Exploring the “density-benefit” relationships of alien species

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Statement of originality

I declare that, to the best of my knowledge, the content of this thesis is my own work. This thesis has not been submitted for any other degree or purpose. I also certify that the intellectual content of this thesis is the product of my own work and that all the assistance received in preparing this thesis has been acknowledged. All information sources and literature used have been referenced appropriately.

Amelia M. Saul

Authorship attribution statement

The Appendix of this thesis is published as O’Rourke et al. 2020. I contributed to the core ideas of the work and assisted with manuscript editing.

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As supervisor for the candidature upon which this thesis is based, I can confirm that the authorship attribution statement above is correct.

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Abstract

Exploring the “density-benefit” relationships of alien species

The disastrous impacts of invasive alien species are well-documented. However, there is growing evidence that some alien species can also have positive effects in their new environments, adding complexity to alien species management. Classic density-damage relationships are used to determine cost effective densities at which to control alien populations and limit their adverse effects. In this thesis I propose that the ecological benefits of alien species are also related to population density. First, I hypothesised the different types of relationships between population density and ecological benefits that may be provided by alien species. I then investigated the "density-benefit" relationships of three common alien species and tested my predictions through a series of manipulative field experiments. In my first data chapter, I investigated the effect of population density on the pollination behaviour of alien black rats, *Rattus rattus*, that provide a pollination function for an Australian native plant, *Banksia ericifolia*. I found that a greater population density of black rats spent a lower proportion of time in physical contact with, and foraging on, *Banksia* inflorescences. Therefore, black rats at high densities behave in a way that may reduce their pollinator efficacy. I next investigated the effect of density upon the role of an alien plant, *Lantana camara*, providing refuge for small native reptiles, *Lampropholis delicata* and *L. guichenoti*. I found that the abundance of reptiles was related to *L. camara* density in a U-shape, showing a benefit at high densities only. I found that this plant increased in structural complexity when in high densities, demonstrating an effect of density upon its growth form which then enhanced its value to native species. In my third data chapter, I conducted a simulation experiment to compare the digging activities of native marsupials (*Bettongia leseur* and *Lagotis macrotis*) and alien European rabbits (*Oryctolagus cuniculus*) at different densities. Density, rather than the species of digger (simulated via different artificial foraging pit morphology), was significantly related to the germination and survival of seedlings in artificial pits. However, seedlings grew larger in artificial native pits, indicating a difference in the quality of the ecological function provided by these analogous alien and native species. Together, these results suggest that “density-benefit” relationships need to be integrated into decisions about population density in the management of alien species. Importantly, they provide a mechanism for reconciling the positive impacts of alien species against their negative impacts. Including the benefits of alien species in their management will advance the current understanding of alien species ecology, guide the management of alien species with complex impacts and ensure that significant ecological benefits provided by alien species are not lost unnecessarily.

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Table of Contents

List of Figures

List of Tables

“You must see with eyes unclouded by hate. See the good in that which is evil, and the evil in that which is good. Pledge yourself to neither side but vow instead to preserve the balance that exists between the two.”

Hayao Miyazaki

Chapter 1 General introduction

The management of alien species targets their negative impacts while overlooking the ecological benefits that they sometimes perform. Considering the impacts of alien species holistically provides a nuanced and accurate understanding of their ecology. In this thesis, I propose that the ecological benefits of alien species are density dependent, just like their negative impacts. I refer to the relationship between an alien species' population density and an ecological benefit as a "density-benefit" curve, and I hypothesise that different "density-benefit" curves will have different shapes depending on the species, context and time since introduction. In this first chapter, I explore the rationale for studying the density dependence of alien species' impacts, both positive and negative. My hope is that this approach to alien species will bridge the division within the field of invasion biology, and will advance our current methods of alien species management.

1.1 Managing the negative impacts of alien species

Alien species are pervasive throughout the world (Simberloff et al. 2013) and the current extraordinary rate of species introductions continues to increase with globalisation and climate change (Ricciardi 2007). Alien species can cause a variety of detrimental economic and environmental impacts at different scales (Ehrenfeld 2010). Although not all alien species always cause harm, those that do can have major impacts (Salo et al. 2007, Blackburn et al. 2014). Furthermore, through actions such as land clearing, urbanisation and using fertilisers in agricultural practices, humans are modifying natural environments and creating situations that amplify the impacts of alien species (Ricciardi 2007). Therefore, the problem of alien species is growing, and the world is changing to become less untouched and wild.

Preventing invasions by alien species is the most cost-effective action that we can take in alien species management (Leung et al. 2002). Economic and environmental returns decrease once an alien species gains entry to an area and their invasion progresses (Victorian Government 2010). Although methods for eradication are improving (Simberloff et al. 2013), rarely can an alien species be eradicated once populations have become abundant and widespread (Braysher 2017). Once an alien species is established, it is inefficient to control every population wherever it occurs, so efforts are best targeted to protecting assets such as native species and agricultural systems (Victorian Government 2010, Fleming et al. 2018). However, beyond this phase in the invasion process, when an alien species becomes entrenched within native ecosystems, the complex nature of the ecological role of alien species in ecosystems is not well understood and, as a result, our management options are narrow and not well defined.

The discussion about basing management decisions on the geographic origins of a species (i.e., whether they are an alien species or a native species) has recently moved towards an impact-based management approach (Simberloff 2013, Blackburn et al. 2014, Norbury et al. 2015, García-Díaz et al. 2020). This is useful as, theoretically, impact-based management can be used to navigate the complexity of the social values of both native (Garibaldi and Turner 2004) and alien (Nuñez and Simberloff 2005) species; including in situations where native species have negative impacts (Nackley et al. 2017). However, even in this impact-based approach, there is a significant lack of exploration of the net impacts of entrenched alien species, especially when those entrenched alien species may provide ecological benefits for native species and ecosystems.

1.2 Avoiding a one-sided view of alien impacts

The negative impacts of alien species are very well understood and receive extensive attention in the literature (Ricciardi et al. 2017). Although this attention is justified and necessary, the same attention is not given to the inevitable positive impacts of alien species, especially for entrenched populations. It is unrealistic to assume that every interaction with an alien species will be harmful to native species. Alien species will inevitably provide food for some native species (Li et al. 2011), or indirectly perform ecological functions like pollination (Pattemore and Wilcove 2012) or fungal spore dispersal (Vernes and McGrath 2009) to some extent as they forage. It is likely that more positive interactions will develop over time (Dickman 2007). Overlooking these benefits in research creates a one-sided view of the overall impacts and ecology of alien species (Goodenough 2010); and ecological managers do not have access to crucial information needed in the management of alien species and the conservation of native ecosystems and functions.

The reality is that many alien species are now entrenched in native ecosystems with little chance of eradication, and so require on-going management. Similarly, problematic native species will also require long-term solutions as it may be undesirable to eradicate these species from local areas (Nackley et al. 2017). In the long to medium term, evolution may temper the exaggerated effects of alien species upon native species (e.g, Morrison (2002)), and bring about a reduction in their negative impacts or the extinction of some native species, but the chronic effects of alien species require more investigation (Strayer et al. 2006). Alien species will inevitably transition from being alien to becoming naturalised (or even “native” (Carthey and Banks 2012)) as they form associations with native species. For example, native northern brown bandicoots (*Isoodon macrourus*) now recognise and exhibit the appropriate avoidance behaviours for alien red foxes (*Vulpes vulpes*) in areas where they have coexisted for 150 years (Bytheway and Banks 2019). Therefore, a binary management response, where actions are decided for species according to their native or alien status, cannot fit the nuances of alien species’ impacts as they change through time.

1.3 The problem of the *complex pest*

Entrenched alien species are not simple to manage and their impacts on ecosystems may only be noticeable once irreversible changes have occurred (Vilà et al. 2011). This is because alien species can embed themselves in a complex web of direct and indirect interactions with other species, including becoming involved in beneficial interactions (Goodenough 2010). Dickman (2007) introduced the idea of a *complex pest* to explain how control and eradication efforts for alien species can sometimes have unexpected and unintended results; particularly when interspecies interactions are not considered (Zavaleta et al. 2001, Dickman 2007). For example, the control of one alien species can unexpectedly trigger the rapid population increase of a second alien species (Banks et al. 1998), or it could negatively affect a native species that relied upon the alien species for an ecological benefit. For example, eradication of alien plants in the Azores is likely to be detrimental to a range of endemic land snail species that are more commonly associated with these alien plants than native plants (Riel et al. 2000). A more nuanced examination of the interactions and ecological functions that a species may be involved in will assist in conserving ecosystem functions, and perhaps help with targeting conservation efforts for particular species, as well as foreseeing any unwanted effects of control efforts (Dickman 2007).

Population density, the time since introduction and the condition of the native ecosystem are all parameters that should be considered when determining if interspecies interactions are likely to have formed (Dickman 2007). The probability of species interactions forming increases when alien species are present in high densities and when they have been present in an ecosystem for a long time (Dickman 2007). Unfortunately, we have limited ability to predict the impacts of alien species control measures on dependent native species because the interactions formed between native and alien species are not well understood. Nor is much known about the management strategies available for alien species that have become entrenched in an ecosystem (Zavaleta et al. 2001). If in doubt, Dickman (2007) recommends that a small-scale removal experiment should be conducted prior to any control actions. Other options include modelling and conducting surveys of the community before and after any control actions (Caut et al. 2009). However, this highlights that we need novel approaches to alien species management that combine ecological understanding, network analysis and cost-benefit evaluations.

1.4 Ecological benefits of alien species

As alien species become involved in interaction webs with native species, it is inevitable that some of these interactions will be beneficial. In fact, many instances of alien species providing ecological benefits have been documented (e.g., Dick (2001), Graves and Shapiro (2003), King et al. (2006), Malo et al. (2013) and Wright et al. (2014)). These ecological benefits can be in the form of beneficial interactions with specific native species (e.g., facilitation (Rodriguez 2006)) or through performing ecological functions (e.g., pollination, providing refuge or ecosystem engineering), that benefit a native community (Schlaepfer et al. 2011). For example, in southeastern USA, the novel habitat provided by alien seaweed, *Gracilaria vermiculophylla*, dramatically increases the abundance of native amphipods (*Gammarus mucronatus*) (Wright et al. 2014). Also, in North America, threatened native Lake Erie water snakes (*Nerodia sipedon insularum*) have almost completely shifted their dietary preferences to consuming alien round gobies (*Neogobius melanostomus*) (King et al. 2006). Furthermore, this change to alien prey is likely to have helped native water snakes to attain high growth rates and body sizes (King et al. 2006).

There are also many practical examples of alien species being retained in an ecosystem to provide benefits, especially in regeneration efforts (many are listed by Sotka and Byers (2019)), and sometimes even at the cost of negative effects (e.g., Sogge et al. (2008)). However, there are mixed perceptions of the amount of attention that the benefits of alien species have received in the literature (Cassini 2020). For example, suggestions for more research into the benefits of alien species (e.g., Ramus et al. (2017)) can be met with the response that these positive impacts are already well understood (e.g., Sotka and Byers (2019)). However, although benefits have been identified, most research merely documents the benefits rather than explore their consequences and limitations. Beyond identifying the presence of an ecological benefit, we need to explore and understand the ecology of these interactions to learn how and when they occur and develop management strategies that include them.

1.5 Ecology of the ecological benefits of alien species

We greatly value the ecological benefits of some alien species (i.e. ecosystem services, such as food production, water supply and climate regulation (Silvertown 2015)) but rarely examine how their presence and efficacy change with parameters such as time, context or density. Furthermore, recent calls to conserve ecological functions of native species highlight that this is a gap in community ecology research in general (e.g., Brodie et al. (2018)). A lack of understanding of the ecology of alien species' benefits has unfortunately led to a debate where consideration of the positive effects of alien species is thought to override or undermine negative effects (Simberloff et al. 2011, Russell and Blackburn 2017).

As an alien species becomes entrenched in a native ecosystem, the number of interactions it is involved in, as well as the nature of these interactions, may change as native species benefit, adapt, decline or learn (e.g., similar to the consequences of urbanisation (Start et al. 2019)). Many alien species are generalists, and generalist species are usually involved in many interactions, whereas specialists are involved in fewer (Start et al. 2019). The strengths and importance of these interactions can also be different depending on the species providing them and their density (Stephens and Rowe 2020). Population density also is likely to play a part in how effectively ecological benefits are provided (Soule et al. 2003). As the control of an alien species' population deals with reducing and changing population density (Norbury et al. 2015), this is an important variable to explore to determine how it will interact with any ecological benefits being provided so they may be incorporated in management actions.

1.6 Positive impacts and density

The negative impacts of pest species (including alien species) can be related to their density and the relationship understood through density-damage curves (Yokomizo et al. 2009, Norbury et al. 2015, Bradley et al. 2019). Such curves can then be used to identify a threshold density at which to control a pest so that it does not have costly negative impacts (e.g., Gooden et al. (2009) and Jones et al. (2013)). This approach ensures that resources are not wasted on control actions that may not be needed to achieve an outcome of reducing impacts (Choquenot and Parkes 2001). These relationships are frequently used in agricultural contexts, however relatively few studies have looked at using density-damage relationships for conservation (Norbury et al. 2015).

Ecological benefits are likely to be linked to density as changing population density induces behavioural shifts and imposes physical limitations upon individuals. For native species, it is well understood that density affects behaviours related to foraging (Kausrud et al. 2006), mating strategies (Höglund and Robertson 1988, Kokko and Rankin 2006), dispersal (Matthysen 2005) and vigilance (Elgar 1989, Mooring et al. 2004). Since many of these behaviours underpin beneficial interactions and ecological functions, changes to population density are likely to affect how these benefits are provided (e.g., Fontaine et al. (2008) and Stephens and Rowe (2020)). Furthermore, changes in density can also impose physical constraints on an organism's ability to provide a benefit, for example, pollen becomes a limiting resource when there are too many pollinators (Dedej and Delaplane 2003). It has been suggested that native species are conserved at "ecologically effective densities" so that ecological functions are provided optimally (e.g., Soule et al. (2003)) and we can conserve ecological functionality (Brodie et al. 2018). However, we do not yet understand the shapes of these "density-benefit" relationships and how different densities will affect different ecological functions for native or alien species.

1.7 Managing complexity

Complex alien species' impacts arise frequently and ecological managers currently make decisions about actions in the absence of research. For example, the alien plant *Lantana camara* is retained to provide habitat for a colony of native little penguins (*Eudyptula minor*) in Sydney, Australia (S. Guthrie, pers. comm. 2017) and it is also used by regeneration workers as a barrier plant to stop invasion by other species. In both of these cases, the manual and ecological costs of removing this plant are considered to outweigh the costs of retaining it in the ecosystem, even though they have not been quantified. Of course, at all points in alien species management, caution should be applied as alien species' impacts can change with time and context (Vitule et al. 2012, Sotka and Byers 2019). However, the same caution should also be taken to ensure that ecological benefits are not disrupted with control efforts.

Currently, the literature on alien species' impacts generally deals with negative impacts and positive impacts separately. Although recognition for the ecological benefits of alien species is expanding (e.g., Simberloff (2013) and Blackburn et al. (2014)), ecological managers need better information to be able to include these benefits in their management plans and priorities. Addressing both the positive and negative impacts provides a more accurate representation of the ecology of an alien species and it will allow an evaluation of impacts at many different scales as well as meet many different management aims. Furthermore, our current knowledge of density-damage curves provides an opportunity to combine density-damage and "density-benefit" relationships to investigate how population density affects the net impact of an alien species.

1.8 Thesis outline

In this thesis, I introduce the concept of a "density-benefit" relationship and advocate for its use to understand and measure complex alien species' impacts. Then, in my experimental chapters (Chapter 3, 4 and 5), I test the density-dependence of three different types of ecological benefits performed by three of the most widely distributed and problematic alien species in Australia: black rats (*Rattus rattus*), lantana (*L. camara*) and European rabbits (*Oryctolagus cuniculus*). I test these relationships in urban, disturbed forest remnants and a natural, semi-arid Mallee environment, two distinct environments in Australia. I also examine three different mechanisms of benefits from alien species: direct effects through their foraging behaviour or by physically providing refuge habitat, and indirect effects via digging. Furthermore, I test whether the shape of a "density-benefit" relationship may be consistent between an alien species and native species providing the same ecological benefit. More specifically:

- Chapter 2 reviews the theory and current perspectives surrounding the management of alien species' impacts. I introduce "density-benefit" relationships as a means of examining the net impacts of alien species.

- Chapter 3 explores the "density-benefit" relationship between the pollination behaviour of an alien mammal (*R. rattus*) and a native plant (*Banksia ericifolia*) in disturbed forest remnants in the northern suburbs of Sydney.
- Chapter 4 examines the mechanism of a "density-benefit" relationship between an alien plant (*L. camara*) providing refuge habitat for native reptiles (*Lampropholis* spp.) in the remnant forests of Sydney Harbour National Park.
- Chapter 5 examines the "density-benefit" relationship between an alien ecosystem engineer (*O. cuniculus*) and native seedlings and compares this to that of a native ecosystem engineer in a simulation experiment.
- Chapter 6 discusses and synthesises the findings of the previous chapters and provides directions for applications and future research.

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Chapter 2 Density dependence of the ecological benefits of alien species

Author contributions:

A.M.S., C.E.T. and P.B.B. conceived the ideas. A.M.S. wrote the manuscript with critical contributions from C.E.T. and P.B.B.. All authors gave final approval for submission.

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2.1 Abstract

Invasive alien species can be involved in positive species interactions and perform important ecological functions yet, despite numerous calls, these benefits are rarely incorporated into decisions about alien species management. However, ecological functions can be density dependent, and it is likely that the ecological benefits of alien species will vary as their density varies spatially and temporally. Here, we propose multiple ways by which the different ecological benefits of alien species will be density dependent and how “density-benefit” curves can be used to identify thresholds that will inform cost-effective management actions. We describe how mismatching evolutionary history, suboptimal densities and inherent characteristics of alien species in recipient ecosystems will shape the efficacy of the benefits they provide. Incorporating alien species’ benefits in management plans will help avoid unintended consequences of control and preserve ecological functions in novel ecosystems.

2.2 Highlights

- Alien species can reach extreme and variable abundances.
- The negative impacts of alien species are density dependent and can be described with “density-impact” curves.
- There is growing recognition that some invasive alien species provide beneficial effects for native species and ecosystems especially alien species that have been present in an environment for a long time.
- Although not well studied, the ecological benefits of native species may also be density dependent and so populations should be conserved in ecologically effective densities.
- The current rate of environmental change suggests that systems may not survive without the benefits provided by alien species, especially when an alien species is a substitute for an extinct native species.

2.3 Disentangling complex alien species' impacts

Species that are translocated outside of their **native** (see Glossary) ranges, whether by natural or human-assisted means, can have profound impacts (ecological (Ricciardi et al. 2013), social (Pejchar and Mooney 2009), agricultural (Paini et al. 2016) and economic (Hoffmann and Broadhurst 2016) etc.) in their new environments. A release from natural predators, parasites and competitors can allow these **alien species** to eventually reach extremely high densities, and a lack of co-evolutionary history can lead to exaggerated negative effects upon naive native species (Salo et al. 2007). Over time, however, alien species will become involved in a range of direct and indirect **species interactions** within local **ecosystems**. It is inevitable that some of these interactions with **entrenched** alien species will benefit native species. Dickman (2007) coined the term "the complex pest" to describe those alien species that are involved in both negative and positive interactions. If these positive effects are not accounted for, controlling or removing alien species can have unintended harmful consequences for native species (see also (Zavaleta et al. 2001)).

There is, in fact, a growing evidence base of the conservation value that some alien species can have for both native species and ecosystems (Schlaepfer et al. 2011) (Table 2.1). For example, populations of Baltimore checkerspot butterflies (*Euphydryas phaeton*) preferentially use alien English plantain (*Plantago lanceolata*) as a host plant despite the presence of native hosts of equivalent benefit (Brown et al. 2017). Alien species can even provide **ecological functions** (Schlaepfer 2018) and alien prickly pear (*Opuntia ficus-indica*) provides nurseries for native seedlings in the over-grazed shrub-grasslands of Nairobi National Park (Oduor et al. 2018). The interactions and functions provided by alien species may be particularly beneficial in the absence of a native species that would otherwise provide the function. For example, following the extinctions of many native bird species in Hawaii, alien Japanese white-eyes (*Zosterops japonica*) now provide important pollination services for native plants (*Clermontia* spp. (Aslan et al. 2013) and *Freycinetia arborea* (Cox 1983)). Recognition of such positive impacts has led to calls that alien species be managed according to their impacts and functional roles rather than continuing to adhere to the alien-versus-native species dichotomy (Rodriguez 2006; Goodenough 2010; Davis et al. 2011; Bonanno 2016). This dichotomy has been a core tenet in conservation and restoration management, but may no longer be practical for the rapidly changing environments of today (Davis et al. 2011).

Here, we refine the alien-versus-native discussion by proposing that the positive effects of alien species are likely to be density dependent, so that alien species' populations could be controlled to an optimal density to maximise ecological benefits. Previously, the relationship between alien species' densities and their purely positive interactions and functions has not been considered beyond using the term "impact" to acknowledge and incorporate some of their benefits into their overall effects (Norbury et al. 2015). However, we expect that alien species will provide interactions and functions in different ways to native species since the traits inherent to alien species will shape the efficacy of these benefits. Therefore, we propose "density-benefit" curves and suggest their use would guide the appropriate integration of the ecological benefits of alien species into their management.

Table 2.1 Alien species provide many beneficial ecological functions in their new environments.

Function	Example	Refs
Decomposition	Alien earthworms (*Prosellodrilus amplisetosus*) in Ireland provide unique decomposition services by accessing parts of the soil profile that are inaccessible to the native earthworm assemblage	(Melody and Schmidt 2012)
Seed/spore dispersal	Alien black rats (*Rattus rattus*) consume and disperse a variety of native Australian fungus species in the absence of native bush rats (*R. fuscipes*)	(Vernes and McGrath 2009)
Ecosystem engineering	The formation of reefs by alien Pacific oysters (*Crassostrea gigas*) in Sweden support equal or higher macrozoobenthos species abundance and richness than native blue mussel (*Mytilus edulis*) beds	(Hollander et al. 2015)
	In the USA, native polychaete worms (*Diopatra cuprea*) use alien agar seaweed (*Gracilaria vermiculophylla*) to improve the structural integrity of their tubes and enhance access to epifaunal prey	(Kollars et al. 2016)

Herbivory	Grazing by invasive herbivorous fish (*Siganus luridus* and *S. rivulatus*) controls macroalgal growth thereby improving the resilience of Greek marine habitats to ocean acidification	(Baggini et al. 2015)
Host	Alien mammals such as European rabbits (*Oryctolagus cuniculus*), black rats, brown rats (*R. norvegicus*), domestic dogs (*Canis lupus familiaris*) and house mice (*Mus domesticus*) are all hosts for native Australian paralysis ticks (*Ixodes holocyclus*)	(Lydecker et al. 2015)
Pollination	African honeybees (*Apis mellifera scutellata*) are important pollinators of degraded Amazon forest fragments	(Dick 2001)
Predation	Native Australian garden skinks (*Lampropholis delicata*) seem to respond appropriately to predation by alien black rats, which suggests that alien black rats may regulate the skink population at an appropriate level for the native ecological community	(Smith et al. 2017a)
	Depression of native spider populations through predation by alien black rats results in increases of invertebrate abundance and ordinal richness	(Smith et al. 2017b)
Prey	Alien round gobies (*Neogobius melanostomus*) make up >90% of the diet of threatened Lake Erie water snakes (*Nerodia sipedon insularum*)	(King et al. 2006)
	In Portugal, alien red swamp crayfish (*Procambarus clarkii*) make up 67% of native Eurasian otter (*Lutra lutra*) diets and 70% of native black-crowned night heron (*Nycticorax nycticorax*) diets	(Marcal Correia 2001)
Refuge	Alien shrubs (*Rhododendron ponticum*) provide shelter to native British wood mice (*Apodemus sylvaticus*) leading to their increased abundance	(Malo et al. 2013)
	In the USA, native grey catbirds (*Dumetella carolinensis*) build more nests in alien honeysuckle shrubs (*Lonicera* spp.) than in any native shrub species with no adverse effects upon nest predation rates, parental care or fledgling weight	(Gleditsch and Carlo 2014)

2.4 Negative impacts of alien species are density dependent

The density dependent nature of the negative effects of pest species, including alien species, is described by **density-impact curves** (Yokomizo et al. 2009, Norbury et al. 2015, Bradley et al. 2019). For example, in New Zealand, high densities of alien European hedgehogs (*Erinaceous europaeus*) have increased predation pressure on native ground weta (*Hemideina* spp.), resulting in a nonlinear density-impact curve between hedgehog density and weta counts (Jones et al. 2013). In conservation programmes, density-impact curves are central to modern approaches of managing impacts rather than species. By identifying a species-specific target threshold, an alien species can be controlled to a density where they will persist without causing unacceptable damage (see (Blackburn et al. 2011)). Thus, density-impact curves inform targeted and cost-effective management of the impacts of entrenched alien species where eradication is impractical. Density-impact curves are more commonly used in agriculture, and there are current calls to increase their use in conservation (Norbury et al. 2015, O'Loughlin et al. 2019).

2.5 Ecological benefits are density dependent

We argue that, similar to ecosystem processes with negative outcomes, those with positive outcomes will also be density dependent. Recent interest in the conservation of ecosystem functionality has highlighted the density dependence of native ecological functions as a gap in community dynamics worth exploring (Soule et al. 2003, Brodie et al. 2018). Although generally assumed, evidence of density dependence within the species interactions and ecological functions provided by native or agricultural species has only been found in a few studies (e.g., (Dedej and Delaplane 2003, Soule et al. 2003, Koch et al. 2009, DeVore et al. 2020)).

The shape of the relationship between population density and the efficacy of an ecological benefit can have many forms. For example, the density dependent relationship of cane toads (*Rhinella marina*) as effective hosts for native *Amblyomma* sp. ticks is linear (DeVore et al. 2020) whereas the relationship between European honeybee (*Apis mellifera* L.) density and pollination success is hump shaped (Dedej and Delaplane 2003). Different behaviours are involved with providing each ecological benefit successfully, for example, cane toads must shelter in damp environments with their conspecifics to be effective tick hosts (DeVore et al. 2020) and honeybees must collect sufficient pollen loads and deposit them on flowers of the same species in a way that effects fertilisation (Dedej and Delaplane 2003). Changes to population densities can influence these behaviours both socially and physically, which may constrain the efficacy of a benefit. For example, the pollination success of honeybees is eventually limited by high bee densities as the pollen supplies of plants become depleted, causing individuals to collect and carry smaller, less effective pollen loads (Dedej and Delaplane 2003). Understanding the mechanisms of these relationships, their shapes and their context-dependence will allow native species to be conserved in ecologically effective densities (Soule et al. 2003).

2.6 Ecological benefits of alien species are density dependent

Here, we propose that the ecological benefits provided by alien species will also be density dependent, and we call these relationships “density-benefit” curves. Like density-impact curves, “density-benefit” curves will occur in different shapes, strengths and directions (Figure 2.1), and be context- and time-dependent. We predict that variation in the population density of alien species will be associated with behavioural shifts, or place physical limitations upon individuals that, in turn, result in variations to the provision of ecological interactions and functions. For example, increases in the density of alien agar seaweed (*Gracilaria vermiculophylla*) are associated with epifaunal abundance and richness, which use the seaweed as habitat, through positive hyperbolic curves (Ramus et al. 2017). Similarly, increasing cover of alien bitou bush (*Chrysanthemoides monilifera* ssp. *rotundata*) through time is positively and linearly related to native bird and small mammal abundances (O’Loughlin et al. 2019). Nonlinear curves are of particular interest as they can provide more guidance to managers when they identify thresholds or breakpoints. Each “density-benefit” curve is also likely to be context-dependent, and so the shape of a curve has the potential be temporally and spatially unique (Soule et al. 2003).

In Figure 2.1, we hypothesise example “density-benefit” curves for a number of interactions and ecological functions that alien species perform. For example, the efficacy of pollination likely increases proportionately with the density of alien pollinators in the system when at low densities, but comes to a plateau as the availability of pollen (a finite resource) wanes and pollen is dispersed among too many pollinators (Figure 2.1a). The benefits of consuming and dispersing seeds or spores might increase proportionally with alien consumer density until all seeds have been dispersed (Figure 2.1b). Native parasites and pathogens could benefit from increases in alien host density but a threshold may appear if too many hosts cause a dilution effect where parasites and pathogens cannot encounter one another to mate (Figure 2.1c). Alien herbivores can regulate plant growth, but this benefit could change when herbivores become overabundant and exert too much control (i.e., begin killing native plants) (Figure 2.1d). Alien ecosystem engineers at low densities likely create a limited amount of soil disturbance and minimal opportunities for seeds, leaf litter and nutrients to be captured; the efficacy of this benefit could increase until the disturbance rate is too high and seeds, leaf litter and nutrients (finite resources) become spread too thinly over the landscape (Figure 2.1e). The rate of decomposition could rapidly increase with increasing density of an alien decomposer until all the organic waste is decomposed at a rate greater than it is created (Figure 2.1f). At low densities, alien predators may not exert enough downward pressure to affect trophic regulation but this benefit could increase rapidly with predator density (due to the extreme outcomes of predation, i.e. mortality) up to a threshold beyond which native prey may become increasingly more vulnerable to a population crash (Figure 2.1g). The benefits of alien prey at low densities could be limited if the prey is difficult to locate; benefits would increase with density before reaching a plateau when prey become hyperabundant and predators are satiated (Figure 2.1h). At low densities, refuge effects from alien plants are likely limited if difficult to encounter and are competed over; benefits could increase as more refuges are available to native species until a plateau arises when refuges become a limited resource (Figure 2.1i).

Changes to alien species’ densities, whether through control actions or natural population dynamics, will affect the provision of ecological functions and this should be accounted for in management decisions on alien species control. Like density-impact curves, “density-benefit” curves can help avoid unintended consequences of arbitrarily controlling alien species’ density levels (Dickman 2007). “Density-benefit” curves should also directly complement the use of density-impact curves to optimise alien species management; to reduce damaging impacts while maintaining important ecological functions, especially those provided by entrenched alien species. Using “density-benefit” curves in management plans of both alien and native species in disturbed or novel ecosystems would ensure that ecological functionality is conserved.

It is likely that alien species’ benefits and their relationships with population density will be different to those of native species providing analogous ecological functions, due to characteristics that are unique to alien species, especially soon after arrival. Below, we outline some traits of alien species that will influence the mechanisms behind “density-benefit” curves as important avenues for future alien species research.

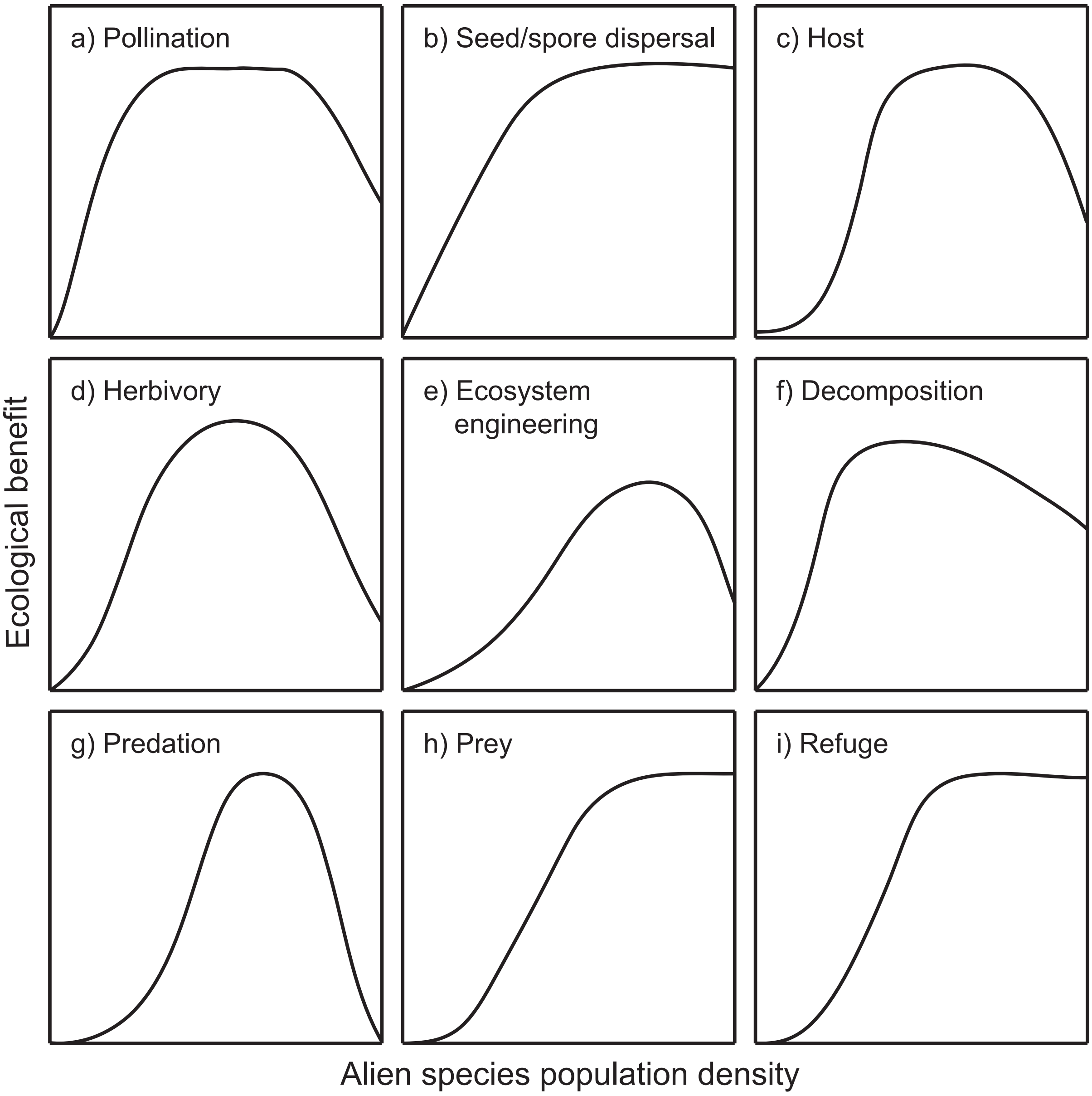

Figure 2.1 Hypothetical potential relationships ("density-benefit" curves) between population density and ecological benefits from interactions (a – c) and functions (d – i) provided by alien species in their new environments. All are curvilinear relationships, with thresholds and plateaus emerging at different density levels. We defined species interactions as actions that primarily benefit one native species, whereas ecological functions provide broader net benefits for an ecosystem.

2.7 Influences on the ecological benefits of alien species

2.7.1 Alien species' densities are often extreme and variable

In their new environments, alien species' densities are often very low or too high since populations are often establishing (i.e., becoming **naturalised**), out of control or being controlled. The efficacy of benefits provided by alien populations in extreme densities (especially in extremely low densities) is likely to be limited by behavioural and physical changes (Figure 2.1). Many entrenched alien populations occur in low densities, similar to those of native species (Hansen et al. 2013). However, when an alien population does reach a high density, this density can be higher than that of comparable native species (Hansen et al. 2013). Alien species' densities will also shift throughout the invasion process in response to management activities and environmental conditions.

The extreme and variable nature of alien population densities may limit the efficacy of their ecological benefits. For example, at low densities, Allee type effects may occur if there are too few individuals present to provide an ecological benefit to the ecosystem (Soule et al. 2003). In Australia, dingoes (*Canis lupus dingo*) in packs perform the role of apex predators by hunting large prey and creating a landscape of fear that protects smaller native mammals from alien predators (e.g., domestic cats, *Felis catus*, and red foxes, *Vulpes vulpes*) (Nimmo et al. 2015). However, if low densities disrupt pack structures, Glen et al. (2007) proposed that lone dingoes may prey upon livestock more frequently, as well as the smaller native mammals that they could otherwise protect. By contrast, high population densities could lead to changes in individual behaviour caused by increased intraspecific competition or physical limitations. For example, territories are often smaller at high densities (Ochiai and Susaki 2002), and individuals may be forced to seek alternative food sources, limiting the efficacy of ecological roles like pollination or seed dispersal. These issues strengthen the case for intervening early in the invasion process, when alien species are in low densities. However, for entrenched alien populations, managing population densities to balance the positive and negative impacts is likely to provide the best outcome for the suite of species they interact with.

2.7.2 Density influences on ecological benefits will change with time

Over time, both the population densities and benefits of interactions with alien species are likely to increase. Alien species do not share a long evolutionary history with their recipient ecosystem and so evolutionary mismatches can occur initially that may affect how appropriately an ecological function is provided. For example, alien bumble bees (*Bombus terrestris*) bypass a species-specific mutualism with a native Japanese plant species (*Corydalis ambigua*) by robbing floral resources, causing a reduction in seed set and fewer legitimate visits by native bumble bees (*Bombus ardens*) (Dohzono et al. 2008). The time since establishment will thus influence the benefits provided by alien species. For example, in Australia, the arrival of cane toads (*Rhinella marina*) severely impacted native predators (such as goannas (*Varanus* spp.) and northern quolls (*Dasyurus hallucatus*)) that have had no evolutionary experience with bufotoxins (Shine 2010). But with learning (e.g., Torresian crows (*Corvus orru*) learning to avoid the toxin glands of cane toads (Donato and Potts 2004)) and micro-evolutionary change (e.g., native common tree snakes (*Dendrelaphis punctulatus*) with smaller heads surviving as they are physically unable to eat cane toads (Phillips and Shine 2004)), the negative impacts on these species have reduced with time. It is therefore important to note that the nature of an ecological function, or interaction, provided by an alien species may shift over time causing changes to the shape of its “density-benefit” curve.

2.7.3 Weak positive impacts can become more important at high densities

The generalist habits of alien species can limit their ability to provide effective ecological benefits, but density may change this. Many alien species tend to have broad diets and habitat specifications, a trait that allows them to establish in new environments, including in disturbed and urban areas. Species involved in many interactions (generalists) can have weak influences within an ecosystem compared to specialists that provide a few stronger interactions (Start et al. 2019). However, the strength of an interaction is not only related to the number of other interactions a species has. For example, native American beavers, *Castor canadensis*, are both generalists and keystone species demonstrating that generalist species can be involved in strong interactions (Marcot & Vander Heyden 2001). Small changes to the density of a strongly interacting species, like American beavers, and the benefits they provide will have repercussions on the balance of an ecosystem (McCann 2000).

Importantly, changes in population density can also affect the strength of an interaction or ecological function, at least for native species. For example, native generalist rodents disperse fungal spores to more habitats, and also become more effective dispersers than specialists when in higher abundances (Stephens and Rowe 2020). Thus, it is possible that an alien species involved in weak interactions may only ever provide substantial ecological benefits when at high densities. Unfortunately, some alien species will also cause more damage when at high densities (Yokomizo et al. 2009).

2.8 Concluding Remarks

Managing the holistic impact of alien species in recipient ecosystems needs to move beyond a simple recognition of potential positive roles amongst the many negative impacts (Simberloff et al. 2013) and towards understanding how these roles will shift with changes in population density. Density benefit curves are also relevant to native species that become overabundant and need to be managed without detrimental effects on their positive ecological roles. We suggest that partnering “density-benefit” curves with density-impact curves can help identify optimal management densities for alien species that reconcile their positive and negative roles (see Outstanding Questions). This is especially important when managing entrenched alien species where eradication is not an option, either due to the cost or the absence of a native species to provide ecological benefits instead. Furthermore, in disturbed and novel ecosystems where restoration is no longer possible, optimising the species density to provide ecological functions will ensure that effective ecosystem functioning is retained. Lastly, accepting that both the positive and negative impacts of alien species will vary with density will help to quell the polarising arguments about overlooking either the negative impacts (e.g., alien species denialism) (Russell and Blackburn 2017) or the positive impacts of alien species (Davis et al. 2011, Davis et al. 2017).

2.9 Outstanding Questions

The following research questions are important to advancing the research and use of “density-benefit” curves.

How can we incorporate both density-impact and “density-benefit” curves to produce a net benefit model for an alien species?

Are all “density-benefit” curves unique? Or is it possible to predict the “density-benefit” curve for an alien species and the type of function it provides?

How does density interact with strong and weak interactions in networks?

Can you measure the functional richness or redundancy of novel ecosystems? If so, how do you measure the effects of adding or removing ecological functions?

How can we achieve a cross-tenure approach to ecosystem and the impacts of alien species e.g., how can we incorporate agricultural species into this debate?

2.10 Glossary

Alien: In this paper, we use the term “alien”, instead of introduced, exotic or non-native, to describe a species that is novel to an ecosystem. Regardless of its geographic origin, and whether or not it arrived by human means, the impacts of a new species will be alien to an ecosystem and, therefore, require research and attention.

Density-impact curve: The relationship between the population density of a pest species (usually an alien species) and its negative impacts within an ecosystem or agricultural system. It is also referred to as a damage function, a density-damage curve, abundance-impact curve or, in agricultural research, a density-yield function. These curves inform cost-effective pest management by identifying the densities at which alien species can remain in an ecosystem while causing minimal damage. If densities rise above a defined threshold, however, control will be needed to avoid unacceptable negative impacts.

Ecosystem: A level of ecological organisation that encompasses the interactions within a community of organisms and the interactions that community has with the abiotic features of their shared environment. The sizes of ecosystems can vary and are dependent upon the observer.

Ecological functions: The ways in which species interact with their biotic and abiotic environments (e.g., seed dispersal, herbivory and decomposition), that ultimately influence the energy flow within an ecosystem.

Ecosystem service: Ecosystem processes (including functions and species interactions) that specifically contribute to the economic gain and wellbeing of humans.

Entrenched: An alien species that is firmly established (widespread and abundant, and involved in interactions with native species) in an ecosystem and is therefore difficult to eradicate.

Evolutionary mismatch: Alien species do not share an evolutionary history with their recipient ecosystems. Therefore, some alien species are not adapted to allow specialised interactions with native species to occur optimally. When this happens, this is an evolutionary mismatch (Sih 2013).

Native: A description of a species that has evolved to survive in the environment and ecosystem where it resides.

Naturalised: The stage in an invasion when a new species is able to reproduce so that its population is self-sustaining.

Species interactions: Interactions between species, or populations of species, that result in positive, neutral or negative outcomes to a population size or performance (e.g., predation, competition, parasitism, mutualism, commensalism and amensalism). Species can be involved in many or few interactions, and different interactions can have different strengths and, therefore, different consequences for the ecosystem should they be disturbed or disrupted.

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Chapter 3 Effects of population density on the pollination behaviour of an introduced pollinator

Author contributions:

A.M.S., C.E.T. and P.B.B. conceptualised the research and designed the methodology. A.M.S. conducted the field research, and collected and analysed the data. All authors were involved in the interpretation of the data. A.M.S. wrote the manuscript with critical contributions from C.E.T. and P.B.B.. All authors gave final approval for submission.

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3.1 Abstract

Alien species can have positive ecosystem effects and undertake behaviours that provide useful ecological functions. However, it is likely that the efficacy of these functions will be related to alien population density, given that population density influences individual behaviour that, in turn, influences how alien species interact with native species. Here, we test how the behaviour of alien black rats (*Rattus rattus*) as pollinators of a native plant (*Banksia ericifolia*) is related to their population density in peri-urban Sydney, Australia. In this system, alien black rats have little prospect of being eradicated and there is evidence that their pollination behaviours for this plant, which has evolved with mammal pollinators, in part replace a role played by lost native pollinators. We estimated the densities of 14 spatially independent black rat populations and examined different behaviours critical to pollen collection, cross-pollination and seed set. On average, black rats spent 67% (± 1%) of their time collecting pollen. Time spent in contact with and foraging on inflorescences linearly decreased with population density, while visitation rates were independent of density. In contrast, behaviours that could affect cross-pollination linearly increased with black rat population density, while behaviours that we predicted would limit pollinator efficacy and seed set, were similar across all population densities. Our results suggest that alien black rats are providing pollination services to a native plant and that this service varies in response to their population density. Without considering the influence of population density upon behaviour, changing the density of alien populations (e.g., through control efforts) may disrupt the beneficial interactions and functions relied upon by native species. However, careful management of alien populations could maintain these ecological functions while reducing negative impacts, especially in disturbed and novel ecosystems.

3.2 Introduction

There is growing evidence of alien species having positive impacts in their new environments through beneficial interactions with natives or by providing ecological functions. For example, in south-eastern USA, native polychaete worms (*Diopatra* *cuprea*) decorate their tubes with alien red seaweed (*Gracilaria vermiculophylla*) (Kollars et al. 2016). The alien seaweed not only anchors the dwelling of the polychaete worm, but attracts its prey by providing substrate for epifauna (Kollars et al. 2016). Native snail kites (*Rostrhamus sociabilis plumbeus*) in the Everglades of Florida, USA, frequently consume alien snails (*Pomacea maculata*) and show equal preference between alien and native snail species (Wilcox and Fletcher 2016). Soil disturbance by alien pigs (*Sus scrofa*) in tropical Australia exposes edible seeds, roots and invertebrates that would have otherwise been unavailable for an assemblage of native birds (Natusch et al. 2017). The efficacy of these functions is wholly dependent upon appropriate behaviours of the alien species being performed often enough and effectively enough to be beneficial. It is well known how behavioural mismatches between alien and native species can lead to negative outcomes and exaggerated impacts (Sih 2013). However, much less is known about the behavioural dimensions of any positive effects and ecological functions of alien species.

Many parameters have the potential to determine the efficacy of positive ecological functions of alien species, including: the length of time the alien species has been present in the ecosystem (e.g., O'Loughlin et al. (2019)), the functional profile of the ecosystem (e.g., Vernes and McGrath (2009)), but also the population density of the alien species (e.g., Ramus et al. (2017)). As the negative impacts of alien species are density dependent (Fleming et al. 2002, Norbury et al. 2015, Bradley et al. 2019), it is likely that the beneficial ecological functions of alien species will be too. For example, pollination success by European honeybees (*Apis mellifera* L., an alien species in the Americas, Australia and Asia) is positively related to colony density (Rollin and Garibaldi 2019). Similarly, in Australia, increasing cover of invasive bitou bush (*Chrysanthemoides monilifera* ssp. *rotundata*) over time supports more native birds and small mammals (O'Loughlin *et al.* 2019) and experimental increases of invasive seaweed (*Gracilaria vermiculophylla*) density positively affects epifaunal abundance and richness (Ramus *et al.* 2017). The mechanisms that drive a relationship between population density and an ecological function are not well understood for native or alien species. However, ecological functions will depend upon a behavioural dimension, which itself can be influenced by density.

It is not well known exactly how population density shapes behaviours that affect the efficacy of ecological functions but there is indirect evidence in the literature. For example, pollination success of blueberry (*Vaccinium ashei* var. 'Climax') plants is nonlinearly related to the density of their pollinators, European honeybees (*Apis mellifera* L.) (Dedej and Delaplane 2003). A hump-shaped relationship occurs because high densities of honeybees pose physical and behavioural limitations upon their pollen loads and movement, curbing their efficacy as pollinators (Dedej and Delaplane 2003). Animal behaviours are well known to be density dependent through studies of grouping behaviours (e.g., Holubová et al. (2019)), spacing patterns (e.g., Vas and Andersen (2015)), foraging (e.g., Cvikel et al. (2015)) and mating strategies (e.g., Höglund and Robertson (1988)). It is also likely then that variation in population density changes the behaviours associated with an ecological function to affect ecological functionality of species in native and novel ecosystems.

Here, we explore the density dependent pollination behaviours of alien black rats (*Rattus rattus*) in the peri-urban forest remnants of Sydney, Australia. Black rats are globally ubiquitous and considered to be one of the worst invasive species due to their severe effects upon island fauna (Veitch 2011). However, in peri-urban areas and fragmented forests, their impacts (either positive or negative) have not been well understood until recently (Banks and Hughes 2012). For example, in these forest remnants of Sydney, the small native mammals that were historically present are locally extinct (Banks et al. 2011, Banks and Hughes 2012) and thus cannot pollinate native mammal-pollinated plants (e.g., Proteaceae species). Black rats frequently visit the inflorescences of one of these species, *Banksia ericifolia* (O'Rourke et al. 2020). Since they forage non-destructively and carry significant pollen loads, it is likely that black rats are providing a pollination function (Saul 2013). However, black rats also have exaggerated impacts on birds via nest predation (Smith et al. 2016), and limit reptile and invertebrate abundance (Smith et al. 2017a). Given these negative impacts, black rats are considered undesirable and a target for population control. Understanding how changes to their density may impact their positive pollination function is important to conserving their positive ecological function in peri-urban areas.

For a non-flying mammal to be an effective pollinator, regular visitation and fidelity to a plant species is required (Carthew and Goldingay 1997). The visitation rate of a pollinator (i.e., number of visits to inflorescences over time) is an indirect indication of pollen collection and transferral (Cayenne Engel and Irwin 2013). When visiting, an effective pollinator must also forage non-destructively and successfully remove a substantial load of pollen from the inflorescence in their fur (Carthew and Goldingay 1997). Lastly, an effective pollinator must transfer that pollen to another inflorescence to effect cross-pollination, fertilisation and seed set (Carthew and Goldingay 1997). As non-flying mammalian pollinators are considered less mobile than flying pollinators, their movement patterns are particularly important for ensuring genetic diversity within the plant population through cross-pollination (Goldingay et al. 1991a). Importantly, each of these stages involves a behavioural dimension.

Pollination by animals should be strongly influenced by the density dependent foraging behaviours of pollinators, but the nature of the effect has the potential to be complex. For example, high density populations will experience more competition for resources (e.g., floral rewards: nectar and pollen) (Davidson and Morris 2001, China et al. 2013). This could result in individuals spending more time at food patches (e.g., inflorescences), rather than risk switching between patches in search of high quality resources (cf. optimal foraging theory). Under this scenario, we expect that individuals will spend more time in physical *contact* with and *foraging* on inflorescences when in high densities. Increased *contact* with an inflorescence results in increased collection of pollen. For example, the amount of time that a sugar glider (*Petaurus breviceps*) interacts with an inflorescence increases the amount of pollen collected in their fur (Goldingay et al. 1991a). However, individuals making fewer switches between plants would also lead to lower *visitation* rates, and fewer cross-pollination opportunities.

Populations with high densities can also experience “dilution effects” where the lowered perceptions of risk from predation can allow individuals to forage for longer (Childress and Lung 2003, China et al. 2013, Carthey and Banks 2015). *Vigilance* is a behaviour that signals an individual’s perception of risk (Bedoya-Perez et al. 2013) and, in high densities, we could expect that individuals will be able to allocate more of their time to *foraging* and display less *vigilance*. Individuals that spend less time in locomotion, or *moving*, (i.e., when switching between patches) will also be able to allocate more time to being in *contact* with an inflorescence, which we also expect to occur at high densities. However, reduced locomotion may simultaneously lower cross-pollination rates.

Increased competition in high density populations could also lead to *destructive foraging*, especially as a result of food stress (Botha and Pauw 2017). *Destructive foraging* combines pollination and herbivory and can reduce the reproductive output of plants directly (e.g., through the consumption of gametes) and indirectly (e.g., by reducing the floral display and limiting visitation) (McCall and Irwin 2006). Black rats are omnivorous and plant matter comprises up to 81% of their diet in the Galapagos Islands (Clark 1982). Specifically, *destructive foraging* (or florivory) by black rats has also been reported in the Canary Islands to affect 10% of a threatened bellflower (*Canarina canariensis*) population (Jaca et al. 2019). Although some pollen collection may occur during *destructive foraging*, future pollen availability, floral display and the eventual seed set will all be impacted.

Mammalian pollinators also regularly *groom*, which results in the removal of pollen in their fur, decreasing their pollen load (Goldingay et al. 1991a, Johnson and Pauw 2014). A negative exponential relationship exists between the time that hairy-footed gerbils (*Gerbillurus paeba*) and striped field mice (*Rhabdomys pumilio*) spend *grooming* and the size of their pollen loads (Johnson and Pauw 2014). However, we do not expect that *grooming* will be related to density dependent foraging behaviours.

In this paper, we established native *B. ericifolia* inflorescences in artificial pollination networks and used motion-sensitive wildlife cameras to record the pollination behaviours listed above of visiting alien black rats at a range of population densities. Many pollinating non-flying mammals are small, nocturnal and cryptic, which necessitates indirect techniques to measure their efficacy as pollinators (Goldingay et al. 1991a). For example, motion-sensitive cameras can allow observations of regular non-destructive floral visitation, while spooling or tracking footprints indicates the transportation of pollen loads to conspecific plants (Carthew and Goldingay 1997). Using artificial pollination networks allowed us to work in sites with different black rat population densities and to track “pollen” transfer among inflorescences in a site.

3.3 Materials and methods

3.3.1 Study species and study sites

Black rats likely established in Australia soon after European settlement (Banks and Hughes 2012) and have since become established in coastal areas (Stokes et al. 2009). As human commensals, they are successful in human-modified environments and may occupy the empty niches of locally extinct native species (Dickman and Watts 2008, Stokes et al. 2009). Due to their generalist diet and arboreal habit (Veitch 2011), they are considered to be potential or partial pollinators of plants in their native India (Pandit and Choudhury 2001, Devy and Davidar 2003), as well as in areas of their introduced range in the Canary Islands (Rodríguez-Rodríguez and Valido 2011), New Zealand (Ecroyd et al. 1995, Pattemore and Wilcove 2012) and Australia (Johnson et al. 2011, Saul 2013).

Banksia ericifolia is a dense, multi-stemmed shrub (up to 5 m high) that occurs in the heath (open sclerophyllous shrublands) and dry sclerophyll forests of coastal, south-east Australia. It is considered mammal pollinated (Carpenter 1978, Paton and Turner 1985, Goldingay et al. 1991b) and exhibits characteristics of a mammal pollinator syndrome: large (8 to 26 cm) inflorescences, a musty smell, flower production in winter and nocturnal production of copious amounts of nectar (Paton and Turner 1985). Black rats frequently visit *B. ericifolia* inflorescences to forage for nectar (O’Rourke et al. 2020) and carry large pollen loads comparable to those carried by native mammalian pollinators (Saul 2013).

We studied black rat pollination behaviour in coastal wet and dry sclerophyll forests, which are common in south-east New South Wales, Australia (Keith 2011). The native fauna typically associated with these vegetation communities includes non-flying mammalian pollinators such as eastern pygmy possums (*Cercartetus nanus*), brown antechinus (*Antechinus stuartii*), bush rats (*Rattus fuscipes*) and sugar gliders (*Petaurus breviceps*) (Schulz and Ransom 2010). However, these mammal species are now mostly absent from the urbanised, small forest remnants of Sydney, where alien black rats occur instead (Banks et al. 2011).

In the austral winter of 2017, we located 14 forest remnants with black rat populations throughout Sydney's northern suburbs (Figure 3.1). Each remnant was small (~1 ha) and separated by at least 500 m to ensure that black rat populations were independent. Although *Banksia* species were present in some of our sites, we ensured that local winter-flowering species (*B. ericifolia* and *B. spinulosa*) were not present to restrict black rats to only forage on the inflorescences from our artificial pollination networks. Motion-sensitive wildlife cameras at each site confirmed that other significant native mammal pollinators were not present.

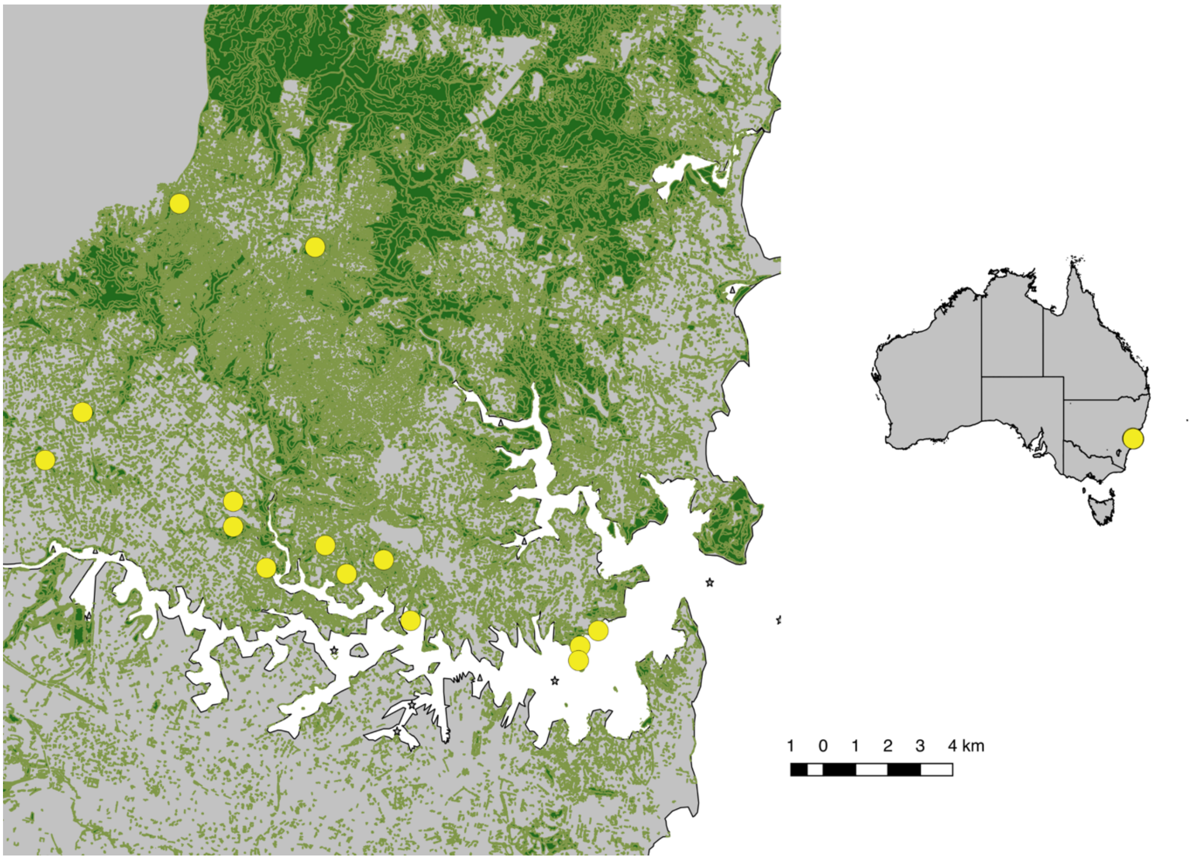

Figure 3.1 Study sites in the northern suburbs of Sydney, Australia, were separated by at least 500 m to ensure independence between black rat populations (n = 14).

3.3.2 Determining the population density of black rats

To index population density at each site, we calculated the relative abundance of black rats using chew-track-cards (white, coreflute plastic cards, 90 x 180 mm, 3 mm gauge, with the channels running along the length) baited with peanut butter (Sweetapple and Nugent 2011). Relative abundance calculated from chew-track-cards is commonly used to estimate the density of mammalian pests, including black rats (Sweetapple and Nugent 2011, Ruffell et al. 2015). Previous work in our study area found a linear correlation between population estimates of black rats from live trapping and the proportion of chew-track-card visits (Smith et al. 2017b). At each site we deployed 36 chew-track-cards in a 1 ha grid (6 x 6) with 20 m spacing (Smith et al. 2017b) by attaching cards to trees (any species) at a height of 30 cm (Sweetapple and Nugent 2011). A pilot trial confirmed that one night was sufficient to calculate relative abundance and avoid saturation (all cards chewed). Bite marks of different mammal species were identified following Sweetapple and Nugent (2011).

The relative abundances at our study sites were representative of the natural range of black rat populations found across Sydney (Hansen et al. 2020) (Figure 3.2). Using the relationship in Smith et al. (2017b), we estimated the population densities of black rats at our sites ranged from 1 – 34 animals trapped on 1 ha. The high end of this range approximates a population density of six black rats per hectare, similar to that measured at a nearby remnant forest in Sydney Harbour National Park (Hansen et al. 2020).

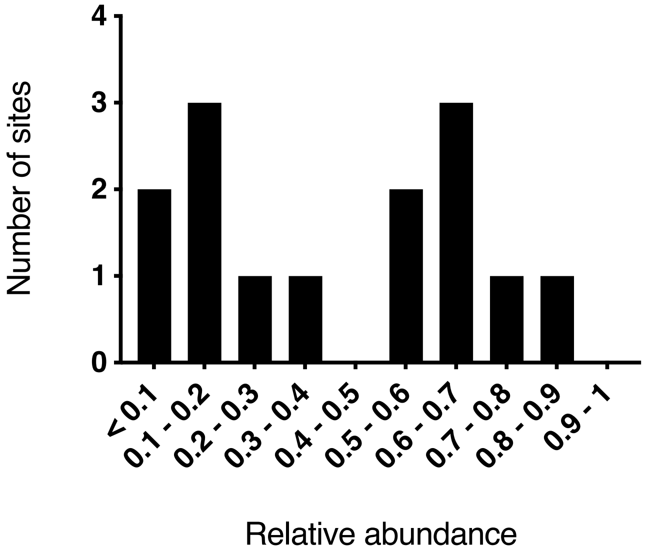

Figure 3.2 Population densities (estimated from relative abundance) of black rats across 14 sites in the northern suburbs of Sydney, Australia.

3.3.3 Artificial pollination networks

To create artificial pollination networks, we collected *B. ericifolia* inflorescences from forests located within 20 km of our experimental sites. Before collection, and before inflorescences opened, we covered each inflorescence with a mesh bag to prevent pollination. Inflorescences were collected and deployed once 50 - 90% open and producing nectar, around five weeks later. We deployed 7-9 inflorescences at each site, with 124 inflorescences deployed in total. A bag of water was attached to the stem of each inflorescence to prevent it from drying out. Inflorescences were then tied to the trunks of small trees or shrubs, 30 cm off the ground, 5 m apart (Figure 3.3), in a grid arrangement to simulate the distribution in natural patches of *B. ericifolia* (Fairley and Moore 2010).

We recorded black rat visitation and behaviours using a motion-sensitive Scoutguard SG560K-2mHD camera set 1 m away from each inflorescence (Meek *et al.* 2014). Cameras were set to film continuous 60 s videos at the highest resolution (1280 x 720) with a normal PIR trigger, which detected movement within a 1 m radius. Inflorescences and cameras were left in the field for five nights.

To track “pollen” transfer by rats within networks, we also dusted two inflorescences per artificial pollination network with different colours of non-toxic ultraviolet fluorescent powder. On collection, inflorescences were placed in separate plastic bags to retain fluorescent powder and prevent contamination among inflorescences. An ultraviolet lamp was then used to detect the presence of fluorescent powder on the other inflorescences in a site which would indicate transferral.

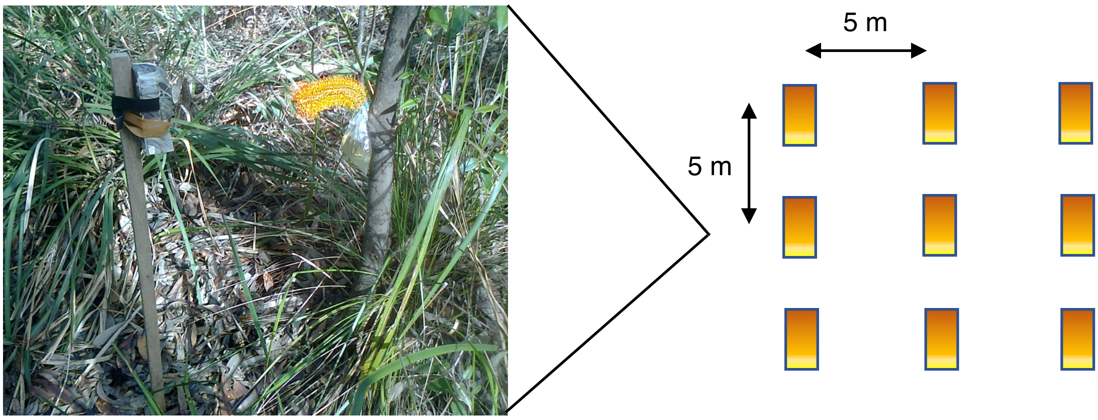

Figure 3.3 Artificial pollination networks consisted of 7-9 cut *Banksia ericifolia* inflorescences, with a water bag tied to the stem, and motion-sensitive cameras arranged in a grid. Photograph by A. M. Saul.

3.3.4 Analyses of pollination behaviours

We analysed 986 videos of black rats detected within our artificial pollination networks. In 9 videos, two black rats were present at the same time and we analysed the behaviours of each rat separately, bringing our sample size to 995 videos. The number of videos analysed per site ranged from 14 to 239, depending on the amount of rat activity at that site.

We defined a visit as a black rat making physical contact with an inflorescence sometime during a video. All detections of black rats were analysed, including videos where rats made no contact, so that behaviours that impede pollination (e.g., *moving* and *vigilance*; Table 3.1) would be recorded. To calculate the mean *visitation rate* of independent foraging bouts for each site, we excluded visits that were not separated from others by five minutes. Inspection of time gaps between successive videos showed that the duration of foraging bouts rarely exceeded five minutes.

Pollination behaviours were scored with the event recorder software JWatcher (Blumstein et al. 2019) according to an ethogram we developed (Table 3.1). Multiple observers were blinded to site and were tested for intra-observer reliability using the JWatcher reliability routine. We quantified the proportion of time that each animal spent in physical *contact* with and *foraging* on inflorescences, *grooming*, in locomotion (*moving*), *vigilant* or *destructively foraging* (Table 3.1). The proportion of time that black rats spent in contact with inflorescences was not mutually exclusive to the other behaviours. However, all other behaviours were mutually exclusive.

Table 3.1 Ethogram for video analysis of black rat pollination behaviours.

Behaviour	Definition	Effect on pollination
contact	Animals physically touching the inflorescence	Incidental collection or transferral of pollen
foraging	Clearly licking to collect nectar and pollen	Pollen may be collected or transferred, use of floral rewards
grooming	Licking and washing fur	Removal of pollen from fur, decreasing pollen load
moving	Animals were in motion e.g., running, walking, climbing, jumping	Impedes foraging but may result in cross pollination
vigilance	Still, sniffing the air, alert	Impedes foraging and pollination
destruction	Clearly chewing or ripping out flowers	Although pollen collection could still occur, damage to flowers is caused, limiting pollen availability and eventual seed set

3.3.5 Statistical analyses

We used the residuals from each of our models to verify that pollination behaviour variables were normally distributed and that we could assume homogeneity of variances following Zuur et al. (2010). Outliers were identified using Cleveland dot plots and outlier boxplots and were all retained in our dataset unless stated otherwise. R^2 values and inspection of the model residuals indicated the strength of each regression. We verified the assumptions of independence and absence of residual patterns in our models by plotting residuals against fitted values. All data exploration and analyses were carried out using JMP Pro 13 (SAS) software (SAS Institute Inc. 2019).

We conducted a linear regression to understand the relationship between black rat population density (relative abundance) and visitation rate (mean number of independent visits per night over five nights). To understand how population density affects pollination behaviours of black rats, we conducted separate linear regressions between the proportions of time (whilst in sight) that black rats allocated to being in *contact*, *foraging*, *grooming*, *moving*, being *vigilant* and *destructively foraging* and the relative abundance for each artificial pollination network. We log transformed the variable *vigilance* to improve the spread and distribution of the model residuals. Non-transformed data are presented in our figures.

One site was excluded from statistical analyses as black rats did not visit the artificial pollination network on the first night of the experiment, leaving 13 sites. Although rats at this site foraged on inflorescences on subsequent nights, their pollination behaviour differed from populations at other sites (e.g., rats spent a high proportion of time *moving* (42% ± 0.08) and a low proportion of time *foraging* (19% ± 0.07)). We did not detect any patterns in our experimental set up, the size, vegetation class or presence of predators at this site that could explain these dramatic behavioural differences.

3.4 Results

Black rats visited *B. ericifolia* inflorescences and foraged for nectar in all 14 artificial pollination networks (although one of these sites was later excluded from our analyses). Rats typically crawled all over the inflorescences and, in 360 of 986 videos (37%), clung to them for more than 50 seconds. Most visits occurred on the first (54%) and second (30%) nights. We also detected inter-inflorescence transfer of ultraviolet fluorescent powder in 11 artificial pollination networks.

3.4.1 Pollination behaviours

Visitation rates at sites ranged from 1.4 to 18.5 visits per night (Table 3.2, Figure 3.4) and, at all sites, black rats spent a high proportion of their time in *contact* with inflorescences (55 - 77%), which was negatively related to their relative abundance (Table 3.2, Figure 3.5a). Besides being in *contact* with inflorescences, black rats spent most of their time *foraging* (39 - 66%), which was also negatively related to their relative abundance (Table 3.2, Figure 3.5b).

Table 3.2 Linear regressions between pollination behaviours of black rats and their relative abundance measured with chew-track-cards. Significant *p* values (where ∝ < 0.05) are indicated in bold text.

Response	Equation	F value	d.f.	*p* value	R^2	Figure
visitation rate	$y = 4.000 + 7.130x$	2.582	1, 11	0.134	0.190	3.3
contact	$y = 0.730 - 0.159x$	7.676	1, 11	**0.018**	0.411	3.4a
foraging	$y = 0.555 - 0.163x$	5.431	1, 11	**0.040**	0.331	3.4b
grooming	$y = 0.036 - 0.017x$	1.363	1, 11	0.268	0.110	3.4c
moving	$y = 0.133 + 0.153x$	16.436	1, 11	**0.002**	0.599	3.4d
vigilance (log transformation)	$y = -1.805 - 0.794x$	4.553	1, 11	0.056	0.293	3.4e
destruction	$y = 0.041 + 0.026x$	0.368	1, 11	0.557	0.032	3.4f

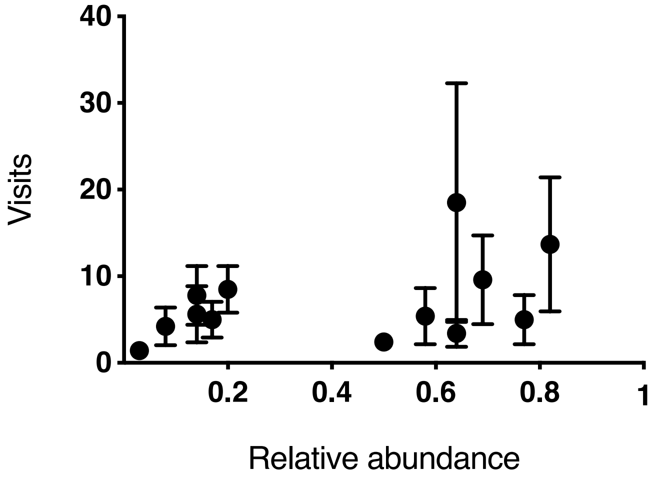

Figure 3.4 Mean visitation rate (± S.E.) per night (for 5 nights) was not related to black rat population density. The relationship between the number of independent visits per night by black rats to *Banksia ericifolia* inflorescences in artificial pollination networks (n = 13) and black rat relative abundance.

The proportion of time that black rats spent *grooming* was small (1 - 5%) and not related to their relative abundance (Table 3.2, Figure 3.5c). However, the time that black rats spent *moving* (12 - 31%) was positively related to their relative abundance (Table 3.2, Figure 3.5d). The time that black rats spent *vigilant* (7 - 31%) was negatively related to their relative abundance but not statistically significant (Table 3.2, Figure 3.5e). Finally, the time that black rats spent foraging destructively (0 – 16%) was not related to the relative abundance of black rats (Table 3.2, Figure 3.5f) and, at three sites, black rats did not destructively forage at all. *Visitation rate* was also not related to black rat relative abundance.

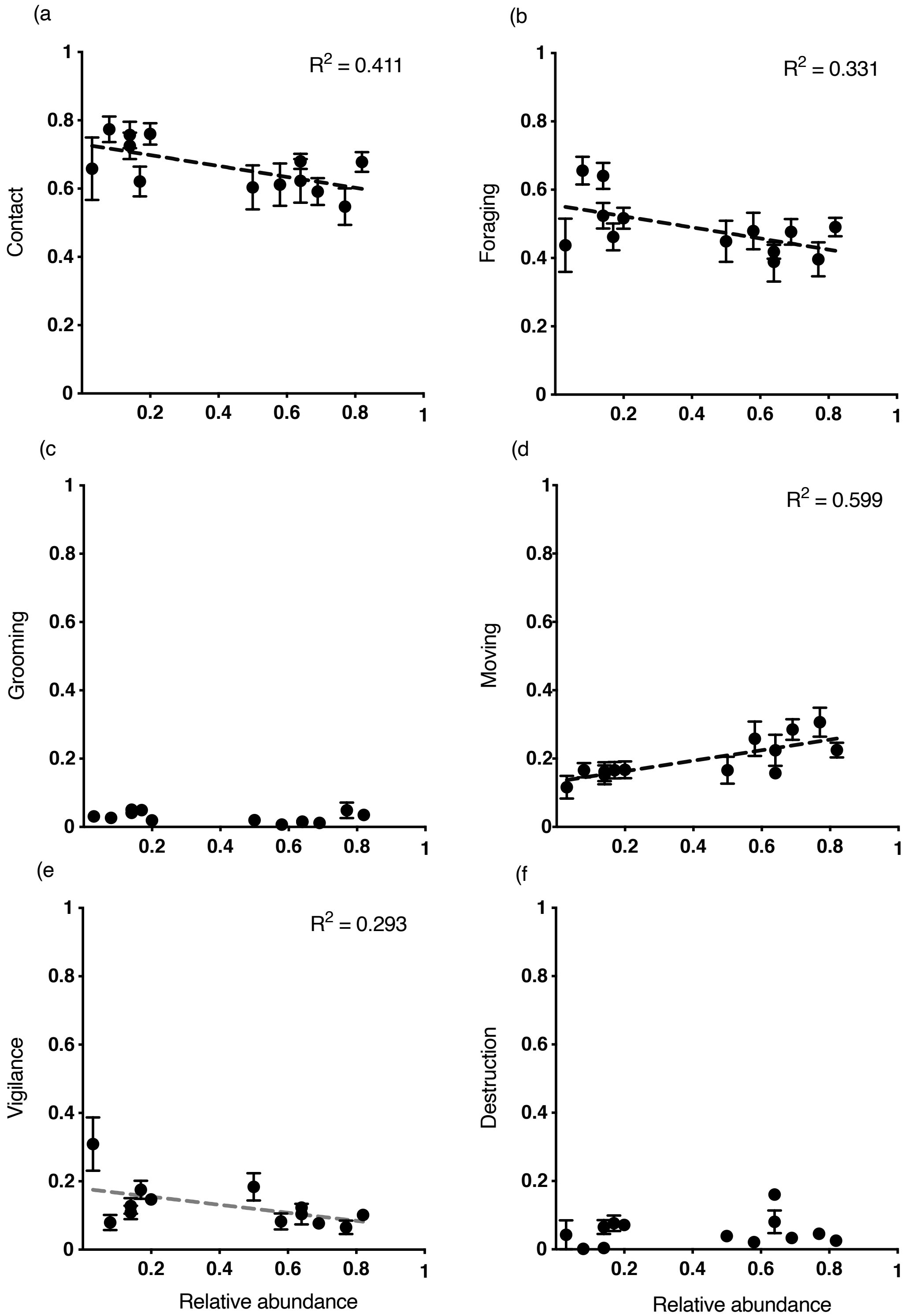

Figure 3.5 The relationship between black rat density and pollination behaviours. Relationships between the mean (± S.E.) proportions of time (during 1 minute videos) that black rats spent exhibiting pollination behaviours in artificial pollination networks (n = 13) and black rat relative abundance: a) being in physical contact with *Banksia ericifolia* inflorescences, b) foraging for nectar on inflorescences, c) grooming, d) locomotion (*moving*), e) displaying vigilance, and f) destructively foraging. A grey dashed line indicates a relationship that is near statistical significance.

We used linear regressions to analyse the relationships between relative abundance and the mean proportion of time that black rats spent in *contact*, the mean amount of time (in seconds) spent in *contact* and the total number of independent visits. Because 84% of visitation happened on the first two nights, we performed analyses on these nights separately (Table 3.3, Figure 3.6). Only the total time that black rats spent in *contact* was related to relative abundance and only on the second night (Table 3.3, Figure 3.6d).

Table 3.3 Linear regressions between pollination behaviours of black rats and density estimates on different nights of the experiment. Significant *p* values (where $\propto < 0.05$) are indicated in bold text.

Response	Equation	F value	d.f.	*p* value	R^2	Figure
Mean *contact*, first night	$y = 0.705 - 0.044x$	0.218	1, 11	0.650	0.019	3.5a
Mean *contact*, second night	$y = 0.754 - 0.172x$	2.568	1, 11	0.137	0.189	3.5b
Mean time (s) in *contact*, first night	$y = 32.903 – 6.804x$	2.920	1, 11	0.116	0.210	3.5c
Mean time (s) in *contact*, second night	$y = 34.328 – 23.381x$	7.316	1, 11	**0.021**	0.399	3.5d
Total visits, first night	$y = 4.844 + 37.782x$	3.251	1, 11	0.099	0.228	3.5e
Total visits, second night	$y = 10.991 + 1.317x$	0.035	1, 11	0.856	0.003	3.5f

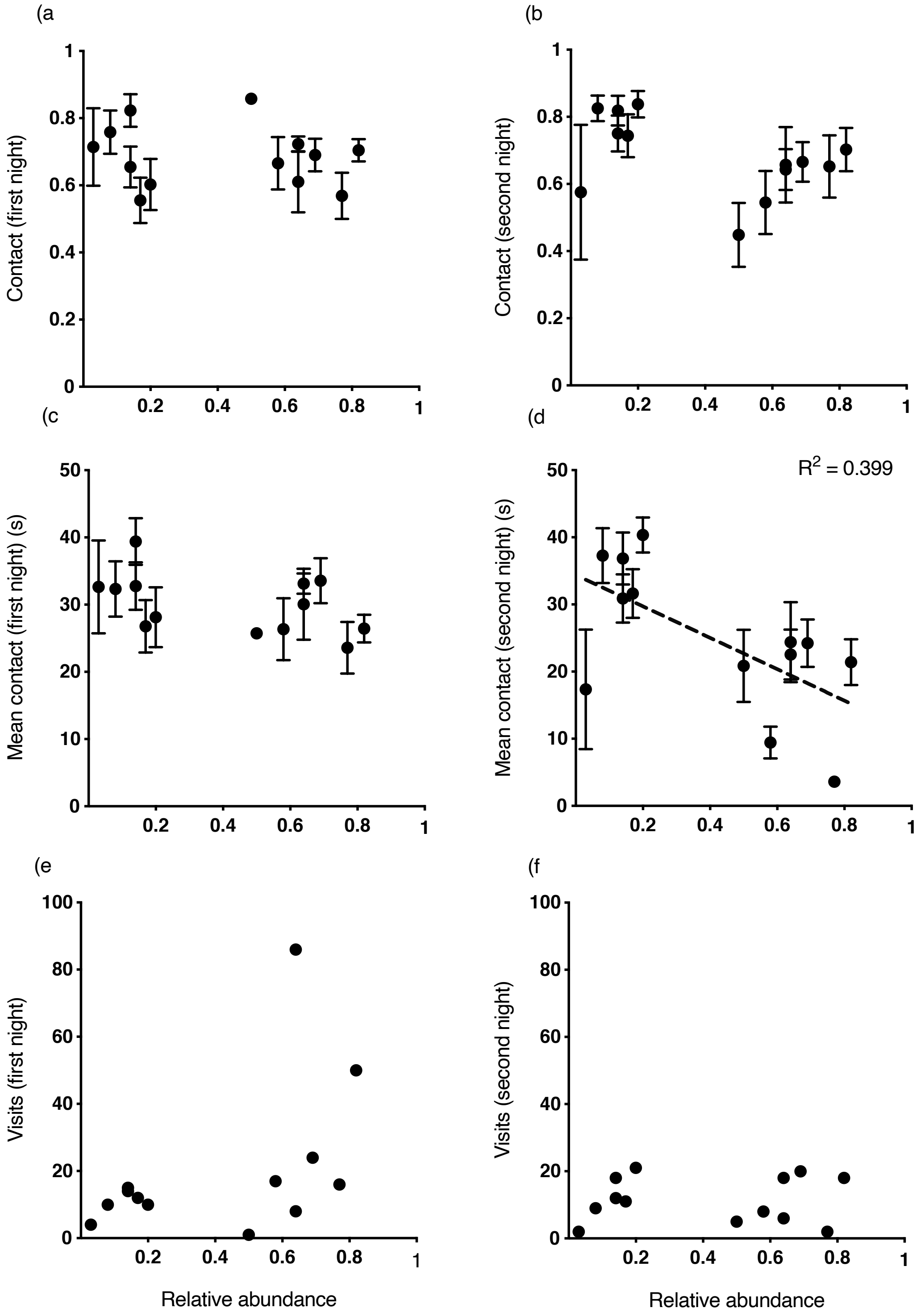

Figure 3.6 Relationships between pollination behaviours of black rats and abundance estimates were different between the first and second nights of the experiment: a) mean (± S.E.) proportion of time spent being in physical contact with *Banksia ericifolia* inflorescences on the first and b) second nights, c) mean time (s) (± S.E.) being in contact with inflorescences on the first and d) second nights, and e) the number of independent visits to inflorescences on the first and f) second nights.

3.5 Discussion

We found that important pollination behaviours of alien black rats were related to their population density, but not all behaviours. Furthermore, we found that some behaviours were related to density in a way that may have conflicting outcomes for pollination efficacy. Black rats rapidly discovered inflorescences, visiting them at 13 of 14 sites within the first night of the experiment. We also detected ultraviolet fluorescent powder transfers at 11 sites indicating strong potential for a role in pollination. However, black rats in sites with higher population density allocated less time to interacting with native *B. ericifolia* inflorescences and spent less time in *contact* with and *foraging* on inflorescences compared to black rats at lower densities, indicative of poor pollination performance at higher densities. Black rats were also less *vigilant* when in high densities (although this result was not significant) but they spent more time *moving,* which would promote pollen transfer and pollination success. *Visitation rates* and the proportion of time that black rats spent *grooming* or *destructively foraging* were not density dependent. Thus, as alien black rats are using native *B. ericifolia* inflorescences as a food source, they are likely to be pollinators of this species (see also (Saul 2013) and (O'Rourke et al. 2020)) and their pollination behaviour is density dependent in complicated ways.

At high densities, black rats foraged for the shortest amount of time, which would limit the amount of pollen collected in their fur (e.g., sugar gliders (Goldingay et al. 1991a)). Optimal Foraging Theory predicts that individuals from high density populations will choose to forage for longer at one patch, rather than risk missing out by searching for better quality resources elsewhere (Davidson and Morris 2001, China et al. 2013). Instead, we found the opposite relationship. This may have been related to individuals in high densities rapidly depleting the floral rewards out of our inflorescences, prompting individuals to search for other food. Resource depletion has consequences for pollination efficiency, for example, blueberry plants produced less fruit when pollinated by European honeybees in high densities since each individuals carried a reduced pollen load (Dedej and Delaplane 2003). Although overall, we found a negative relationship between contact time and density, this relationship was absent on night one but then appeared on night two. High densities of black rats would have only been affected by resource depletion by the second night of the experiment, resulting in shortened visits to inflorescences (but not visitation or time allocation) and potentially reduced pollen loads (Figure 3.5d). Our cut inflorescences may have had limited ability to replenish nectar supply between nights so that they may have started to dry out on the second night of the experiment. Natural *B. ericifolia* inflorescences produce nectar continuously with higher production rates occurring at night (Paton and Turner 1985). However, rates of nectar production do vary from day to day, and between plants, likely according to environmental conditions (e.g., temperature, rainfall and humidity) (Paton and Turner 1985). Although we did not measure the nectar production of our cut inflorescences, we did provide them with a water source, and some inflorescences had not dried out by the time they were collected after the experimental period. Many inflorescences, though, had their water bags punctured by black rats causing the water to drain out and inflorescences to dry. Given the limitations of our artificial set up, it is important to understand whether black rats will continue to return to natural *B. ericifolia* inflorescences throughout the flowering season to establish their efficacy as pollinators.

Although we selected sites that were of similar sizes and had no winter-flowering Banksia species present, we were not able to control for background community composition and complexity. That black rats visited artificial pollination networks on the first night of the experiment shows that our inflorescences were attractive, either as a resource or for their novelty, over other food sources at that time. In general, the effect of the presence of other food sources upon pollination behaviours would depend on the availability and value of those resources to individuals. As with most ecological field studies, we may have only sampled a subset of the population at each site (i.e., individuals that would choose to visit chew cards and/or artificial pollination networks (see Garvey et al. 2020)) but no residual patterns were found in our data, therefore we are confident that there were no notable differences between our sites that could have affected black rat behaviour.

Black rats were frequent visitors to *B. ericifolia* inflorescences as compared to other small mammal pollinators of Proteaceae species elsewhere. For example, in separate studies at least one native mammal visited *B. spinulosa* inflorescences every 24 hours (Carthew 1993) and only five visits by pygmy possums to *B. integrifolia* inflorescences were observed over 13 nights; rodents visit South African *Protea* spp. up to four times per night (Zoeller et al. 2016). In comparison, we found that, on average and across all sites, black rats made 0.57 ± 0.03 independent visits per inflorescence per each night of the experiment, with a maximum of 45 visits in one night to one inflorescence. However overall visitation rates were not related to density.

Most black rat visits (84%) occurred within the first two nights of our experiment, probably because floral rewards were low by the third night. Price and Banks (2012) reported similar neophilic behaviour by black rats rapidly investigating artificial nests treated with domestic quail (*Coturnix japonica*) odours. Without the reward of real quail eggs, visits to nests dropped by the third day of the experiment (Price and Banks 2012). As generalist foragers, black rats learn to ignore unrewarding cues and will not investigate them again, even when a reward is provided in the future (Price and Banks 2012, Bytheway et al. 2013). This is not ideal behaviour for an effective pollinator as, to effect cross-pollination, pollinators must visit other flowers from con-specific individuals within a short time. Our use of ultraviolet fluorescent powder did confirm that some cross-pollination was affected by black rats within artificial networks, but we do not know the timeframe for this. However, in previous work, one black rat individual was positively identified visiting two *B. ericifolia* inflorescences within the same night (Saul 2013). Furthermore, natural *B. ericifolia* inflorescences can continue to produce nectar for 2-3 weeks (Lloyd et al. 2002) which would sustain rewards to motivate returning black rats to revisit and transfer pollen.

Other important pollination behaviours were independent of black rat population density. As expected, black rats spent little time grooming on an inflorescence, which could otherwise limit their pollination role, and grooming was not related to population density. Pollen loads can be reduced by grooming, for example, the time that hairy-footed gerbils (*Gerbillurus paeba*) and striped field mice (*Rhabdomys pumilio*) spend grooming is exponentially related to their pollen loads, where the number of pollen grains in their fur is reduced to almost zero after one minute of grooming (Johnson and Pauw 2014). Nonetheless, excluding these rodents from *Leucospermum arenarium* inflorescences significantly reduces seed set, demonstrating that pollination is effected even with a potentially limited pollen load (Johnson and Pauw 2014). Rats are well known for their grooming and at least in an observational laboratory study spend up to 40% of their time grooming, especially after eating or interacting with novel objects (Bolles 1960). In contrast, individuals in our artificial pollination networks only spent up to 5% of their time grooming, probably as this behaviour reduces time available for behaviours more important to fitness outcomes. 94% of samples taken from the snouts of black rats contain *B. ericifolia* pollen, and black rats carry similar pollen loads to those of native mammalian pollinators (Saul 2013), further demonstrating that grooming is unlikely to limit pollen collection.

Destructively foraging (eating the inflorescences rather than just the floral rewards) occurred at most sites but this behaviour was also not density dependent. We had hypothesised that destructive foraging might increase at higher densities e.g., due to food stress from competition. Destructive foraging can occur when predators seek other potential prey in the flowers, not just nectar. For example, many *Banksia* species are predated upon by moth larvae, that attack both inflorescences and seed cones, and parrots (mainly black cockatoos, *Calyptorhychus funereus latirostris*) that attack inflorescences in search of these moth larvae (Scott 1982, Lamont and Leeuwen 1988). However, we only observed black rats eating flowers and not necessarily damaging the rachis of the inflorescences. It is possible that observed destructive foraging was done by a few individuals. For many pest species, damage is the result of unusual behaviours of a subset of individuals (Swan et al. 2017). In any case, *Banksia* inflorescences are made up of hundreds of individual flowers, which could be an important defence to predation since it is highly likely that some flowers will be unharmed (Scott 1982). Therefore, *B. ericifolia* may still be able to produce seed following a destructive foraging event by individual black rats (Goldingay et al. 1991b).

Behaviour is known to be density dependent (Holling and Buckingham 1976, Childress and Lung 2003, Bonsall et al. 2003, China et al. 2013), but the flow-on effects upon ecological functions had previously not been explored, especially for an alien species. Our results highlight that the effects of density on the behaviours of a population (driven by other factors such as social interactions and food stress) can be complex. Therefore, the impacts of these behaviours upon the efficacy of an ecological function, such as pollination, will also be complex. The influence of density is likely to be simpler for ecological functions that have fewer behavioural dimensions (e.g., ecosystem engineering) or when behaviour is not relevant (e.g., functions provided by plants). For alien species that provide some positive services, understanding the density dependence of their behaviour will help to reduce negative impacts whilst conserving ecological functions that may otherwise be lost.

Our results suggest alien black rat behaviour at inflorescences makes them good candidates as pollinators of native *B. ericifolia,* but some of these behaviours are density dependent. Black rats showed high fidelity to inflorescences in our artificial pollination networks, particularly on the first and second nights of the experiment. They were quick to find the new resources, they foraged readily and mostly non-destructively. Furthermore, we detected potential evidence for successful cross-pollination. However, the effects of population density produced variation in their behaviours, which is likely to impact their efficacy as pollinators in complex ways. Black rats in high densities foraged for less time, which would limit their pollen collection abilities, but they moved more, which might provide more opportunity for effecting cross-pollination. Our research highlights the need to consider how density dependent behaviours shape ecological functions, as this will both inform and open up many avenues for conservation, whether it is finding compromises in alien species management or in the restoration of native systems.

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Chapter 4 How density affects the positive effects of an alien plant: native skink use of *Lantana camara* in urban Sydney, Australia

Author contributions:

A.M.S., C.E.T. and P.B.B. conceptualised the research and designed the methodology. A.M.S. conducted the field research, and collected and analysed the data. All authors were involved in the interpretation of the data. A.M.S. wrote the manuscript with critical contributions from C.E.T. and P.B.B.. All authors gave final approval for submission.

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4.1 Abstract

The impacts of alien plants are often complex and include both negative and positive effects on native species. Ecological managers can be faced with the challenge of weighing up the outcomes of management (e.g., removal) against any conservation benefits provided by alien plants. We suggest that the positive effects of alien plants can also be related to their density. Like density-damage relationships that help determine the level of population control needed to curb undesirable effects of alien species, “density-benefit” relationships can help determine how to optimise their ecological benefits. To test this, we investigated how the density (measured as cover) of invasive lantana in a patch (*Lantana camara*) is related to the abundance of native skinks (*Lampropholis* spp.) that use lantana patch edges as refuge. We trapped skinks using pitfall traps at twelve spatially distinct sites in Sydney Harbour National Park, Australia. Skink abundance was related to lantana cover through a U-shaped relationship and also decreased with the number of lantana patches in a plot. This suggests that significant benefits from lantana to native skinks only exist when cover is at its highest as this tends to correspond to a more structurally complex growth form with hard edges. Understanding that the density of an invasive alien plant species affects its beneficial effects will allow ecological managers to explore the more subtle interactions between alien and native species.

4.2 Introduction

Alien plants have complex impacts on their new environments. A recent meta-analysis found that alien plants can reduce the fitness and growth rates of resident plant and animal species, but they can also provide ecosystem functions such as increased nutrient cycling and microbial activity (Vilà *et al.* 2011). To understand the net conservation outcomes of any intervention against alien plants, the positive effects of alien plants must be weighed up against their harmful, negative effects. For example, in eastern United States, invasive hybrid cordgrasses (*Spartina* spp.) provide habitat for endangered Californian clapper rails (*Rallus longirostris obsoletus*) but their transformative negative impacts upon native saltmarsh ecosystems have been used to justify their removal (Lampert *et al.* 2014). Conversely, in southwestern United States, invasive Eurasian tamarisk (*Tamarix* spp.) is retained to provide breeding habitat for a number of endangered native birds, including yellow-billed cuckoos (*Coccyzus americanus*) and willow flycatchers (*Empidonax traillii*) where native vegetation has been lost or degraded (Sogge et al. 2008). Although many other native birds do not benefit from the presence of tamarisk, native riparian vegetation may not return after its removal (Sogge et al. 2008), and so tamarisk is considered to have a net benefit to the ecosystem. Failing to understand and take into account the benefits of these alien plants may result in unwanted, unexpected consequences for native species (Zavaleta et al. 2001, see also Dickman 2007).

However, the mere presence of an alien plant in an ecosystem is unlikely to fully characterise the complex nature of its impacts, and its population density will likely play an important role. The influence of population density in negative interactions between alien and native species is often explained through density-damage curves (Yokomizo et al. 2009, Norbury et al. 2015, Bradley et al. 2019) that can identify impact thresholds (Gooden et al. 2009). These relationships are used to inform cost-effective control decisions (Norbury et al. 2015). It is likely that beneficial effects of alien plants are also related to their abundance and there is anecdotal evidence supporting this. For example, following removal, the extent of re-establishment of alien bitou bush (*Chrysanthemoides monilifera* ssp. *rotunda*) influences the abundance of small native birds and mammals that use the plant as a source of food and refuge (O'Loughlin et al. 2019). Similarly, the overall impacts of an alien seaweed (*Gracilaria vermiculophylla*) upon coastal ecosystem functions are positive, context-dependent and vary across seaweed density (Ramus *et al.* 2017). Understanding how density affects ecological benefits, such as ecological functions and interactions, would allow alien plant populations to be controlled to a density level where benefits to native species are conserved, but negative impacts are reduced. This will be especially useful for the control of established alien plants that cannot be eradicated and for conserving ecological functionality in novel ecosystems (Hobbs et al. 2006).

In this paper, we explore the density dependent component of the interaction between the alien plant, lantana (*Lantana camara*), and small native reptiles (*Lampropholis delicata* and *L. guichenoti*, hereafter "skinks"). Lantana has been established on the east coast of Australia for over 160 years (Sharma et al. 2005) and is often the target of bush regeneration efforts. It is listed as one of 32 Weeds of National Significance for its invasive nature since it is easily spread and grows fast, especially in disturbed landscapes with high nutrient and sun availability (Virkki et al. 2012). Lantana has a variable and novel growth pattern that can change from sprawling canes to dense, prickly thickets (Figure 4.1) depending on the light conditions (Goyal and Sharma 2019). In disturbed ecosystems and where the structural complexity previously provided by native plants has been lost, lantana is thought to provide habitat for small birds (e.g., superb fairy wrens, *Malurus cyaneus* (Parsons et al. 2016) and bell miners, *Manorina melanophrys* (Lambert and McDonald 2017)), small native mammals (e.g., bush rats, *Rattus fuscipes* (Gleen 2013)) and native reptiles (including skinks (Virkki et al. 2012)). Lantana may have particular use at the edges of remnant vegetation by reducing deleterious edge effects for native animals (Gleen 2013) and buffering invasion from other alien plant species. Edge effects arising at the junction of two different habitats can consist of biotic and abiotic changes that may benefit species according to their biological requirements (Schlaepfer and Gavin 2001).

Figure 4.1 a) Lantana (*Lantana camara*) patches are composed of many interweaving canes, stems and leaves and can form b) an extremely dense patch with a hard, distinct edge. Photographs by M. Lai.

Skinks are ubiquitous in human-modified areas such as gardens (Burgin 1993) and forest edges (Anderson and Burgin 2002) and are often abundant in vegetation invaded by lantana (Virkki et al. 2012). This is probably because both lantana and skinks thrive in areas with canopy gaps and increased sunlight (Kanowski et al. 2006, Virkki et al. 2012). Edge habitats often have higher temperatures and sunlight penetration than interior habitats (Murcia 1995), and so they can be exploited by generalist reptiles (Schlaepfer and Gavin 2001) (Figure 4.2). Generalist species with flexible habitat requirements may be less negatively affected by alien plants.

Skinks require habitats with a heterogeneous structure allowing them to shuttle between sun and shade (Martin 2013, Hacking et al. 2014). Maintaining an optimum body temperature is critical for foraging, avoiding predators, digestion and, ultimately, growth and reproduction (Torr and Shine 1993, Webb and Shine 1998). Alien plants can disrupt the structure of a habitat so that small reptiles are not able to reach their optimum body temperature (Valentine et al. 2006, Downes and Hoefer 2007, Hacking et al. 2014). Skinks also require open areas with deep leaf litter (Howard et al. 2003) for hunting invertebrates (Lunney et al. 1989), camouflage (Valentine et al. 2006) and detecting the approach of predators (Prosser et al. 2006). Alien plants can produce leaf litter that is too shallow, or that interferes with camouflage (Valentine et al. 2006), and the presence of alien plants can decrease the invertebrate diversity (Samways 1996). Although lantana typically produces a dense litter cover (Stock 2005) at a depth that is similar to that of uninvaded sites, shading from patches may significantly reduce litter temperatures (Martin 2013).

The dense vegetation structure of lantana may be beneficial by providing refuge from predators. Skinks require access to retreat sites for refuge from predators such as snakes (e.g., yellow-faced whip snakes, *Demansia psammophis* and eastern small-eyed snakes, *Rhinoplocephalus nigrescens* (Downes and Shine 2001)), native birds (e.g., magpies, *Gymnorhina tibicen*, kookaburras, *Dacelo novaegineae* and Australian ravens, *Corvus coronoides* (Anderson and Burgin 2002)) and rodents (e.g., alien black rats, *Rattus rattus* and native bush rats, *R. fuscipes* (Smith et al. 2017)). In general, little is known about how alien plants may provide refuge for native reptiles, apart from anecdotal evidence (e.g., bitou bush, *Chrysanthemoides monilifer spp. rotunda*, sheltering reptiles from domestic cats and dogs (Winkler et al. 2008)).

Figure 4.2 A skink (*Lampropholis guichenoti*) basking at the edge of an extremely dense patch of lantana (*Lantana camara*) in Sydney Harbour National Park. Photograph by M. Lai.

We expected that skinks use the edge of a lantana patch as a basking-retreat-site interface. Skinks thermoregulate at the edge, retreating into the core of the patch when approached by predators. However, the edge benefits are not likely to continue into the core of the lantana patch since both sunlight and ambient temperatures are reduced within lantana patches (Martin 2013), as well as invertebrate diversity (Samways 1996). Therefore, we hypothesise that the availability of lantana patch edges should influence the abundance of skinks by improving their ability to thermoregulate safely and invertebrate availability, but higher densities of lantana will lead to reduced edge area and thus reduced skink abundance (Figure 4.3, Mechanism).

Geometrically, smaller patches of lantana will have relatively more edge available than undesirable core area, whereas larger patches will have more core area (Figure 4.3, Prediction 1). Therefore, we expected that the increasing cover of lantana in a plot would be related to increasing skink abundance, and that skink abundance would reach a plateau at high densities when plots become dominated by core areas. In turn, we also expected that the number of lantana patches would also affect skink abundance. A plot with more patches would have more lantana edge available to skinks than a plot with a single lantana patch (Figure 4.3, Prediction 2). Therefore, we expected that skink abundance would also increase with the number of patches in a plot.

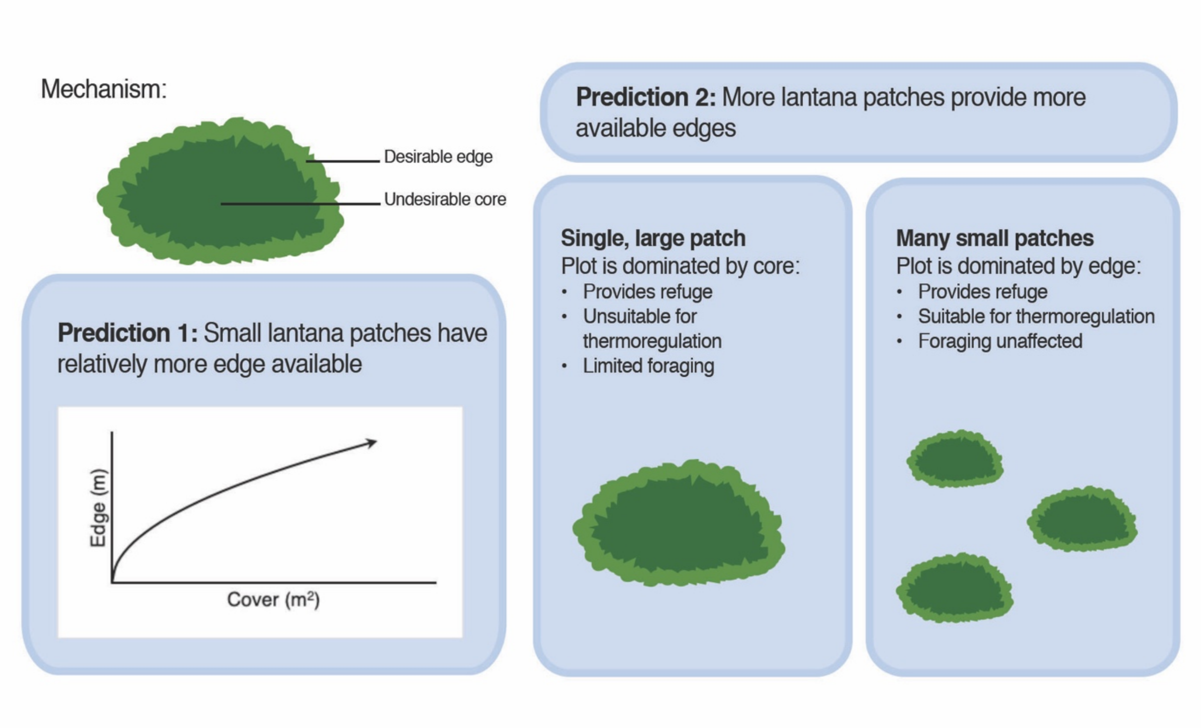

Figure 4.3 The desirable edges of lantana (*Lantana camara*) patches allow native skinks to bask safely. The undesirable core of the patch provides skinks with refuge but is unsuitable for thermoregulation or foraging. The relationship between the amount of desirable edge and undesirable core habitat is affected by increasing lantana cover and different numbers of lantana patches.

4.3 Methods and materials

4.3.1 Study area

We studied the effect of lantana (*Lantana camara*) density on the abundance of small (< 55 mm) native reptiles (*Lampropholis delicata* and *L. guichenoti*: Scincidae) in Sydney Harbour National Park, Sydney, Australia (lat 33°50’S; long 151°15E). Sydney Harbour National Park comprises a collection of isolated bushland precincts, ranging in size from 9 to 183 ha, that are surrounded by an urban matrix. Our experiment was conducted in two of these precincts, Bradleys Head (31 ha), and Middle Head (including Clifton Gardens; 52 ha), that include a mix of coastal sandstone ridgetop woodland (dominated by *Angophora costata*, *Eucalyptus botryoides* and *E. piperita,* and containing an understorey of *Acacia* spp. and *Banksia integrifolia*), coastal sandstone gulley forest (dominated by *A. costata*, *E. punctata* and *E. tereticornis*) and coastal scrub (dominated by *A. costata, B. integrifolia* and *Allocasuarina distyla*), all with varying degrees of invasion by lantana (NSW Government 2012). The national park has a long history of disturbance and modification, in particular for military use during the 19th century, and so features old fortifications along with rocky foreshores, sandstone slopes and cliff faces (NSW Government 2012).

We set up 12 plots of 100 m^2 (10 m x 10 m), representing five skink home ranges (Anderson and Burgin 2002), throughout Middle Head and Bradleys Head. We selected plots with open vegetation to ensure that skinks would be present, and we aimed to capture a gradient of lantana density (Figure 4.4). All plots were spaced more than 50 m (the maximum distance between any plots was 2 900 m) apart to ensure independence between skink populations given that the largest home range recorded for *Lampropholis* spp. in Sydney is 20.2 m^2 (Anderson and Burgin 2002).

Figure 4.4 Coastal sandstone ridgetop woodland invaded by lantana (*Lantana camara*) at Bradleys Head, Sydney Harbour National Park. Photograph by M. Lai.

4.3.2 Lantana density and microhabitat characteristics

During November and December of 2017, we surveyed the percentage of lantana cover (*mean lantana cover*), the number of lantana patches (*total lantana patches*), and a suite of microhabitat characteristics that could influence skink presence and abundance in each plot (see Table 4.1). A patch of lantana did not necessarily correspond to an individual plant, so we defined a patch as lantana plants that formed a clump that was not joined to others, thus having a unique edge. Microhabitat structures can influence reptile assemblages by driving the availability of resources, basking opportunities and refuge (Virkki et al. 2012). We adapted microhabitat characteristics identified as essential to skink presence from Mather (1989) and Anderson and Burgin (2002). We also used the methods developed by Gleen (2013) to survey the three dimensional qualities ("architecture") of the vegetation in our plots. To make sampling easier, we subdivided each 100 m^2 plot into 5 m x 5 m quarters and surveyed each quarter separately. We averaged our results from each quarter to produce a total for the whole plot. Counts of lantana patches and “architecture” features, however, were totalled across the quarters (Table 4.1).

4.3.3 Native skink abundance

We trapped skinks using plastic pitfall traps (height: 117 mm, base diameter: 85 mm, diameter at top: 98 mm, volume: 700 ml) installed so that the lip was flush with the ground. Each container had drainage holes in the base, and a damp sponge and some leaf litter as sources of moisture and cover for captured skinks. Pitfall traps were arranged in clusters of four with each trap at the cardinal point of a 1 m^2 square. Four trap clusters were installed in each plot, with one 1 m^2 cluster at the centre of each quarter. This specific arrangement has been used successfully to index skink numbers in the area (Smith et al. 2017). We opened traps at 8 am each morning and checked and closed them at 4 pm. Each plot was trapped for three consecutive days, resulting in 576 trap days.

For each captured skink, we measured its mass (g) and snout-vent length (mm), which was used to assign them to a size-age category following Joss and Minard (1985). We also temporarily marked each individual uniquely under the chin with a non-toxic, permanent marker to allow us to estimate the population size through recaptures. However, no individuals were re-caught, so we estimated skink abundance as the minimum number known alive (MNKA; (Krebs 1966)).

Traps were set during November 2018 to January 2019, during the Austral summer. We collected weather data from The Bureau of Meteorology website to identify weather conditions that may have influenced our trapping results (www.bom.gov.au): daily maximum temperature (°C), overnight minimum (°C), precipitation (mm), mean wind speed (km/h), cloud cover (8ths), relative humidity (%) and sun hours from the weather station at Observatory Hill, Sydney (lat 33°51’S; long 151°12E). We closed traps on rainy days or days with predicted maximum temperature outside of the range: 26 to 34°C.

4.3.4 Statistical analyses

We checked our datasets for outliers, collinearity and independence using the method of data exploration outlined by Zuur et al. (2010). Assumptions of homogeneity of variance and normality were investigated using model residuals plotted against fitted values, and datasets were square root transformed if these were violated (e.g., the *total small objects* variable). Linear regressions were used to test the effect of *mean lantana cover* and *total lantana patches* on the abundance of skinks. We used Akaike's Information Criterion (AIC) to select the model with the best fit. The relationship between skink abundance and *mean lantana cover* had the lowest AIC value (64.5) when fitted with a quadratic linear model. The relationship between skink abundance and *total lantana* patches had the lowest AIC value (59.5) when fitted with a linear model.

Relationships between habitat characteristics, weather variables and skink abundance were investigated with Pearson correlations, including between *mean lantana cover* and *total lantana patches*. After fitting models, we checked the model residuals against each covariate in the model and each covariate not in the model, and for temporal and spatial dependency.

To reduce the number of variables and to explore the interactive effects between them, we performed a Principal Components Analysis using our 15 habitat variables. Eleven principal components (PC) were produced, and the first four PCs accounted for 24.12%, 20.1%, 14.53% and 11.78%, respectively, of the total variation in our dataset. We then used stepwise regression analysis to develop a model for predicting the abundance of skinks based on these PCAs. All exploration and analyses were carried out in JMP Pro 13 (SAS) software (SAS Institute Inc. 2019).

Table 4.1 The suite of microhabitat characteristics, including lantana density, patches and "architecture", measured to explain skink abundance in 100 m^2 plots at Sydney Harbour National Park.

Habitat characteristic	Survey method	Reference
Mean lantana cover (%)	Estimated visually to the nearest 5% within each plot quarter.	(Gleen 2013)
Total lantana patches	Direct counts of separate lantana patches per plot.	
Mean lantana height (cm)	Direct measurements of the tallest point of each lantana patch were taken with a 1 m ruler. A mean was produced per plot quarter.	
Mean bare ground (%)	Estimated visually within a 1 m^2 quadrat tossed randomly once in each plot quarter.	(Mather 1989, Anderson and Burgin 2002)
Mean grass cover (%)	Estimated visually within a 1 m^2 quadrat tossed randomly once in each plot quarter.	(Mather 1989, Anderson and Burgin 2002)
Mean leaf litter cover (%)	Estimated visually within a 1 m^2 quadrat chosen randomly once in each plot quarter.	(Mather 1989, Anderson and Burgin 2002, Gleen 2013)
Mean litter depth (cm)	Direct measurements taken with a ruler within a 1 m^2 quadrat chosen randomly in each quarter. The mean of four measurements was produced per plot quarter.	(Mather 1989, Anderson and Burgin 2002) (Gleen 2013)
Mean understorey density (0-3; habitat architecture)	Visually estimated and assigned categories: 0 No vegetation, 1 Light, 2 Medium, 3 Dense. The mean of four measurements was produced per plot quarter.	(Gleen 2013)

Mean understorey height (cm)	Directly measured with a 1 m ruler. The mean of < 8 measurements was produced per plot quarter.	(Mather 1989, Gleen 2013)
Mean tree canopy cover (%)	Visually estimated once from the centre of each plot quarter.	(Mather 1989, Anderson and Burgin 2002, Gleen 2013)
Total low cavities (habitat architecture)	Direct counts of cavities formed by vegetation, where the foliage layer began at a height less than 1 m per plot.	(Gleen 2013)
Total high cavities (habitat architecture)	Direct counts of cavities formed by vegetation, where the foliage layer began at a height more than 1 m per plot.	(Gleen 2013)
Total fallen trees or logs (habitat architecture)	Direct counts of fallen trees or logs per plot.	(Mather 1989, Gleen 2013)
Total homogeneity (habitat architecture)	Direct counts of highly dense vegetation patches per plot.	(Gleen 2013)
Total small objects	Direct counts of objects (rocks, rubbish etc.) smaller than a soccer ball (22 cm in height and diameter) per plot.	(Mather 1989, Gleen 2013)
Total large objects	Direct counts of objects (boulders etc.) larger than a soccer ball (22 cm in height and diameter) per plot.	(Mather 1989, Gleen 2013)
Total other	Direct counts and notes of any other features of the plot (e.g., cliff faces, bare sandstone bedrock, brush turkey (*Alectura lathami*) mounds, and remnants of fortifications).	

4.4 Results

We found that skink abundance was related to *mean lantana cover* through a quadratic linear model ($F_{(2, 9)} = 4.836$, $p = 0.0375$, $R^2 = 0.52$; Figure 4.5a). The relationship was U-shaped, where more skinks were caught in plots with the lowest and highest lantana cover. On the other hand, skink abundance was linearly related to the number of lantana patches in a plot ($F_{(1,10)} = 6.241$, $p = 0.032$, $R^2 = 0.38$; Figure 4.5b) and fewer skinks were caught where there were more lantana patches. Our 12 plots contained a range of lantana cover (0.8 – 80 %) and lantana patches (2 - 11). No correlation was found between *mean lantana cover* and *total lantana patches* (Pearson's r = -0.31, p = 0.333).

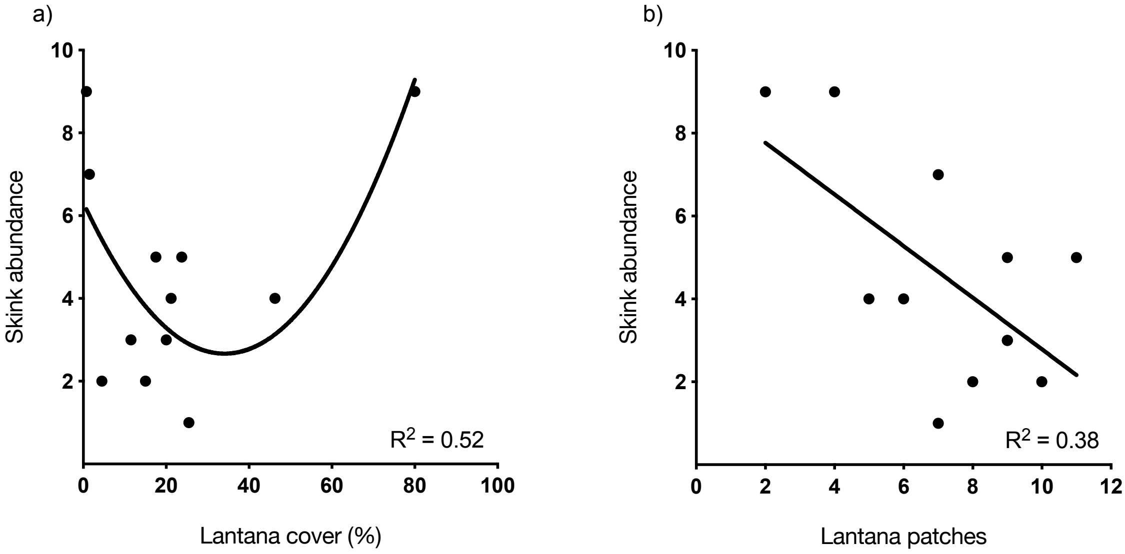

Figure 4.5 The relationship between the abundance of skinks (measured as the minimum number known alive) and percent cover of lantana (a) and the number of lantana patches (b) in 100 m^2 plots (n = 12).

Most microhabitat characteristics were consistent between plots (Table 4.2) apart from *mean lantana cover* (0.75 – 80 %), *mean lantana height* (62.5 – 270.8 cm), *mean grass cover* (13.8 – 73.8 %), *mean leaf litter cover* (18.8 – 76.3 %), *mean understorey height* (100 – 207.3 cm), *mean tree canopy cover* (17.5 – 63.8 %) and *total small objects* (0 – 60), which had the widest ranges. Skink abundance was negatively correlated with *mean lantana height* (Pearson's $r = -0.601$, $p = 0.039$) and *mean tree* *canopy cover* (Pearson's r = -0.601, p = 0.039) (Table 4.3). *Mean lantana height* and *mean tree canopy cover* were themselves linearly correlated (Pearson's r = 0.625, p = 0.03; Table 4.3).

Table 4.2 Summary of survey results of habitat characteristics that could influence native skink abundance in each 100 m^2 plot (n = 12).

Habitat characteristic	Mean ± s.e.
Mean lantana cover (%)	22.3 ± 6.4
Total lantana patches	7.3 ± 0.8
Mean lantana height (cm)	185.6 ± 15.5
Mean bare ground (%)	10.3 ± 3.2
Mean grass cover (%)	36.5 ± 5.7
Mean leaf litter cover (%)	47.4 ± 5.6
Mean litter depth (cm)	3.5 ± 0.4
Mean understorey density (0-3; habitat architecture)	2 ± 0.1
Mean understorey height (cm)	163.3 ± 9.6
Mean tree canopy cover (%)	37.8 ± 4.9
Total low cavities (habitat architecture)	2.7 ± 0.6
Total high cavities (habitat architecture)	3.0 ± 0.6
Total fallen trees or logs (habitat architecture)	6.8 ± 1.3
Total homogeneity (habitat architecture)	2.1 ± 0.6
Total small objects	13.3 ± 5.3
Total large objects	11.6 ± 1.9
Total other	3.3 ± 0.7

Table 4.3 Results of linear correlations between skink abundance and habitat characteristics in 100 m^2 plots (n = 12). Stars indicate significant *p* values ($\alpha > 0.05$).

Habitat characteristic	**Pearson's *r***	**n**	***p* value**
Mean lantana height (cm)	-0.601	12	0.039*
Mean bare ground (%)	0.223	12	0.486
Mean grass cover (%)	-0.167	12	0.604
Mean leaf litter (%)	0.12	12	0.735
Mean litter depth (mm)	-0.007	12	0.983
Mean understorey density (1-3)	0.027	12	0.933
Mean understorey height (cm)	-0.449	12	0.143
Mean tree canopy cover (%)	-0.601	12	0.039*
Total low cavities	-0.051	12	0.875
Total high cavities	-0.372	12	0.234
Total fallen trees/logs	-0.36	12	0.250
Total homogeneity	0.008	12	0.980
Total other	0.052	12	0.872
Total small objects	-0.173	12	0.590
Total large objects	-0.337	12	0.284
Mean lantana height (cm) x mean tree canopy cover (%)	0.625	12	0.030*

Skink abundance was negatively and linearly related to Principal Component 4 ($F_{(1, 10)} = 21.114$, $p = 0.001$; Figure 4.6). The fourth Principal Component had the highest positive loadings for the microhabitat variables: *mean lantana height*, *mean tree canopy cover* and *total high cavities*.

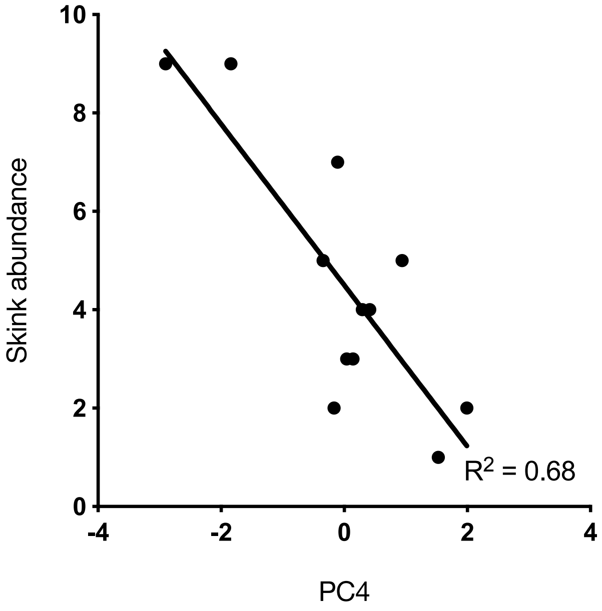

Figure 4.6 The relationship between the abundance of skinks (measured as the minimum number known alive) and Principal Component 4, formed from microhabitat characteristic measurements taken from 100 m^2 plots (n = 12).

Skink abundance was influenced by weather variables that described the amount of sun, including cloud cover (Pearson's *r* = -0.623, *p* = 0.023) and sun hours (Pearson's *r* = 0.597, *p* = 0.031; Table 4.4). However, variation in these weather values was spread across trapping weeks, so we are confident that the weather did not affect our results.

Table 4.4 Results of linear correlations between skink abundances and weather variables retrieved from the Bureau of Meteorology website and skink abundance per trapping day (n = 13). Stars indicate significant *p* values ($\alpha > 0.05$).

Weather variable	Pearson's *r*	n	*p* value
Relative humidity (%)	-0.209	13	0.493
Overnight min (ºC)	-0.381	13	0.199
Daytime max (ºC)	-0.095	13	0.757
Cloud cover (8^{th})	-0.623	13	0.023*
Wind strength (km/h)	-0.262	13	0.437
Sun hours	0.597	13	0.031*

4.5 Discussion

We found that density (measured as percentage cover) of alien lantana was related to native skink abundance through a U-shaped curve. This result shows that lantana only provided benefits to skinks when present in very high densities, above a threshold of approximately 40% cover. At low densities, from 0 – 40% cover, the presence of lantana provided decreasing benefits to skinks and so could even be considered a cost. We observed that the largest patches of lantana also tended to be the most structurally complex, thus providing a clear, hard edge that skinks could use to balance their thermoregulation needs and safety. We consistently observed skinks moving or basking in the sun at the edge of large, dense lantana patches, retreating into the patch when approached. The edges and interiors of many other lantana patches were undefined since most plants had a sprawling growth form. Therefore, only lantana patches that were extremely structurally complex would have formed a useful basking-retreat-site interface for native skinks.

We found that the number of lantana patches in a plot was negatively and linearly related to skink abundance. More skinks were present when there were fewer lantana patches in a plot and less edge habitat, which was opposite to our predictions. Again, small patches tended to lack the hard edge properties, (characteristic of high densities and when lantana patches were large and structurally complex) that we found to be beneficial to skinks. The presence of these small, scrappy patches probably decreased the habitat quality for skinks in comparison to the native vegetation. There were also fewer patches at higher densities of lantana since patches began to merge together, however we found no statistical relationship between *mean lantana cover* and *total lantana patches*.

The U-shaped relationship between lantana density and skink abundance indicates that lantana only provides benefits when in extreme densities. Although alien plants can provide refuge from predators (Winkler et al. 2008), often small reptiles actively avoid alien plants with a complex vegetation structure since this alters the microclimates that reptiles need for thermoregulation (Hacking et al. 2014). For example, when presented with stands of native grasses and alien grader grass (*Themeda quadrivalvis*), rainbow skinks (*Carlia schmeltzi*) prefer native grasses despite an increase in predation pressure (Hacking et al. 2014). This is because temperatures in sites invaded by grader grass do not reach the preferred body temperature for skinks (Hacking et al. 2014). Similarly, *L. delicata* in experimental cages with high cover of alien blue periwinkle (*Vinca major*) resort to climbing to the canopy of these plants to access sunlight, resulting in decreased body weights and clutch sizes (Downes and Hoefer 2007). Although we did not take microclimate measurements, lantana may create cooler and shadier conditions in invaded sites (Martin 2013). Therefore, reduced skink abundances could be explained by the altered microclimates in plots where lantana patches did not provide a distinct, hard edge with beneficial effects. Future studies are needed to investigate how far into a lantana patch beneficial thermoregulation opportunities persist. Techniques such as giving-up density experiments (Bedoya-Perez et al. 2013) or predation experiments using model skinks (e.g., Anderson and Burgin (2002) and Hacking et al. (2014)) would also be useful to establish the perception of predation risk by skinks, and the actual predation risk at the edge of lantana patches, respectively.

Alien plants, including lantana (Samways 1996), can impact the abundance and diversity of invertebrates, however, in a vegetation community similar to our study site, the presence of lantana did not have an effect on invertebrate assemblages (Martin 2013). Skinks are also flexible in their diet and their hunting style (Lunney et al. 1989). We expected that foraging opportunities would be limited within the interior of a lantana patch, whereas the edge area is beneficial for skinks because they can thermoregulate in safety and so improve their foraging ability in the surrounding matrix. The direct effect of lantana upon foraging opportunities for skinks is unclear.

Alien plants can have exaggerated impacts on small-bodied native reptiles with small home ranges, by modifying a large proportion of their habitat (Martin 2013). Lantana provides novel habitat structure in wet and dry sclerophyll forests, and its presence may decrease *L. delicata* abundance by half, in comparison to skink abundance in intact native vegetation (Martin 2013). In this study, the average density of lantana was 35% so we would expect low skink numbers given we trapped the fewest skinks in lantana densities of approximately 40%. Although we did not recapture any skinks, the numbers that we caught were higher than in a previous study conducted in the same area using the same technique: an average of 10 skinks caught over one hectare (Smith et al. 2017). Therefore, we are confident that our results are representative of the skink populations in Sydney Harbour National Park.

Apart from *mean lantana cover* and *total lantana patches*, the other microhabitat characteristics related to skink abundance were *mean lantana height* and *mean tree canopy cover*, which were themselves positively correlated. These relationships were further supported by the results of our Principal Components Analysis. The growth of lantana varies with the conditions available, for example, lantana tends to grow taller when there is less sunlight (Goyal and Sharma 2019), which would explain the correlation between *mean lantana height* and *mean tree canopy cover*. Furthermore, the negative relationship between *mean tree canopy cover* and skink abundance is probably be due to sun availability as skinks prefer open canopies (Kanowski et al. 2006, Virkki et al. 2012). Therefore, there is a negative association between sunlight, skink presence and the climbing growth forms of lantana. Lastly, the trapping success of skinks was correlated with high sun hours and low cloud cover, two measurements of sun availability.

The success of management is often reported by the amount of alien plants that have been removed. However, there are currently calls to measure the success of control through the responses of native species (O'Loughlin et al. 2019). We have found that density is related to the benefits that lantana provides for skinks. The U-shape of the "density-benefit" relationship for lantana, shows that benefits are limited when this plant is in intermediate densities and not providing a distinct, hard edge. However, density-damage curves show that the negative effects of lantana also arise at high densities (Gooden et al. 2009). Our results suggest ecological managers must decide between completely removing lantana or retaining patches with high structural complexity to support skink abundance whilst mitigating the negative impacts to native plants. It is likely that removing the structurally complex patches of lantana will negatively affect skinks, but ineffective removal of lantana could be worse. Therefore, maximal removal should be the goal. Ultimately, long-term investigations are needed to detect or understand any fitness consequences that different densities of lantana may cause to skink populations.

We have shown that the ecological benefits of an entrenched alien plant are density dependent. Lantana at high densities likely provides opportunities for basking in safety to native skinks, due to the edge effects arising with a novel, structurally complex growth form. “Density-benefit” relationships could allow ecological managers to control an alien plant to an optimal density without wasting effort and resources, particularly in the case of an established alien plant that cannot be eradicated. The density of an alien plant is commonly measured as the amount of land that it covers (e.g., Gooden et al. (2009)). This can be quickly estimated visually, and land managers aim to reduce alien plant cover through control techniques such as manual removal, herbicide use and burning (O’Loughlin et al. 2019). A deeper understanding of the way that the density of a species affects its beneficial effects will allow ecological managers to explore the more subtle interactions between alien and native species. “Density-benefit” relationships also provide a tool with which to consider and incorporate the ecological benefits of both alien and native plant species into management plans.

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Chapter 5 Density influences the ecosystem engineering role of an alien species

Author contributions:

A.M.S., C.E.T. and P.B.B. conceptualised the research and designed the methodology. A.M.S. conducted the field research, and collected and analysed the data. All authors were involved in the interpretation of the data. A.M.S. wrote the manuscript with critical contributions from C.E.T. and P.B.B.. All authors gave final approval for submission.

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5.1 Abstract

Beneficial ecological functions provided by established alien species are not well understood, and so are often overlooked by practitioners in decision-making. However, knowledge of these benefits can be useful in the conservation of some native species or when aiming to restore functionality in a novel ecosystem. Since some ecological functions are density dependent, their efficacy will be limited by behavioural and physical changes that arise at certain densities. Therefore, fluctuations in population densities of alien species (e.g., through control efforts) could also impact potential benefits. We explored the density dependence of ecosystem engineering by alien European rabbits (*Oryctolagus cuniculus*) in an Australian semi-arid ecosystem and predicted that seedling recruitment would be influenced by foraging activity density. We simulated and compared the digging activities of rabbits and native marsupials by creating artificial foraging pits in nine density levels. In each pit, we measured the abundance and species richness of seedlings, estimated surviving seedling "biomass" and tracked seedling survival over three months. To examine whether pit density also affects the conditions within pits, we measured changes in soil infilling, leaf litter capture and temperature. Seedling recruitment was affected by increasing pit density with fewer seedlings germinating when pit density was either extremely low or high. Although artificial rabbit pits were smaller, warmer and collected more leaf litter than artificial native pits, the abundance, species richness and survival of seedlings were similar in the two pit shapes. Estimated survivor "biomass", however, was not related to pit density and was higher in artificial native marsupial pits. This finding suggests that differences in the growing conditions exist between the two pit shapes. Entrenched alien species, like rabbits in Australia, will have multiple direct and indirect interactions with native species in their new environments, including some that are beneficial. We show that a beneficial ecological function is related to the population density of an alien species, and so could be disrupted by management efforts if not acknowledged or misunderstood. Furthermore, as rabbits are unlikely to be eradicated, careful long-term management of their population densities may maximise the benefits they provide.

5.2 Introduction

Alongside the well documented negative effects of invasive alien species upon biodiversity, there is growing recognition that some alien species can have positive effects in their new ecosystems. For example, alien Japanese white-eyes (*Zosterops japonicus*) have become the sole pollinators of native Hawaiian *Clermontia* spp., following declines of native birds (Aslan et al. 2013), and, in southern England, alien shrubs (*Rhododendron ponticum*) positively influence the abundance of native wood mice (*Apodemus sylvaticus*) by providing shelter from aerial predators (Malo et al. 2013). Although many alien species have devastating social (Pejchar and Mooney 2009), ecological (Graham et al. 2018) and economic impacts (Hoffmann and Broadhurst 2016), they may simultaneously support native species (Rodriguez 2006, Schlaepfer et al. 2011, Emer et al. 2015, Stout and Tiedeken 2016, Natusch et al. 2017), and this complexity is often overlooked in management decisions. The negative impacts of established alien species that cannot be eradicated are influenced by their population density (Yokomizo et al. 2009, Norbury et al. 2015) and it is likely that their positive effects will be too.

The efficacy of ecological functions performed by native and agricultural species is acknowledged to be density dependent (Brodie et al. 2018) but this has only been confirmed by a few studies (Dedej and Delaplane 2003, Soule et al. 2003). For example, when pollinator density is low, visitation rates and, therefore, the reproductive success of plants is limited (Spears 1987). As the density of pollinators increases, so does the efficacy of their pollination. At high densities, however, changes can occur in the behaviour of pollinators leading to inadequate pollination. For example, competition for pollen can lead to individuals switching to pollinate a different plant species (Fontaine et al. 2008) or the finite amount of pollen available could be spread too thinly among plants (Dedej and Delaplane 2003). The relationship between a species' density and a beneficial ecological function will likely vary in shape, direction and strength, just as density-impact curves will (Bradley et al. 2019), and can be context- and time-dependent (Soule et al. 2003). Therefore, rather than simply controlling entrenched alien populations to mitigate their damage, understanding how changes to their density influences ecological functions will be essential to the management of an ecosystem as a whole.

In this paper, we focus on the relationship between the density of an alien species, the European rabbit (*Oryctolagus cuniculus*), and the ecosystem engineering functions it provides. Ecosystem engineering is the creation or modification of habitat and the alteration of resource availability by one species for others (Jones et al. 1994). Several alien species provide benefits to native species through ecosystem engineering. For example, alien agar seaweed (*Gracilaria vermiculophylla*) provides habitat for native epifauna (Ramus et al. 2017) and alien pigs (*Sus scrofa*) increase food availability for native birds by turning over soil and exposing small invertebrates and seeds (Natusch et al. 2017). In Australia, there are many native mammalian engineers, including burrowing bettongs (*Bettongia lesueur)* and greater bilbies (*Macrotis lagotis*), that create foraging pits as they dig for food such as grubs, tubers, roots and fungi. These pits trap seeds, leaf litter, soil and water (Gutterman and Herr 1981), and buffer the effects of sun exposure and temperature extremes (Eldridge and Mensinga 2007), providing pockets of favourable germination conditions for plants (James and Eldridge 2007, James et al. 2009). Eventually, pits become completely filled and reach the end of their ephemeral lifespans (Alkon 1999). Many native engineers that were once abundant are now either extinct or in decline following compounding impacts such as land clearing, drought, competition with alien herbivores, altered fire regimes (Morton 1990) and predation by alien cats (*Felis catus*) and red foxes (*Vulpes vulpes*) (Short and Turner 2000).

European rabbits are medium-sized, alien mammals that are widely abundant in Australia. They became established in the wild in Australia in 1859 (Myers et al. 1994) and have since become a significant agricultural and ecological pest (Eldridge et al. 2006). Grazing by rabbits suppresses regeneration of native trees, shrubs and pasture, and they are in direct competition for burrows and food with native species such as burrowing bettongs, bilbies and greater stick-nest rats (*Leporillus conditor*) (Myers et al. 1994). In arid Australia, rabbit populations are irruptive in response to favourable climatic conditions and the availability of forage and shelter (Stodart and

Parer 1988). During boom periods, a lack of predators and parasites allows rabbit populations to reach exceptionally high densities such that they have been typically difficult to control, for example, rabbits outside of Arid Recovery in South Australia fluctuate between densities of 10 and 70 individuals km^{-2} (James et al. 2011). Managers and farmers employ population control techniques such as warren destruction (Eldridge et al. 2006), the release of diseases, shooting, baiting and building rabbit-proof fences (Myers et al. 1994) to curb rabbit numbers, as eradication seems unlikely.

In addition to warrens, their communal belowground structures, rabbits create small pits when foraging (Eldridge and Koen 2008). Similar to the pits of native species, rabbit pits provide beneficial conditions for germination in resource-limited landscapes through litter and seed capture (James et al. 2009) although, in some cases, similar abundances of seedlings have been found on equivalent “non-pit” surfaces (James et al. 2011). Since this latter research was conducted at sites where rabbit density is low due to local management practices, it is possible that ecosystem engineering is a density dependent ecological function and that low densities could limit rabbit pits from providing comparable ecosystem benefits to those of native pits.

We created artificial rabbit pits and measured the effect of different pit densities on seedling recruitment and pit conditions. As the shape of rabbit pits also affects their efficacy (James et al. 2009, James et al. 2011), we compared them to artificial pits of native ecosystem engineers with the same density treatments. Pits act as wind and water traps for seeds and interference among pits likely determines the distribution of seeds and subsequent seedlings (Boeken et al. 1998, Eldridge 2011). For example, in semi-arid woodlands of Australia, the density of artificial short-beaked echidna (*Tachyglossus aculeatus*) pits affects the distribution of soil and seeds during rainfall (Eldridge 2011). Similarly, the density of artificial native porcupine (*Hystrix indica*) pits in the Negev Desert, Israel, affects the abundance of plants (Boeken et al. 1998). Therefore, we hypothesised that when pit density is low, the low probability of seed, leaf litter and nutrient capture or retention would result in few seedlings germinating in either pit shape. At intermediate pit densities, seedling abundance should increase, but at high densities, intense interference among pits should cause resource- and seed-limitation, reducing seedling germination. Additionally, we expected that the beneficial effects of rabbit pits will be similar to those of native ecosystem engineers when rabbit pits are in similar densities.

5.3 Methods

5.3.1 Study site and species

We worked at Scotia Sanctuary, a private reserve of 64 000 ha, owned by the Australian Wildlife Conservancy in western New South Wales, Australia. The reserve contains a fenced enclosure (4 000 ha) where alien mammals, such as cats, foxes, goats (*Capra hircus*) and rabbits, have been removed and endangered native ecosystem engineers have been reintroduced, including burrowing bettongs and greater bilbies. Scotia Sanctuary sits within a semi-arid region of Australia and experiences irregular rainfall (annual mean of 257 mm) with hot summers (daily mean of 17-33 °C) and mild winters (daily mean of 5-17 °C) (Finlayson et al. 2008).

Burrowing bettongs and greater bilbies are medium-sized, native, nocturnal marsupials that were historically common in the area, with estimated densities of more than 1.5 individuals per hectare (Noble et al. 2007). Burrowing bettongs became extinct in mainland Australia during the 1960s and were re-introduced to the enclosure at Scotia Sanctuary in 2004 from surviving island populations (Finlayson et al. 2008). Bilbies too would have been common (densities of 1 - 2 individuals per km^2 is typical of bilbies in the Northern Territory (Southgate 1987)) and, although they are still present on the mainland, the species has experienced a severe range contraction and is extinct in New South Wales (McDonald et al. 2015). The decline of both species is probably due to predation by alien foxes and cats, along with dingo (*Canis lupus dingo*) predation (Allen and Fleming 2012), farming and competition with rabbits (Short and Turner 2000).

We surveyed the natural pits of bettongs, bilbies and rabbits in two adjacent sites (4 ha) on either side of the enclosure fence; bilbies and bettongs were only present inside the enclosure and rabbits were present outside of the enclosure in low densities due to periodic control by sanctuary staff. The adjacent sites contained a similar vegetation community and soil profile: a combination of *Eucalyptus* with mixed shrubland, and mixed shrubland (Finlayson et al. 2008) on calcareous soils (Calcarosols) with sandy, loamy sand textures and deep profiles (Eldridge et al. 2012).

5.3.2 Experimental design

In October 2015, we measured the dimensions of natural bettong, bilby and rabbit pits (n = 30) at Scotia Sanctuary. As it is difficult to distinguish reliably between bettong and bilby pits, we grouped them as “native” following James and Eldridge (2007), James et al. (2009) and James et al. (2011) . We determined the mean length, width, depth, and excavation angle of natural pits, and the most common orientation of the mound of ejected soil. We used this information to help us design our artificial pits. From these dimensions, we also estimated the volume of natural native pits using the formula for a cylinder ($V = \pi . r^2 . h$) or an elliptic cylinder ($V = \frac{1}{2} a . \frac{1}{2} b . \pi . h$; to account for distortion in older pits), and we used the formula for a triangular prism ($V = \frac{1}{2} b . h . l$) to estimate the volume of natural rabbit pits. We identified recent natural pits (determined by the presence of high, soft soil ejecta mounds, little leaf litter and no seedlings) to ensure we were not recreating eroded pits. Natural native pits were longer ($F_{(1, 58)} = 12.04$, p = 0.001, $\eta^2_p = 0.17$; Figure 5.1a), wider ($F_{(1, 58)} = 36.36$, $p < 0.0001$, $\eta^2_p = 0.39$; Figure 5.1b) and deeper ($F_{(1, 58)} = 59.49$, $p < 0.0001$, $\eta^2_p = 0.51$; Figure 5.1c) than natural rabbit pits, with larger volumes ($F_{(1, 58)} = 83.18$, $p < 0.0001$, $\eta^2_p = 0.59$; Figure 5.1d). These results confirm previously observed differences between the pit shapes (James and Eldridge 2007).

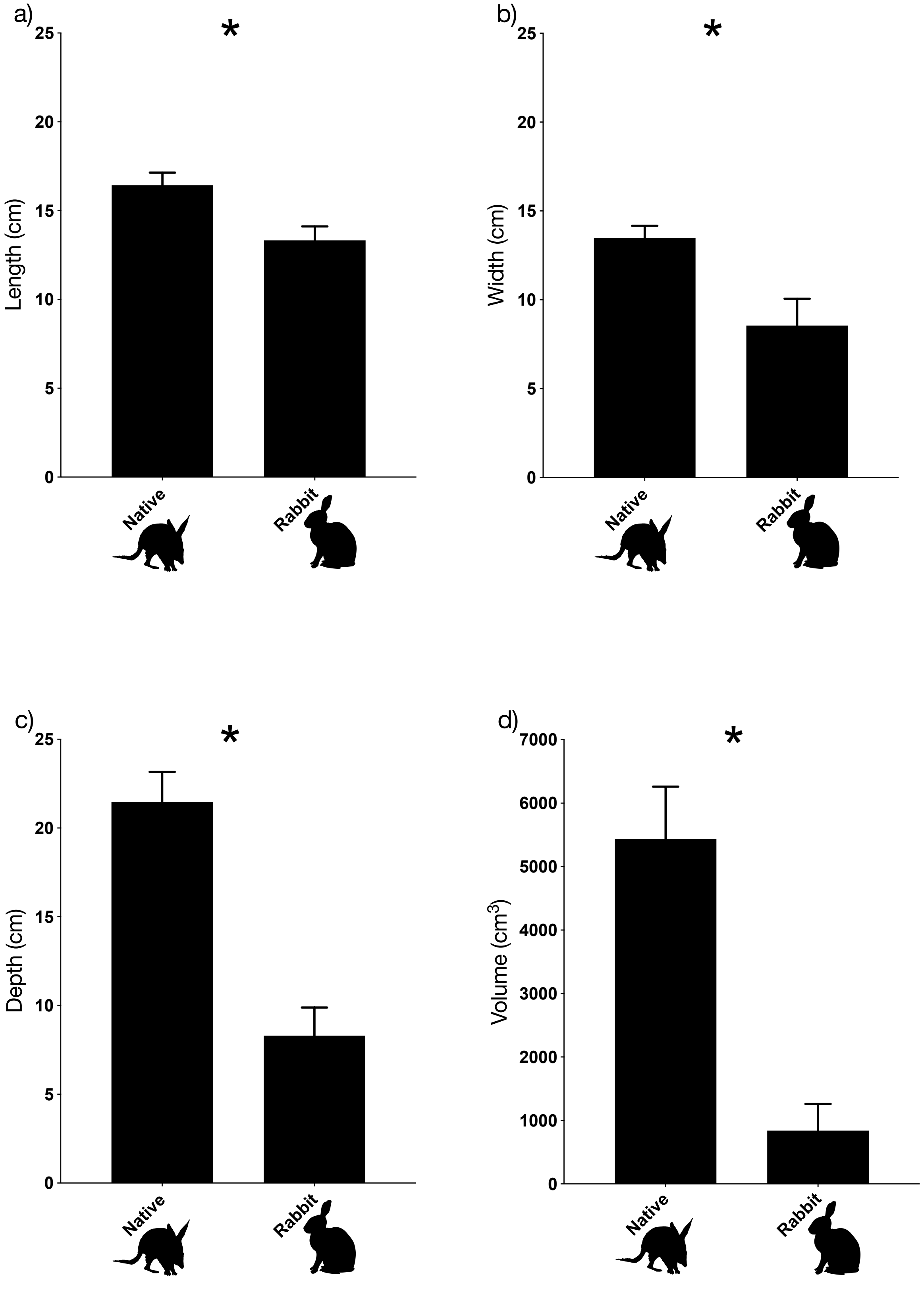

Figure 5.1 Mean (+ S.E.) length (a), width (b), depth (c) and volume (d) of natural native and rabbit foraging pits at Scotia Sanctuary, NSW (n = 30). Native pit volumes were calculated from the formula for a cylinder and rabbit pits were treated as triangular prisms. The stars denote significant differences (where < 0.05).

We then created artificial pits that replicated natural native and rabbit pit shapes (a technique previously used in Garkaklis et al. (2003), James et al. (2010), Eldridge (2011) and Valentine et al. (2017)) (Figure 5.2). This allowed us to control the age of these pits and to set them up within specific density treatments. Although natural native and rabbit pits vary in size, we created standardised artificial pits based on the average dimensions of natural pits we surveyed at Scotia Sanctuary. Artificial native pits were made with an auger (with a diameter of 15 cm, angled at 45°, to a depth of 22 cm to create an approximate pit volume of 3888 cm^3) and we dug artificial rabbit pits with a modified trenching shovel (14 cm x 9 cm, angled at 28°, to a depth to 9 cm, to create an approximate pit volume of 567 cm^3). Loose soil was removed from freshly dug pits with a trowel and piled up on the west side of artificial native pits and the south side of artificial rabbit pits (reflecting the most common orientation of soil ejecta mounds in natural pits found in our surveys).

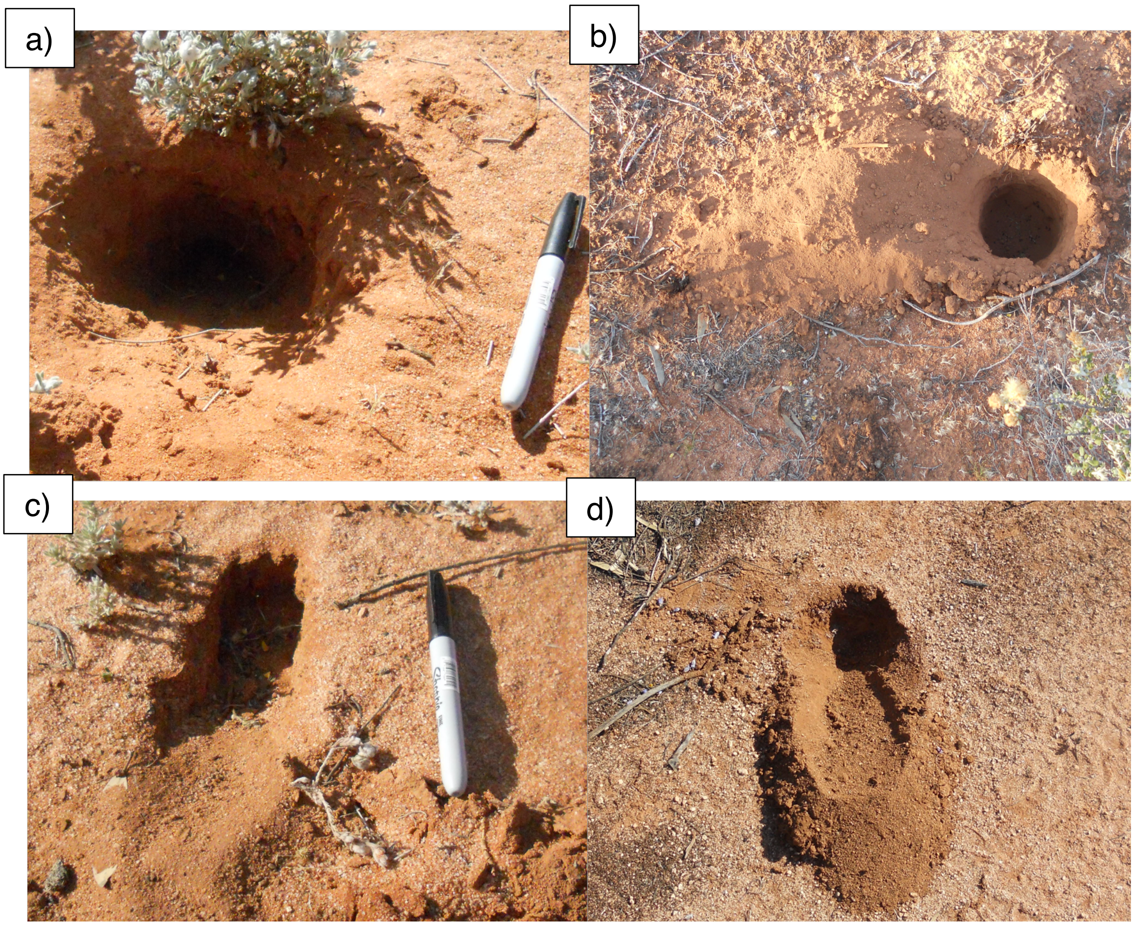

Figure 5.2 a) Natural and b) artificial native foraging pits and c) natural and d) artificial rabbit foraging pits at Scotia Sanctuary, NSW. Felt tip pen measures 13.8 cm. Photographs by A. M. Saul.

We quantified densities of natural native pits (inside the enclosure) and rabbit pits (outside the enclosure) using parallel transects that were 20 m long and spaced 15 m apart (n = 25). Every five metres we dropped a 1 m^2 quadrat and counted the number of pits that were completely inside it (five quadrats per transect). As pits can be present in the landscape for six months to two years (James et al. 2011), we only included recent pits in our surveys to understand the density at which ecosystem engineering mammals create pits. We carried out an additional transect that targeted an area where there was an unusually high density of natural native pits (5 ± 0.84 pits m^{-2}) and report the results here rather than include them in our analysis. The density of natural native pits was higher than that of natural rabbit pits (residual deviance = 11.79, *d.f.* = 48, likelihood ratio *p*-value < 0.0001; Figure 5.3) also supporting the results of previous studies (James and Eldridge 2007, James et al. 2011).

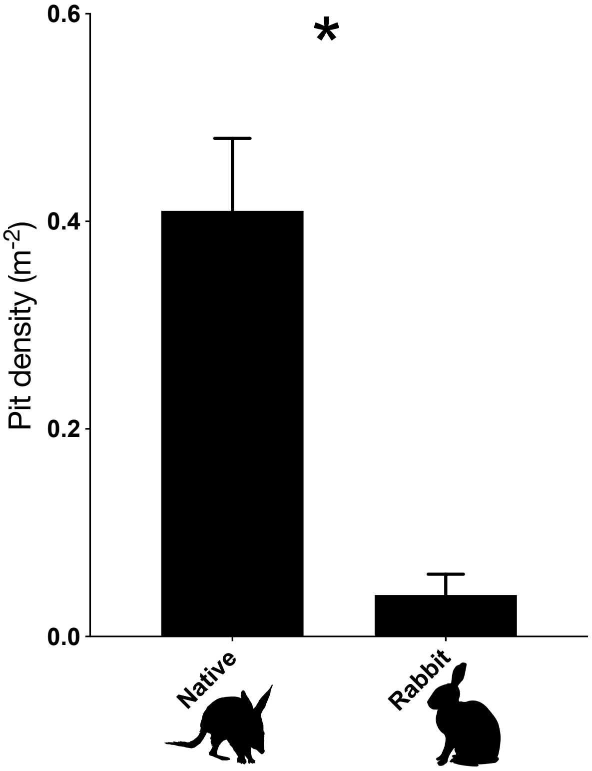

Figure 5.3 Natural native and rabbit pits at Scotia Sanctuary, NSW were counted along transects (n = 25) to find the mean (+ S.E.) density of natural pits per m^2 of each species at Scotia Sanctuary, NSW. The star denotes a significant difference (where < 0.05) between the species.

To simulate the effect of variation in density upon seedling recruitment in artificial native and rabbit pits, we chose density levels that reflected the densities of natural native and rabbit pits at Scotia Sanctuary (1, 2, 4, 8, 16 and 20 pits per 4 m^2 plot), as well as extreme densities (36, 48 and 64 pits per 4 m^2 plot) (Kreyling et al. 2018). Our chosen densities also ensured that artificial pits were distributed uniformly in every plot. We set up a grid of 80 plots in our site outside of the enclosure fence and randomly assigned a pit shape (two levels) and a density treatment (nine levels) to each plot. Each density and shape combination was replicated four times. Setting up our simulation experiment outside of the enclosure fence limited disturbance by digging mammals as native engineers were not present and rabbits were only present in low numbers. We detected minimal disturbance to pits throughout our surveys. We included an additional eight control plots that had zero artificial pits (and no natural pits) to control for the effect of pits on seedling germination. However, these control plots were later excluded from our analyses as the conditions occurring on "non-pit" surfaces are not equivalent to those occurring within artificial pits. To ensure independence from factors that might influence the accumulation of seeds, leaf litter, nutrients or water in pits, plots were separated by 20 m and the grid was 20 m from fences and roads. We expected that different artificial pit densities would affect the capture of seeds, which would be reflected in the abundance and species richness of germinated seedlings. However, we were not able to determine seed capture rates or the presence of seeds already in the seed bank as this would have required destructive sampling of artificial pits. We are confident that the randomisation and replication of our treatments overcomes issues of variation across this patchy landscape.

5.3.3 Pit condition and plant responses

To understand how pit shape and density influence germination conditions and the lifespan of a pit, we measured the volumes (as a proxy for soil infilling), leaf litter capture and the temperature of artificial pits after ten months. We measured the dimensions (length, width and depth) of each artificial pit and calculated the volume from these results using the formula for an elliptical cylinder in artificial native pits to account for distortion (we did not observe distortion in artificial rabbit pits). To avoid destructive sampling, leaf litter capture was graded using a scale of litter visibility at the base of artificial pits, where: 1 = No litter, 2 = Minimal litter (more soil visible than litter), 3 = Moderate litter (more litter visible than soil), 4 = Soil covered by litter, and 5 = Soil covered with a dense layer of litter. Lastly, we measured the difference between the surface temperatures at the base of artificial pits (the mean of four readings from different pits) and adjacent (taken from the corner of each plot at the same time) “non-pit” soil taken from the corner of each plot at the same time. All measurements were recorded between 10:00 and 11:00. Soil moisture was consistently recorded as zero, so soil moisture was excluded from our analysis.

After ten months (August 2016) we surveyed the abundance and species richness of germinated seedlings in artificial native and rabbit pits. We classified seedlings by morphospecies (hereafter, referred to as “species”) in the field with descriptions, photographs and a herbarium. We counted the seedlings that were present within artificial pits rather than in the soil ejecta mounds or “inter-pit” spaces of the plots (following Garkaklis et al. (2003), James et al. (2011)) to examine how the density and shape of artificial pits interfere with resource capture and the resultant effects upon seedling recruitment.

After 13 months (November 2016), following rain, we re-surveyed the abundance and species richness of the seedlings in each artificial pit, referring to our descriptions, photographs and herbarium from the previous trip, to determine individual seedling survival and any new recruitment in the interval between surveys. Although new recruits may have germinated and senesced during this interval, we assume this would have been consistent across our treatments. We measured the tallest and widest points of each seedling and used the product of these measurements, in cm^2, to create an estimate of “biomass” of surviving seedlings per artificial pit.

5.3.4 Statistical analyses

The dimensions (length, width, depth and volume) of natural native and rabbit pits were log transformed and compared using one-way Analysis of Variance (ANOVA) tests. The densities of natural pits were not normally distributed and so were compared using a Poisson generalised linear model (GLM) with a log link function, which is typically used for count data.

The effects of artificial pit density and shape on artificial pit volume, leaf litter capture and temperature were compared using two-way ANOVA tests. We square root transformed the variable *volume* and performed Tukey's HSD *post hoc* tests.

We used Poisson GLMs to examine the effects of artificial pit shape and density on seedling abundance and richness after ten months. Our factorial models included the covariates *pit shape* (categorical with two levels), *density* (categorical with nine levels) and the interaction term *pit shape x density.* Both seedling abundance and richness datasets were square root transformed prior to analyses to reduce the effects of multiple zeroes and overdispersion.

The abundances of surviving seedlings and new seedlings after 13 months were also square root transformed and modelled using Poisson GLMs. These factorial models were the same as above. Estimated survivor "biomass" (also square root transformed) was overdispersed despite the transformation and so we fitted this GLM with a negative binomial distribution and log link function in R Studio (version 1.1.463).

Before analyses, we used the protocol described in Zuur et al. (2010) to explore our datasets in JMP Pro 13 (SAS Institute Inc. 2019). One outlier was identified and removed as this plot had experienced a localised seed fall and was not comparable to the others. Following the recommendations in Zuur and Ieno (2016), model assumptions were verified by plotting residuals against fitted values, against each covariate in the model and each covariate not in the model. We also assessed the residuals for spatial dependency. Although plots were spaced out, and treatments were replicated and applied randomly, some patterns were noticed in the residuals when plotted against spatial variables. Models were tested with and without these spatial variables and they did not affect the results. Therefore, we have excluded them from the analyses presented here. All statistical analyses were carried out in JMP Pro 13 (SAS Institute Inc. 2019) unless otherwise stated.

5.4 Results

Artificial pit density, not shape, had a significant effect on the abundance (Figure 5.4a) and species richness (Figure 5.4b) of seedlings in both artificial rabbit and native pits after 10 months (Table 5.1). Overall, seedling abundance and species richness were highest at 2, 16 and 36 artificial pits per plot. After 13 months, the abundances of surviving seedlings (Figure 5.5a) and new seedlings (Figure 5.5b) in artificial pits were significantly affected by artificial pit density and not artificial pit shape (Table 5.2). Again, the highest values for both responses were measured at densities of 2, 16 and 36 artificial pits per plot. Conversely, the estimated “biomass” of surviving seedlings in artificial pits was significantly different between the artificial pit shapes (Figure 5.6) and not affected by artificial pit density.

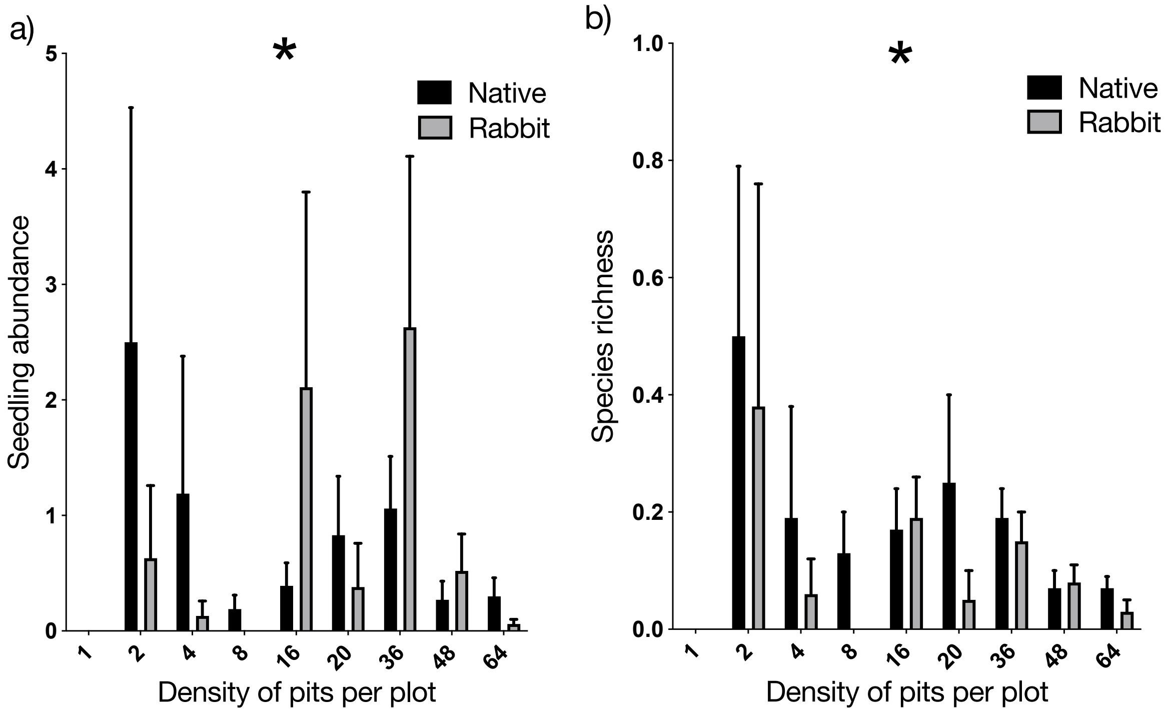

Figure 5.4 Artificial pit density (per 4 m2 plot) had a significant effect (where < 0.05, denoted by a star) on the mean (+ S.E.) abundance of seedlings growing in pits after 10 months (a; n = 4). Artificial pit density also had a significant effect (where < 0.05, denoted by a star) on mean (+ S.E.) species richness of seedlings (b; n = 4).

Table 5.1 Output of Poisson GLMs that tested the responses of seedlings to artificial pit shapes and densities after 10 months. Significant *p* values (where < 0.05) are in bold.

Response	Covariate	Residual deviance	d.f.	Likelihood ratio *p*
Seedling abundance	Shape	39.95	54	0.99
	Density			**<0.001**
	Shape*density			0.42
Richness	Shape	17.57	54	0.99
	Density			**0.001**
	Shape*density			0.66

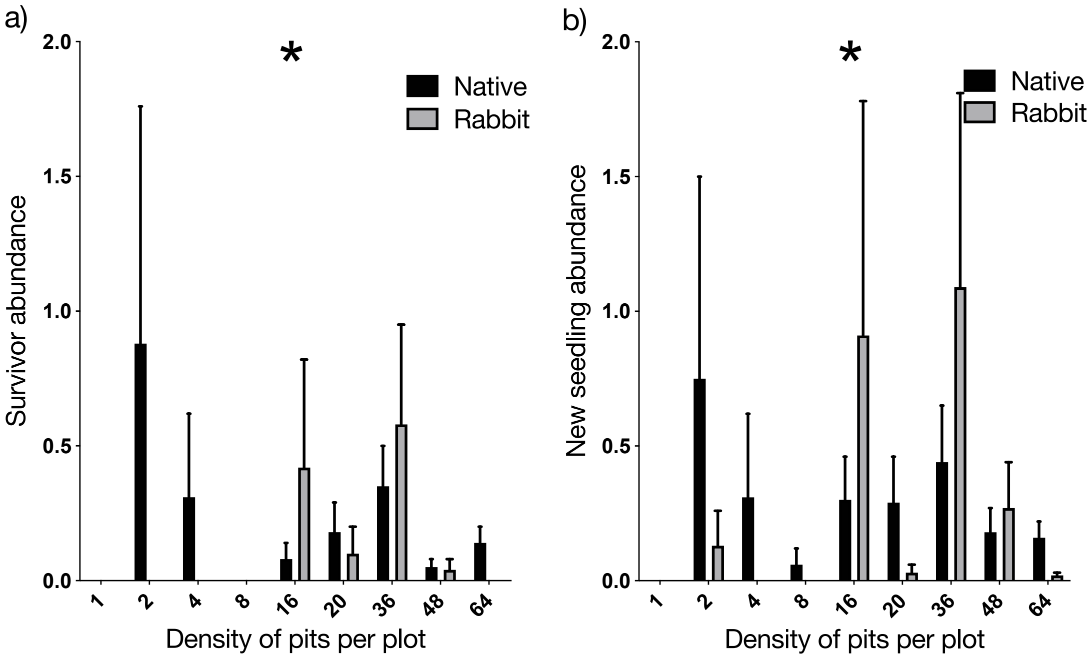

Figure 5.5 Artificial pit density (per 4 m^2 plot) had a significant effect (where < 0.05, denoted by a star) upon the mean (+ S.E.) abundance of surviving seedlings in artificial native and rabbit pits (a; n = 4). “Survivors” were seedlings that were recorded in both of our surveys (10 months and 13 months after experimental set up). Artificial pit density also had a significant effect upon the mean (+ S.E.) abundance of new seedlings in artificial pits (b; n = 4). “New seedlings” were only recorded in our survey taken 13 months after experimental set up and so must have germinated after 10 months.

Table 5.2 Output of Poisson GLMs that tested the responses of surviving and new seedlings to artificial pit shape and density. We recorded surviving seedlings in both surveys after 10 months and 13 months, whereas new seedlings were only recorded 10 months after experimental set up. Surviving seedling “biomass” was estimated from the product of the tallest and widest point of each seedling (measured after 13 months, in cm2). We tested the response of survivor “biomass” to artificial pit shape and density with a negative binomial GLM. Significant p values (where < 0.05) are in bold.

Response	**Covariate**	**Residual deviance**	**d.f.**	**Likelihood ratio p**
Survivor abundance	Shape	19.99	54	0.99
	Density			**<0.0001**
	Shape*density			0.07
New seedlings	Shape	22.98	54	0.99
	Density			**<0.0001**
	Shape*density			0.30
Survivor “biomass”	Shape	53.45	68	**0.006**
	Density			0.58
	Shape*density			0.22

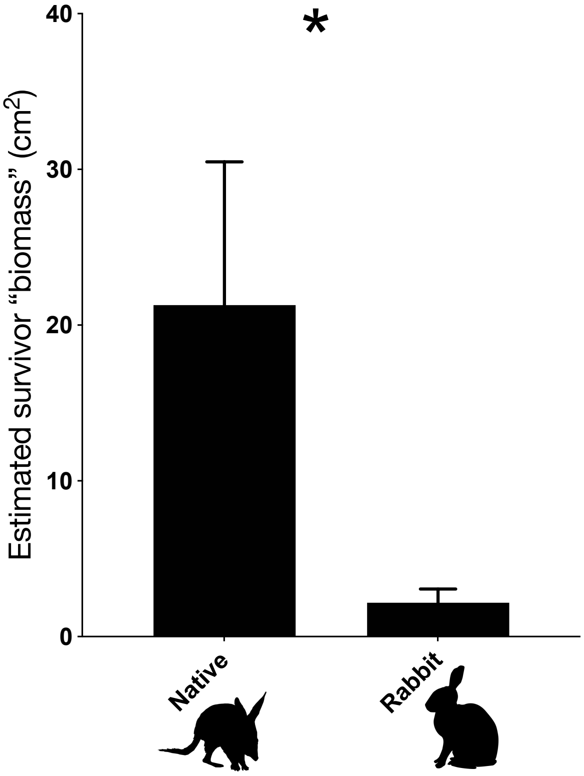

Figure 5.6 Mean (+ S.E.) “biomass” of surviving seedlings in pits (estimated from the product of the tallest and widest points of each seedling in cm^2) was significantly different (where < 0.05, denoted by a star) between artificial native and rabbit pits (n = 36). Surviving seedlings were recorded in both surveys, 10 months and 13 months after setting up. Survivor “biomass” was estimated from measurements taken during the survey after 13 months.

Artificial pit density had a significant effect on the volume of artificial rabbit and native pits (Figure 5.7a) after 10 months (Table 5.3). Artificial native pits, which were created with larger volumes than rabbit pits, remained larger 10 months later (Figure 5.7b). We recorded more leaf litter in artificial rabbit pits than in native pits (Figure 5.7c) but found no effect of artificial pit density on leaf litter capture. Artificial native pits were cooler, and rabbit pits were warmer, than adjacent “non-pit” soil temperatures (Figure 5.7d). Artificial pit temperature was also not affected by artificial pit density. All models differed significantly from null models and model validation indicated no problems.

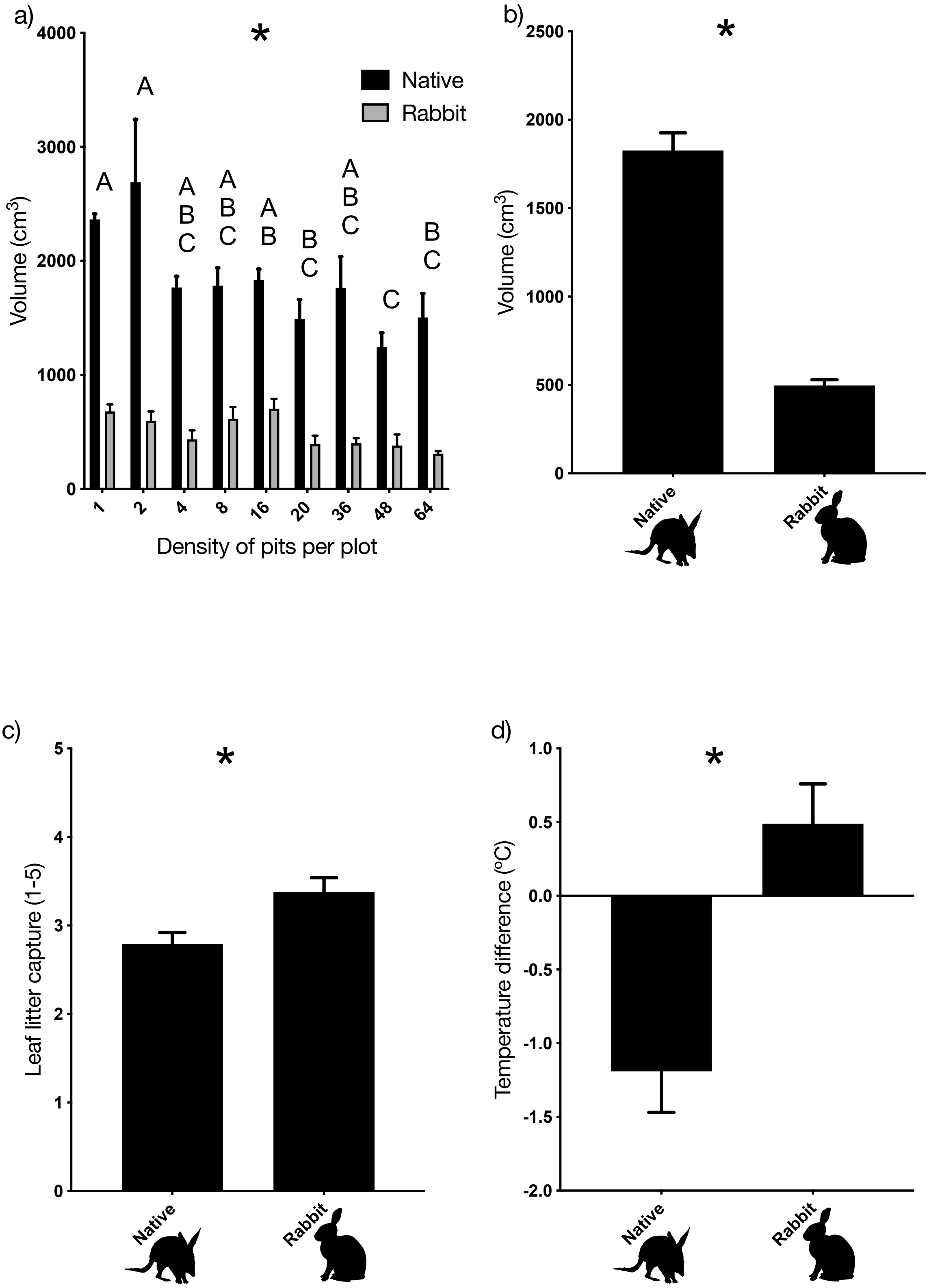

Figure 5.7 Artificial pit density (per 4 m^2 plot) had a significant effect (where < 0.05, denoted by a star) on the mean (+ S.E.) volume of artificial pits after 10 months (a; n = 4). Shared letters indicate that results of density treatments (n = 9) are statistically similar. There was also a significant difference between the mean (+ S.E.) volumes of the two artificial pit shapes (b; n = 36). The amount of leaf litter in artificial native and rabbit pits was measured using a descriptive scale from 1-5 (where 5 denotes a pit containing a dense layer of litter) and the mean (+S.E.) amount of leaf litter in pits was significantly

different between artificial pit shapes after 10 months (c; n = 36). We measured the difference between the surface temperature in artificial pits and adjacent "non-pit" soil. Artificial native and rabbit pits had significantly different mean (+ S.E.) temperature differences (d; n = 36).

Table 5.3 Output of ANOVAs that tested the effects of artificial pit shape and density on pit volume, leaf litter capture and pit temperature. Significant *p* values (where < 0.05) are in bold.

Response	Covariate	F value	d.f.	p value	η^2_p
Volume	Shape	353.96	1	**<0.0001**	0.87
	Density	4.88	8	**0.0001**	0.42
	Shape*density	1.37	8	0.23	0.17
Leaf litter capture	Shape	8.07	1	**0.006**	0.13
	Density	1.44	8	0.20	0.18
	Shape*density	0.65	8	0.73	0.09
Temperature difference	Shape	19.09	1	**<0.0001**	0.26
	Density	0.63	8	0.75	0.09
	Shape*density	1.22	8	0.30	0.16

5.5 Discussion

Our results demonstrate that the efficacy of an ecological function is density dependent (Soule et al. 2003, Brodie et al. 2018, DeVore et al. 2020). We simulated the digging effects of native and alien ecosystem engineers and found that the density of artificial pits affected the abundance and species richness of germinated seedlings. Furthermore, there were no statistical differences in plant responses to the shapes of artificial rabbit and native pits. Overall, our results support our hypothesis: the greatest number of seeds germinated at intermediate pit densities. Although conditions in the two artificial pit shapes were different, only the estimated "biomass" of surviving seedlings was strongly influenced by artificial pit shape. This suggests that disparities do exist in the efficacy of ecological functions provided by analogous species.

Foraging pits, and the seedlings within them, go through successional stages. Pits gradually accumulate soil, leaf litter and seeds until they eventually disappear into the surrounding landscape (Mallen-Cooper et al. 2019). Only ten months after setting up, we found artificial pits at all successional stages but containing only small seedlings.

Notably, artificial pits in plots with higher densities tended to have the smallest volumes indicating a potential link between artificial pit density and infilling rates. Three months later, following rain, new seedlings and plants producing flowers were present in artificial pits. This suggests that beneficial conditions and nutrients persisted in artificial pits, possibly through continued runoff capture (Boeken et al. 1998), from litter decomposition (Steinberger and Whitford 1983) or provided by arbuscular mycorrhizal fungi (Valentine et al. 2018).

A large amount of leaf litter should create an environment that limits seed germination yet, despite artificial rabbit pits capturing more litter, we did not find a difference in seedling abundances between artificial native and rabbit pits. There are conflicting views on the benefits of leaf litter for seedling germination in foraging pits. Leaf litter that is buried by soil breaks down and provides small amounts of nutrients that may be used by seedlings (Steinberger and Whitford 1983). However, up to 60% of above-ground leaf litter in desert systems is actually broken down through exposure to the solar radiation (photodegradation), which means that, for exposed leaf litter, nutrients are often lost through photochemical mineralization (Austin and Vivanco 2006). Large amounts of leaf litter in pits can also limit seed-soil contact, hindering the germination and survival of seedlings, but the presence of leaf litter also conserves moisture in the underlying soil (Fowler 1986). Even though larger pits capture larger volumes of leaf litter (Eldridge and Mensinga 2007) and shallow pits may not retain litter (James et al. 2009), we found more artificial rabbit pits that were full of litter than artificial native pits, despite artificial rabbit pits being smaller overall. This finding could be an artefact of using a descriptive scale, which was created to avoid destructively sampling artificial pits, but it demonstrates that artificial rabbit pits were effective litter traps. Pits with leaf litter also tend to have cooler temperatures (Eldridge and Mensinga 2007), yet we found that artificial native pits were cooler than adjacent ground temperature, despite containing less leaf litter, and this temperature difference was larger than that for artificial rabbit pits. The lower temperature is probably due to the greater depth of artificial native pits compared to rabbit pits ten months after setting up. Deeper pits may provide shade for leaf litter and reduce the chance of photodegradation (James et al. 2011).

For the most part, pit density, rather than shape, affected seedling abundance and richness in artificial pits. However, we found that estimated survivor "biomass" was wholly affected by artificial pit shape. Since conditions were also different between pit shapes, the conditions in artificial native pits could have improved seedling growth, e.g., through higher nutrient content and microbial activity levels (Valentine et al. 2018). The natural pits of native bettongs and bilbies also contain higher concentrations of labile carbon than rabbit pits (although all pits contained more labile carbon than the surrounding ground) (James and Eldridge 2007). These differences in conditions and nutrient content are likely due to the greater depth of native pits that increase resource retention (James and Eldridge 2007, James et al. 2011). Therefore, despite similarities in other plant responses between both artificial pit shapes, the difference in the estimated "biomass" of survivors signals a reduced efficacy of ecosystem engineering by alien rabbits compared to native bettongs and bilbies.

Pit density had the greatest effect upon seedling germination, species richness and survival in artificial pits, demonstrating that ecosystem engineering is a density dependent ecological function. Artificial native pits tended to support higher seedlings recruitment at a density of 2 pits per plot (0.5 pits m^{-2}). This density is similar to the natural native pit density (0.41 ± 0.07 pits m^{-2}) at Scotia Sanctuary. Artificial rabbit pits tended to support the most seedlings at greater densities (16 or 36 pits per plot; 4 or 9 pits m^{-2}), which are analogous of high (e.g., the high density of natural native diggings at Scotia Sanctuary, 5 ± 0.84 pits m^{-2}) or extreme pit densities. No seedlings germinated in artificial native or rabbit pits at the lowest density (1 pit per plot; 0.25 pits m^{-2}). Interestingly, this was most similar to the density of natural rabbit pits (0.04 ± 0.02 pits m^{-2}) at Scotia Sanctuary. Despite being an irruptive species, most censuses of rabbit pit densities occur at conservation sanctuaries where their populations are likely to be curbed by local management efforts. Our results confirm that the efficacy of ecosystem engineering by rabbits is limited by the low density of their pits, which limits the creation of fertile patches, (James and Eldridge 2007, James et al. 2011). Managing the population so that pits are created at higher densities will improve this. However, extremely high densities of pits also limit their benefits and so managing the rabbit population so that pit densities do not reach these levels is important too.

Therefore, our results show that changes in population density will have impacts upon the efficacy of an ecosystem function.

Routine control of pest species density, without consideration of the ecological functions they provide, can result in unintended and unexpected outcomes (Zavaleta et al. 2001, Dickman 2007), particularly when those ecological functions are density dependent. In the case of ecosystem engineering by rabbits, the lowest densities of artificial pits, which were equivalent to natural pit densities, had worse effects than high densities, which did support seedling germination and growth. Our results suggest that plant recruitment would benefit from even a slightly higher abundance of rabbits, particularly where there are also low numbers of native digging mammals (i.e., outside of predator-proof enclosures). Increasing rabbit numbers can come at the cost of amplifying their negative impacts, such as limiting recruitment and recovery of seedlings through overbrowsing (Lange and Graham 1983), and altering the physical and chemical structures of surface soils through warren construction (Eldridge and Koen 2008). Therefore, when long-term control, rather than eradication, is the goal, density-impact relationships can guide management to minimise damage (Yokomizo et al. 2009, Norbury et al. 2015) and complimentary “density-benefit” curves could guide management to maximise the provision of ecological functions.

This work comes amidst calls to conserve ecological functions (Brodie et al. 2018), to manage alien species to maximise their positive impacts (Davis et al. 2011, Natusch et al. 2017) and a growing recognition of the density dependence of ecological functions (Dedej and Delaplane 2003, Koch et al. 2009, DeVore et al. 2020), including those provided by alien species (Ramus et al. 2017). Our work confirms that the ecological benefits of both native and alien species are dependent on population density (Soule et al. 2003) but careful consideration is required, when deciding to rely on an alien species to provide an ecological function, to mitigate negative impacts on other species. However, being overly cautious has only led to inaction in this area (Shackelford et al. 2013). Although frameworks (e.g., Blackburn et al. (2014)) and useful tools (e.g., density-impact curves (Yokomizo et al. 2009, Norbury et al. 2015, Bradley et al. 2019)) are available to determine the overall impact of an alien species, these techniques do not always have the resolution to identify beneficial interactions with alien species that can be applied for maintaining ecosystem functions. Therefore, we encourage the acknowledgement and careful inclusion of the density dependent benefits of alien species in their management, particularly when restoring ecosystem functionality and resilience in novel ecosystems (Schlaepfer et al. 2011), and when native species are absent.

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Chapter 6 General discussion

Alien species can be involved in interspecies interactions and ecological functions that are beneficial to native species and their ecosystems. In this thesis, I investigated the density dependence of these positive impacts through case studies using a range of common alien species in different environments. I showed that “density-benefit” curves were apparent for each alien species and found that the shape and strength of the relationship was different for each system. In this final chapter, I summarise my findings, explore their limitations and the future directions that they offer, and propose solutions to current alien species management problems.

In Chapter 2, I presented the theoretical concept of “density-benefit” curves that may be used to guide alien species management. Given the density dependence of the negative impacts of alien species, I theorised the different ways that the ecological benefits of alien species would also be density dependent. My hypotheses were that these relationships would apply to a wide range of ecological benefits provided by alien species, and that “density-benefit” curves would often be nonlinear and may be unique to the alien species providing the ecological benefit in that environment. I explained why characteristics inherent to alien species (extreme densities, changes in their impacts over time and being generalist species) can shape the nature of these ecological benefits and I offered directions for future research.

In my next chapters, I tested experimentally the density dependence of different ecological benefits provided by alien species in Australian ecosystems. I showed (in Chapter 3) that alien black rats (*Rattus rattus*) in Sydney have likely formed a mutualistic interaction with a native plant species, *Banksia ericifolia*, where black rats are potential pollen vectors in return for nectar and pollen food resources. I found that measures of potential pollinator efficacy were negatively proportionate to the population density of alien black rats. Rats at higher densities had different pollination behaviours compared to rats at low densities, such as more movement, that limited the amount of time that rats spent foraging on inflorescences. I demonstrated (in

Chapter 4) how the alien plant, lantana (*Lantana camara*), facilitates native skinks (*Lampropholis delicata* and *L. guichenoti*) by providing a basking-retreat-site interface. The abundance of skinks was nonlinearly related to the cover of lantana in a U-shape, and negatively related to the number of lantana patches. The benefits of lantana were limited by physical changes to the structural complexity of the plant, and only arose at high densities. I then used a simulation experiment (in Chapter 5) to explore how, through their modification of the landscape, alien European rabbits (*Oryctolagus cuniculus*) indirectly benefit native plant species by providing an environment for seedlings to germinate. I found that their impact is density dependent and similar to that of analogous native marsupials. The abundance and species richness of native seedlings displayed complex, nonlinear relationships with artificial rabbit and native marsupial pit densities. The limitations of this benefit at higher and lower densities were likely caused by the interference between artificial pits at high densities, and a reduced probability that seeds would collect in artificial pits at low densities. Overall, these three ecological benefits, each provided by a common alien species, were density dependent. Therefore, simply stating that alien species can have positive ecological impacts does not account for the complexity and ecology of these interactions. It is also highly likely that ecological functions, whether provided by alien or native species, will be density dependent, but we are only just beginning to understand the shapes of such relationships and the ecological drivers behind them.

In this general discussion, I will discuss the implications of my findings for alien species management through three broad themes:

1. Living with alien species in a changing world
2. Managing the net impacts of alien species
3. Conserving ecosystem functions

6.1 Living with alien species in a changing world

The natural world is currently experiencing massive changes and increasing rates of biodiversity loss (Johnson et al. 2017) caused by habitat destruction, climate change, invasive alien species, pollution and overexploitation (Mazor et al. 2018). The combined effects of these drivers create new phenomena that place further stress on ecosystems (Strayer 2010). For example, global warming has provided new opportunities for alien species to expand their ranges and to increase reproductive output (Walther et al. 2009). Therefore, human activity is creating a world that favours alien species. Preventing species introductions is the best option to manage the threat of novel alien species. But for entrenched alien species, we must learn how to sustainably and holistically manage their impacts; especially where we rely upon the ecological benefits they provide to native species.

Native species, too, are shifting their ranges and moving into areas where they were never previously found (Báez and Collins 2008). Under traditional definitions, these species can still be referred to as “native” to the country or region they are in, but they may move into new ecosystems where they could have undesirable novel effects. For example, sugar gliders (*Petaurus breviceps*), that are native to mainland Australia, were introduced to Tasmania and currently have novel predatory impacts upon critically endangered swift parrots (*Lathamus discolor*) (Campbell et al. 2018). It has been proposed that displaced native species be referred to as “neonative” and be managed separately from resident native species (Essl et al. 2019). The potential impacts of these “neonative” species need to be approached with caution, and “density-benefit” curves can be used to manage the net impacts of these species. Furthermore, using a separate name to classify these species emphasises that their impacts are unknown. Overall, this situation highlights the need for context-dependent and impact-focussed management for all species, native, “neonative” and alien.

We have already accepted the net benefits of some alien species, in particular, domestic and agricultural species. These species are sometimes referred to as examples of alien species that provide ecosystem benefits and services, e.g., domestic wheat (*Triticum aestivum*) is considered a desirable species (Simberloff et al. 2011) although its value to native ecosystems is not discussed. We value these species almost to the point of ignoring their negative impacts upon native ecosystems such as disease transfer (Hollings et al. 2013), nutrient runoff (Woodward et al. 2012), pesticide use (Gibbs et al. 2009) and habitat loss (Norris 2008). However, when these alien species escape into “natural” environments, they are designated as “feral” (when animals) and their negative ecological impacts are well understood (e.g., Nogueira-Filho et al. (2009)). Conversely, native species that invade agroecosystems are also often considered to be undesirable pests for their economic impacts, e.g., eastern grey kangaroos (*Macropus giganteus*) damage grain crops in Australia (Hill et al. 1988). Given that commensal species have a long association with humans and human-modified environments, it has even been suggested that these species be referred to as “native” when they occur in an urban area, and “alien” when they escape into “natural” areas (Banks and Smith 2015). Even species held in zoos and aquaria could be considered so far removed from any “natural” environments that it is mostly irrelevant to consider their origins. However, there are initiatives from some zoos to provide habitat for local wildlife on their grounds (Taronga Conservation Society Australia 2020) and the conservation work carried out by zoos through captive breeding and translocation efforts (Gilbert and Soorae 2017) sees species moved from zoos into “natural” environments. Therefore, is it useful for the conservation of biodiversity to have dichotomies? To separate “natural” environments from human-modified environments, and native species from alien species, rather than focussing on managing impacts holistically?

Given this complexity, the textbook dichotomy of alien and native species arguably no longer covers the spectrum that exists in nature. We need a broader view of alien and native species, and more tools to manage them successfully and sustainably. In my thesis, I propose that we take a nuanced approach to alien species and their impacts, by considering the web of interactions they may be involved in and by aiming to conserve their ecological benefits through the use of “density-benefit” curves.

6.2 Managing the net impacts of alien species

Although the positive impacts of alien species are receiving attention in the literature (Rodriguez 2006, Schlaepfer et al. 2011, Davis et al. 2011), and there are now many examples of alien species retained in ecosystems for various ecological benefits (Sogge et al. 2008, Sotka and Byers 2019), much of the discourse on alien species still focusses on their negative impacts (Simberloff 2013, Blackburn et al. 2014, Ricciardi et al. 2017). This propagates the notion of a dichotomy between the negative and positive impacts of alien species, as well as the inherent goodness of native species versus the “badness” of alien species. To combat this oversimplified narrative, research and discussion of alien species need to continue to move towards understanding the net impacts of these species (Shackelford et al. 2013). I have argued throughout this thesis that it is inevitable that alien species will come to form beneficial interactions with some native species in their incipient environments (Dickman 2007). Conservation managers need databases, frameworks and tools for making decisions on when and how to manage these species where they are entrenched and unlikely to be eradicated. Acknowledging and understanding that the impacts of alien species are complex and context-dependent is necessary to ensure that management actions are effective and appropriately prioritised.

“Density-benefit” curves can be used to identify how efforts to control the population of an alien species, carried out to mitigate negative impacts, will affect the important ecological functions they provide. This would ensure that any unexpected consequences of changing the population density of an alien species may be avoided (Zavaleta et al. 2001, Dickman 2007) and its ecological functions are not lost unnecessarily. For example, in Chapter 4, I found that lantana provided maximal benefits to native skinks when in high densities. However, lantana also negatively impacts native plant communities when in high densities (Gooden et al. 2009). As a consequence, complex decisions will need to be made when alien species provide desirable functions but also have negative impacts that require management. For example, Eurasian tamarisk shrubs (*Tamarix* spp.) have caused hydrological changes resulting in the degradation of riparian vegetation but have also become important nesting habitat for endangered willow flycatchers (*Empidonax traillii extimus*) (Sogge et al. 2008). Due to their importance to native bird species, tamarisks have been allowed to persist. Research into “density-benefit” curves, as I have explored in this thesis, could help to understand the density at which tamarisks are needed to provide these benefits optimally whilst allowing for some mitigation of their negative impacts.

To optimise population management decision-making, “density-benefit” curves should be used in conjunction with density-damage curves to identify how population density is related to both the negative and positive impacts of an alien species. For example, the “density-benefit” curve that I found for alien rabbits (Chapter 5) suggests that their role as ecosystem engineers will be limited if pits are created at low densities, presumably when the animals themselves are in low densities. To provide germination opportunities for native plants, pits must be created at intermediate densities. However, a density-damage curve (or “yield-density” curve, in this case), shows that increasing densities of alien rabbits affect wool production through overgrazing (Fleming et al. 2002). These two functions could then be combined into a single model or used separately. The net benefit of an alien species may be calculated by subtracting the damage from the benefits (e.g., Morris et al. (2010)), for example, the costs to wool production could be subtracted from the benefits of ecosystem engineering at different alien rabbit densities. After understanding the effects of population density upon the net impacts of an alien species, cost-benefit analyses can then be applied, to prioritise conservation actions. For example, hybridised cordgrasses (*Spartina* spp.) have caused changes to the wetlands of Silicon Valley, including the loss of many native bird and plant species. However, the *Spartina* hybrids provide habitat that supports the endangered California clapper rail (*Rallus longirostris obsoletus*). It was ultimately decided that hybrid *Spartina* must be removed for the good of all the other species, but carefully so that alternate habitat could be provided to the endangered rail (Lampert et al. 2014). Even if an alien species must be removed, any positive impacts should be identified so that they can be accounted for during the removal process and, if possible, replicated by native species.

The negative impacts of an alien species, through density-damage curves, can be measured on a species level (e.g., Jones et al. (2013),) a community level or a biodiversity level (Norbury et al. 2015). Measuring a species’ impact at too broad a scale can mean that important interactions are not detected (Dickman 2007). For example, feral cats (*Felis catus*) were removed from Macquarie Island, but the extent of their predatory effects upon alien rabbits was unknown; their removal resulted in the release of alien rabbit populations and subsequent vegetation shifts (Bergstrom et al. 2009). On the other hand, “density-benefit” curves can target both interspecies interactions (a benefit to a single species, as I found in Chapters 3 and 4) and ecological functions (a benefit to a community of species, as I found in Chapter 5). The use of “density-benefit” curves would allow examination of the effects of alien species control, or removal, upon fine scale interactions before the control actions are carried out.

My results in this thesis demonstrate that the shapes of “density-benefit” curves will be different for each organism, ecological function and habitat, emphasising the need for context-dependent alien species management. Interestingly, the shapes of the curves that I measured were different from what I had hypothesised in Chapter 2, and this highlights the complexity with which “density-benefit” relationships can emerge. Although it may not be realistic to explore the “density-benefit” relationship for each alien species before applying management actions, it is feasible and recommended in situations where an alien species is frequently controlled or where a threatened native species may be relying upon benefits provided by the targeted species. Nevertheless, it is crucial that the beneficial effects of alien species are always considered and that ecological managers understand that changing the population density of an alien species can have flow-on effects. For example, the density dependent pollination behaviours of alien black rats are linearly and negatively related to their population density (Chapter 3). This means that controlling black rats to a lower density will not impact their pollination role, which is crucial given that native mammals are not present in the area to provide this function instead (Banks et al. 2011). Also, reducing the density of black rats may mitigate any negative effects that they have e.g., their predatory effects upon native bird eggs (Smith et al. 2016). The “density-benefit” curve for lantana providing refuge for native skinks is U-shaped (Chapter 4), which suggests that lantana should either be completely removed, or retained in structurally complex patches that form when density is high. Lantana has extremely varied impacts, providing habitat (e.g., Parsons et al. (2016) and Lambert and McDonald (2017)) and food (Date et al. 1995) to a number of native species, but also negatively impacts native vegetation (Gooden et al. 2009) and habitat structure for other native reptile species (Virkki et al. 2012). Although a number of native Australian plant species have similar structurally complex growth forms to lantana (e.g., native raspberries, *Rubus* spp., and wattles like prickly Moses, *Acacia verticillata*), and these plants may be effective substitutes, they may not be able to form the hard edges that were beneficial to native skink species. Therefore, to conserve native skinks, lantana might be retained in structurally complex patches but in low enough densities to form a mosaic with natural vegetation so that the habitat requirements of many species may be satisfied. Lastly, the "density-benefit" curves for alien rabbits and native marsupials as ecosystem engineers are complex and do not provide clear management guidance except for highlighting the importance of density (Chapter 5). Before controlling alien rabbits, a small-scale removal experiment should be carried out first to avoid any unexpected effects. Further research may be needed to find a curve that clarifies the density dependent relationship. However, these findings did show that analogous species can provide the same ecological function at different levels of efficacy. Furthermore, it is likely that the shapes of these "density-benefit" curves are unlikely to remain the same throughout time as the nature of the interaction between alien and native species evolves.

My findings in Chapter 5 show that population density is not the only parameter affecting the efficacy of an ecological benefit, but also differences in the ecology and behaviours of the species providing it. Not all ecological benefits are provided equally, as different species will provide ecological benefits at different strengths. (However, the strength, or efficacy, of an ecological benefit may be improved by increasing the density of the species providing it (Stephens and Rowe 2020)). Species will also be involved in different numbers of interactions, i.e. strongly interactive and weakly interactive species will be involved in many or few interactions respectively (Brodie et al. 2018). As alien species tend to be generalists, they are expected to be involved mainly in weak interactions but can become entrenched within complex interaction webs with multiple other species (Start et al. 2019). Therefore, alien species management needs to be informed by community ecology to unpick these interaction webs when controlling or removing an alien species.

6.3 Conserving ecological functions

My thesis complements a growing interest in the density dependent ecological functions performed by native species (Soule et al. 2003, Koch et al. 2009, DeVore et al. 2020). In particular, my ideas stemmed from early calls to conserve native species at "ecologically effective" densities to ensure that their ecological functions are provided to their full capacity (Soule et al. 2003). Recovery plans for threatened species aim to increase population densities to reduce extinction risk, rather than conserving ecological functions. However, having a species present in a system is not enough; it needs to be present at the correct population density level to play an effective ecological role. This brings about the question: should ecological interactions and functions be listed as within their own conservation unit? Expanding our understanding of the density dependence in the ecological roles of both alien and native species will greatly increase accuracy in setting targets for restoration for both native and novel ecosystems (Brodie et al. 2018). I would argue that "density-benefit" curves should be applied to native species as well as alien species to help achieve this goal. It is highly likely that both native and alien species will be needed in the future conservation of ecological functions.

Given the urgency for conserving ecosystem functionality in a rapidly changing world, some conservation biologists have called for bold ecological interventions. For example, rewilding is the practice of returning ecosystem functions to areas where they have been lost due to local extinctions of species that provided important functional roles. This can involve the return of lost native species (e.g., passive or translocation rewilding) (Perino et al. 2019) or even new species (e.g., Pleistocene rewilding) that might provide the required ecological function (Jørgensen 2015). For example, the yellow-crowned night heron (*Nycticorax violace*a) was reintroduced to Bermuda to control over-abundant native blackback land crabs (*Gecarcinus lateralis*) (Wingate 1982). It was confirmed by fossil evidence that this heron was present in Bermuda in prehistoric times, but it is likely to have been a resident more recently too (Wingate 1982). As such, with rewilding, the time scales since extinction can range from a few hundred years to a few thousand years, which begs the question: is a species that has been absent for thousands of years still native to that location? With the complete extinction of some species, rewilding is not possible, but it has been suggested that a closely related species (albeit an alien species) may also be able to provide the ecological functions needed to restore an ecosystem (Griffiths et al. 2010). Alien giant Aldabra tortoises (*Aldabrachelys gigantea*) were introduced to Round Island, offshore to Mauritius, to replace the lost seed-dispersal role previously provided by native giant *Cylindraspis* sp. tortoises, with apparent success (Griffiths et al. 2010). Although such interventions are not suitable for many alien species, and they require excellent planning, experimental trials, thorough risk assessments and contingency plans, they demonstrate some of the possibilities for including alien species in conservation solutions. However, these progressive interventions cannot succeed without a density dependent approach. Managers carrying out these interventions must consider the density at which returned, or new, species will provide an ecological function, and predict when high densities will start to incur net costs.

On the other hand, new concepts in conservation such as *conciliation biology* (Carroll 2011) and *novel ecosystems* (Hobbs et al. 2014) have received criticism (Russell and Blackburn 2017) despite, or because of, their lack of active intervention. The philosophy of *conciliation biology* recognises that many alien species are now permanent in their new ecosystems, and so focusses on the long-term management of their mixed and novel effects (Carroll 2011). Further, *conciliation biology* utilises evolutionary theory to provide a management approach that is responsive to change over time (Carroll 2011). *Novel ecosystem* is a term describing communities of species that never previously existed, having arisen following environmental change and human actions such as land degradation or species introductions (Hobbs et al. 2006). These conciliatory approaches focus on the sustainable, long-term management of ecosystems, and the pragmatic acceptance that alien species are a permanent fixture in them. Therefore, a density dependent approach, using “density-benefit” curves, will achieve net benefits for the conservation of native species and ecological functions, and a reduction in the damage of alien species.

6.4 Conclusions

I hypothesised that density-dependent positive impacts will be typical for alien species (and native species too). This density dependence is caused by behavioural (e.g., Chapter 3) and physical changes (e.g., Chapter 4 and 5) caused by individuals in response to increasing population density. I found that three common alien species all perform density-dependent positive roles in their new ecosystems. Each "density-benefit" relationship had a different shape, strength and complexity level. Furthermore, they were unique to each species, as demonstrated by the subtle differences between the "density-benefit" functions of analogous alien European rabbits and native marsupials in Chapter 5. I discussed the necessity to research and manage the net impacts of alien species. Focussing on a dichotomy between positive and negative impacts oversimplifies their ecology and the complexity of interactions that alien species form with native species.

It seems that the acceptance of many alien species in *novel ecosystems* is inevitable. As such, we need to move beyond simple arguments to remove alien species because they have undesirable impacts or to conserve them because they provide some benefits, without considering any further complexity. Moreover, there is not enough money in conservation to conserve native species at the densities we need them to provide ecological functions, and not enough money to eradicate alien species. Incorporating a density dependent approach to population control efforts would seem to be a viable option for cost-effective conservation of ecological functions and impact mitigation. My hope is that the findings I have made in this thesis provide a useful first step towards this approach.

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Appendix.

Limits to alien black rats (*Rattus rattus*) acting as equivalent pollinators to extinct native small mammals: the influence of stem width on mammal activity at native *Banksia ericifolia* inflorescences

By Rebecca O'Rourke, Jennifer Anson, Amelia Saul and Peter Banks

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ORIGINAL PAPER

Limits to alien black rats (*Rattus rattus*) acting as equivalent pollinators to extinct native small mammals: the influence of stem width on mammal activity at native *Banksia ericifolia* inflorescences

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Abstract Alien species are a major cause of species extinctions globally and the effects of introductions can become substantial, especially once aliens become entrenched and impossible to eradicate. Some entrenched aliens may assume niches of extinct native species that are functionally similar, but the capacity of an alien to perform specialised ecological processes is unknown. Here we examine the potential for the alien black rat (*Rattus rattus*) to effectively pollinate native *Banksia ericifolia* in heath at North Head, Sydney where endemic mammalian pollinators such as brown antechinus (*Antechinus stuartii)* and eastern pygmy-possums (*Cercartetus nanus*) had been locally extinct prior to recent reintroductions. Using artificial inflorescences, we compared the use of inflorescences, visit frequency and duration of alien black rats to reintroduced natives according to the stem diameter of the inflorescence. Black rats were the most frequent visitor and they spent similar or more time at artificial inflorescences as natives, but they also spent more time visiting inflorescences with thicker stem diameters. In contrast, the native mammals visited artificial inflorescences regardless of the stem thickness. We suggest that, as black rats are heavier than the native mammals, this could limit their capacity as substitute pollinators of *B. ericifolia*. This finding shows the importance of understanding the extent of the benefits of aliens before relying on them as functional replacements for extinct natives.

Keywords Niche displacement · Pollination · *Rattus rattus* · Alien

Introduction

Invasive alien species (hereafter referred to as alien(s)) are a major cause of species extinctions globally and their impacts on native biota can become substantial, especially once aliens become entrenched and impossible to eradicate (Mooney and Cleland 2001). However, entrenched aliens will develop a complex web of interactions, both direct and indirect (Dickman 2007), and their effects on ecosystem components and processes can be beneficial or negative (Davis et al. 2011). The negative impacts of competition with, and predation on, native species are well known (see reviews by Mooney and Cleland 2001; Pejchar and Mooney 2009) and can lead to niche displacement and altered ecological processes. However, aliens may also assume roles played by extinct functionally similar native species and provide positive ecosystem

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services (Davis et al. 2011). For example, black rats (*Rattus rattus*) consume and presumably disperse a wide range of fungal taxa in fragmented forests of northern NSW, Australia where native rodents have been extirpated, and may fill a functional role that would otherwise be absent (Vernes and McGrath 2009). At the same time, substantial niche overlap with established aliens may hamper the ability of reintroduced natives to reclaim their functional roles and challenges the value in reintroducing natives if there is an ostensibly ecologically similar alien species already in the ecosystem (Corlett 2016). The multifaceted nature of entrenched alien interactions within a system poses a dilemma where managing the negative impacts of aliens (Bonanno 2016) may also cause the loss of ecological benefits when aliens fill the niches of lost native species (Dickman 2007).

It is highly likely, however, that entrenched aliens may only partially fill the functional roles of lost native species. Many ecosystem functions provided by native species have been fine-tuned by evolutionary processes and result in adaptations of both the function provider and recipient, especially for specialist interactions like mutualisms where efficacy is key (Schupp et al. 2017). For example, many pollination systems require particular adaptations of the pollinator to increase the correct delivery of pollen to flowers (Johnson and Steiner 2000). In contrast, aliens are typically generalists in their habitats and diets, and do not have the same evolutionary history within the ecosystem as native species. For example, *Ficus racemigera* and *Freycinetia sulcata* seeds from New Caledonian rainforests germinate effectively after passing through the digestive tracts of native frugivores (Duron et al. 2017). When ingested by black rats, however, more seeds are destroyed and take longer to germinate, suggesting that black rats are less efficient at seed dispersal than natives (Duron et al. 2017). Therefore, it is important to understand the nature of any functional gaps between native and alien providers of ecosystem functions when considering the impact of removing aliens (Seddon et al. 2014b). These issues are also relevant when considering using introductions of alien species to restore ecosystem functions in environments where native providers are extinct [e.g. proposals for rewilding from Corlett (2016)].

Although the negative impacts of black rats in mainland Australian systems have, until recently, been poorly understood compared to elsewhere (Banks and Hughes 2012), we now understand that they compete with native rodents (Stokes et al. 2009), have negative predatory effects on bird nests (Smith et al. 2016) and act as hosts of diseases (Banks and Hughes 2012). On the other hand, there is some evidence that black rats can act as pollinators. In New Zealand, it was suggested that black rats partially pollinate at least two species of flowering plants, including a Proteaceae species, which may help compensate for the loss of endemic vertebrate pollinators (Pattemore and Wilcove 2012). There is also potential for this phenomenon to occur in our study area where introduced black rats are in high numbers and pollinate a native *Banksia* species (Saul A., unpublished data) in lieu of locally absent native pollinators such as brown antechinus (*Antechinus stuartii*), eastern pygmy-possums (*Cercartetus nanus*) and bush rats (*Rattus fuscipes*).

In Australia, small, non-flying mammals are considered to be important pollinators of numerous flowering plants, especially in the Myrtaceae and Proteaceae families (Carthew and Goldingay 1997). Morphological features of these plants reflect an evolutionary relationship with mammalian pollinators (Carpenter 1978). For instance, *Banksia ericifolia* inflorescences possess several features associated with a mammal pollination syndrome such as hooked styles, copious amounts of sugary nectar produced at night, a musky scent and robust inflorescences (Carpenter 1978). Native mammals that visit and carry the pollen of this species include brown antechinus (Goldingay 2000), sugar gliders, eastern pygmy-possums (Goldingay et al. 1991a) and bush rats (Carpenter 1978). Although they are more likely to bear fruit if they are cross-pollinated (Goldingay et al. 1991b), *B. ericifolia* plants typically have a low fruiting rate, and it is not yet understood whether this is due to a lack of pollinators or a lack of resources, or both (Paton and Turner 1985). It has been suggested, given that *B. ericifolia* is an obligate re-seeder (rather than a re-sprouter) following fire (George 1981), that it is probably resource-limited due to the resources needed to produce its woody fruits (Copland and Whelan 1989). Nevertheless, in Sydney, the effect of the loss of native mammalian pollinators to this species has not been documented and it is unknown whether alien black rats can provide adequate pollination services to replace this role.

To be effective pollinators, mammals must visit inflorescences regularly, forage non-destructively on nectar and pollen (Biccard and Midgley 2009) and optimise the removal and transfer of pollen loads by visiting for extended periods of time, resulting in the cross pollination of sufficient flowers per inflorescence to enable the plant to set seed (Paton and Turner 1985; Ohara et al. 1994). In Sydney Harbour National Park, black rats visit and spend time at *B. ericifolia* inflorescences, forage non-destructively and carry similar pollen loads to native mammalian pollinators (Saul, A., unpublished data). Whether or not they spend equivalent amounts of time on each inflorescence on a plant compared to native pollinators is not known. In this paper, we examined the potential for alien black rats to act as replacement pollinators of a native *Banksia* species in remnant bushland around Sydney, Australia. Here, native small, non-flying, mammalian pollinators have been extirpated in many areas (Banks et al. 2011) except for recent reintroduction efforts at our study site.

Banksia species have large, robust inflorescences positioned both peripherally and interiorly to the plant such that a broad array of pollinators (birds and mammals) may interact with different individual inflorescences depending on their size and/or willingness to access either exposed or protected inflorescences. Open pollination experiments with *B. aemula* found higher seed sets in the peripheral inflorescences, which was attributed to the preference of native bird pollinators rather than competition for maternal resources (Dalgleish 1999). Importantly, since native mammalian pollinators tend to be relatively lightweight and arboreal (Carthew 1993; Goldingay 2000), they too have the capacity to access these peripheral inflorescences. For example, brown antechinus and eastern pygmy-possums weigh 20–35 g and 17–45 g respectively (Fisher and Cockburn 2006; Harris 2008). Native bush rats, which are less frequent tree climbers (Smith et al. 2016), typically weigh 65–225 g (Strahan et al. 1995). Whereas the black rat, which is an adept climber, are, at their smallest weight, two-thirds greater (95 g) than the bush rat and are 50% heavier at their largest (340 g) (Dickman and Watts 2008).

For black rats to be analogous pollinators to the native small mammal species, they should be able to visit and spend the same amount of time at inflorescences. Even though *B. ericifolia* plants typically have low seed sets, we reason that the more cross-pollination that each plant receives, the chance of setting seed is increased. Since black rats are larger than natives, their ability to access and spend sufficient time at all inflorescences on a plant may be constrained. Therefore, only a select portion of inflorescences per plant may be accessible to be pollinated by the alien. Following this hypothesis, we predicted that black rats may be restricted to visiting the sturdier stems in the interior of *B. ericifolia* plants (which can withstand the animal's weight during foraging), limiting the black rat's efficacy as a pollinator of this species when compared to native counterparts.

Furthermore, black rats can show aggression towards smaller mammals in competitive interactions (Harris and Macdonald 2007; Stokes et al. 2009). Therefore, it is also possible that interference competition at inflorescences between black rats and small native species will limit the natives' ability to pollinate. Studying the interactions between natives and an entrenched alien over a common resource can inform the potential for competition. So, we predicted that a resident black rat would aggressively defend *B. ericifolia* inflorescences and that the smaller natives would be subordinate upon direct encounter resulting in natives temporally and spatially avoiding interspecific encounters with black rats over this resource.

Materials and methods

Study site

We studied small mammalian pollinators at North Head peninsula within the North Head Sanctuary (North Head) in New South Wales, Australia (− 33.817364, 151.296492). The headland is formed by Hawkesbury sandstone bedrock covered in coastal heath vegetation communities including critically endangered Eastern Suburb Banksia Scrub (ESBS) (Lambert and Lambert 2015). The vegetation is characterised by several *Banksia* species, coastal tea tree (*Leptosporum laevigatum*) and grass trees (*Xanthorrhoea spp*) (Clemens and Franklin 1980). Extant native non-flying arboreal mammals at North Head include common brushtail possums (*Trichosurus vulpecula*) and common ringtail possums (*Pseudocheirus peregrinus*), which are both potential incidental pollinators of *B. ericifolia*. Three important small mammal pollinators of *Banksia* species, including *B. ericifolia*, have recently been reintroduced to the headland. In 2014, a bush rat population was reintroduced to the area and reached an average density of approximately 7 ha^{-1} across the headland, with greater densities associated with areas of high-quality habitat (Anson J., unpublished data). Then, in 2017, brown antechinus (n = 34) and eastern pygmy-possums (n = 18) were reintroduced. The aforementioned reintroduced mammal pollinators will hereafter be referred to as "natives". Black rats are in high numbers with densities between 4 and 10 ha (Anson J., unpublished data). It should be noted that several birds at North Head are also likely to be diurnal pollinators of *B. ericifolia* but we do not examine them here.

Artificial inflorescences

To replicate natural inflorescence structure in our artificial inflorescences, we determined the natural variation in the positions (e.g. peripheral or interior) and stem diameters of *B. ericifolia* inflorescences by taking measurements of every inflorescence on five replicate plants of similar heights (2.10–3.65 m).We used digital callipers and a tape measure to quantify the stem diameter (to the nearest mm, taken 1 cm from the inflorescence base), the distance from the inflorescence to the main trunk of the plant (to the nearest cm) and the distance from the inflorescence to the ground (to the nearest cm).

We then used artificial inflorescences positioned throughout plants to measure pollinator visitation. There is substantial variation in *Banksia* species flowering times, and the quantity and quality of nectar produced, both within and among species (Fuss and Sedgley 1990; Wyk 1998). This variability among natural inflorescences within a landscape would have hampered our ability to compare patterns of mammal visitation to inflorescences, especially given the low number of natives available at the time of this study. To standardise a resource suitable for comparing patterns of visitation by different animals, we developed an artificial inflorescence comprising a wire bottle brush that allowed us to control the amount of nectar available to visitors across all replicates. This system also allowed us to position the artificial inflorescences so that we could test visitation to inflorescences with different stem diameters. Through a pilot study, we determined that all target species visited artificial inflorescences between the hours of 18:00–06:00 and visits were regular for at least 3 days after artificial inflorescences were first set up.

We installed 12 wire bottle brushes (15 cm in height) across the headland continually from May 3rd through to August 21st, 2017. These artificial inflorescences were doused in 2.5 ml of a 3:1 water:honey solution by rotating the brush in a Tupperware tray and applying residual solution with a paintbrush or syringe to emulate natural *B. ericifolia* nectar loads (Lloyd et al. 2002). They were then deployed in *Banksia spp* or tea tree (*Leptospermum laevigatum*) plants with a range of stem diameters that captured the natural distribution of inflorescence stems that we had measured. Artificial inflorescences were fastened to stems with zip-ties $\geq$ 1 m above the ground to exclude non-target ground-dwelling mammals that may have been attracted to them, such as short-beaked echidnas (*Tachyglossus aculeatus*) or long-nosed bandicoots (*Perameles nasuta*). As bottle brushes are flexible, we were able to orient our artificial inflorescences to resemble the presentation of natural *B. ericifolia* inflorescences (Fuss and Sedgley 1990; Harden et al. 2000).

We aligned a motion sensitive infra-red camera (ScoutGuard 550V) to each artificial inflorescence. Cameras were set to maximum sensitivity and programmed to record 1-min videos with a break of 5 min between potential triggers during the hours of 18:00–06:00, coinciding with black rat (Cunningham 1991) and native activity times as confirmed in our pilot studies. Artificial inflorescences were filmed for three consecutive nights within a week and then moved to a new site the next week. Nectar was applied once at each site as there was no evidence of decreasing visitation to the artificial inflorescence over the 3 days of filming. Wildlife cameras, with similar specification as ours, have been shown to be reliable in detecting visitations by our target small mammal species (or species of equivalent size) (Gray et al. 2017).

Video analysis

Animal behaviours were analysed using JWatcher software (Blumstein et al. 2006) according to an ethogram containing the following behaviours: "in direct contact" or "not in direct contact" with the artificial inflorescence. The use of the artificial inflorescence was then divided into "successful feeding" (when an animal was seen foraging on the artificial inflorescence) or "failing to feed" (when an animal fell from or was otherwise unable to forage on the artificial inflorescence). Other behaviours included "grooming", "passing by" or "other" (for undescribed behaviours). The frequency of each behaviour whilst the animal was in view of the camera and the time spent exhibiting each behaviour were recorded for each artificial inflorescence replicate.

Statistical analysis

To determine whether the stem diameter of an inflorescence was influenced by its distance from the main trunk, we performed a linear regression. To determine if the average time spent in contact with artificial inflorescences differed among species, a one-way ANOVA was performed. To determine whether the position of an inflorescence influenced visitation, we used linear regressions to compare the stem diameter with the total amount of time that black rats and natives spent in contact with artificial inflorescences.

As there were no recorded incidences of direct encounters between natives and black rats at the artificial inflorescences (i.e. individuals of different species in the same video footage), we looked at whether visits by natives were influenced by prior visitation by black rats. To do this, we determined the time (in minutes) it took until the next native individual visited following a black rat visit. However, due to low counts of natives on the same artificial inflorescence following a black rat visit, we reduced the data to binary form (native presence or absence at an inflorescence after black rat visit on the same night) and analysed them using a logistic regression (Quinn and Keough 2002). To determine whether the nocturnal activity differed between natives and black rats, a Kolmogorov–Smirnoff D test was used to test for differences in the distribution of artificial inflorescence visitation times (Sokal and Rohlf 1969). Normality and homogeneity of variance were confirmed using a Kolmogorov–Smirnov test and Levene's test respectively, and data were transformed when necessary. All statistical analyses were carried out in SPSS (IBM, version 24).

Results

As expected, the stem diameter of natural *B. ericifolia* inflorescences was negatively related to the distance from the main trunk of the plant ($F_{(1,\ 238)} = 529.656$, $p < 0.05$; $R^2 = 0.690$; Fig. 1) indicating that peripheral inflorescences had smaller stems. Most inflorescences had stems with diameters between 5.5 and 10 mm (Fig. 2).

Individual artificial inflorescences were visited by multiple species during the experimental period, with black rats visiting most frequently (212 independent visits), followed by bush rats (53), brown antechinus (19) and eastern pygmy-possums (3). Overall, the average time that mammals spent in contact with artificial inflorescences differed significantly amongst species ($F_{(3,\ 283)} = 6.007$, $p = 0.0006$) with black rats spending more time in contact than brown antechinus (Post Hoc Tukey; Fig. 3).

Artificial inflorescences were fastened to stems with diameters of 3.21–62.35 mm. The total time that black rats spent in contact with artificial inflorescences was positively related to stem diameter ($F_{(1,\ 36)} = 24.409$, $p < 0.001$, $R^2 = 0.404$; Fig. 4) indicating that black rats spent more time visiting inflorescences attached to sturdier stems. In contrast, the amount of time that natives spent in contact showed no relation to stem diameter ($F_{(1,\ 17)} = 0.331$, $p = 0.573$, $R^2 = 0.02$; Fig. 5).

There were no video observations of direct inter- or intra-specific encounters at the artificial inflorescences. However, black rats and natives both visited the same artificial inflorescence at different times within one night on 42% of all visits, suggesting a considerable overlap in the spatial use of this resource. The temporal use of artificial inflorescences by natives was analysed using a logistic regression to predict the presence or absence of natives as a function of the amount of time following a black rat visit. However, the time since a black rat visit did not significantly predict the subsequent presence or absence of native mammals (Wald chi $p = 0.07$). Furthermore, there was a complete overlap in the timing of visitation between pollinator species as the distribution of activity times did not significantly differ between black rats and natives (Kolmogorov–Smirnoff D test, $D = 0.149$, $p > 0.05$; Fig. 6).

Discussion

Black rats were by far the most frequent visitors to artificial inflorescences at North Head. Overall, black

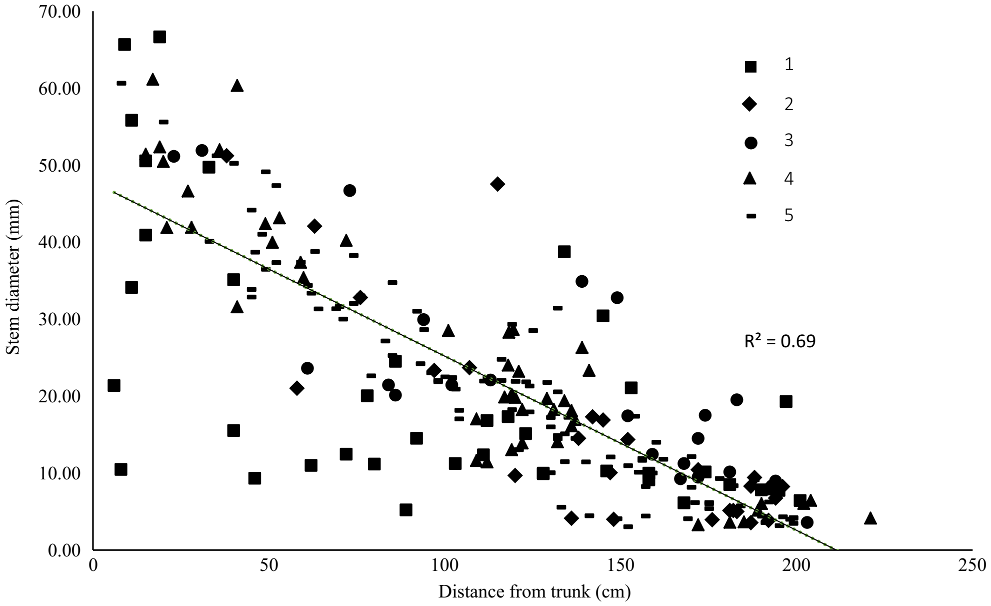
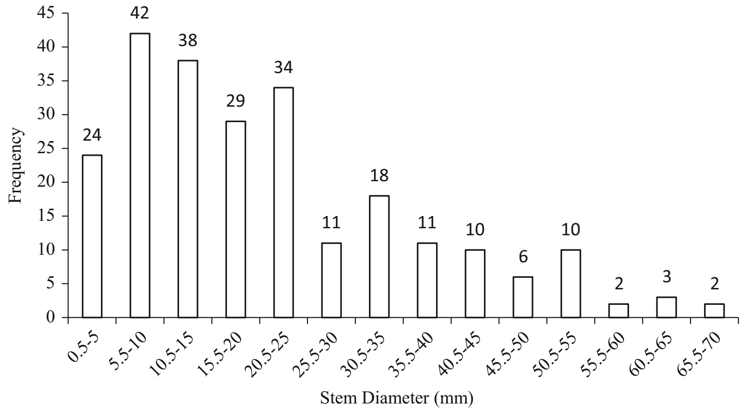


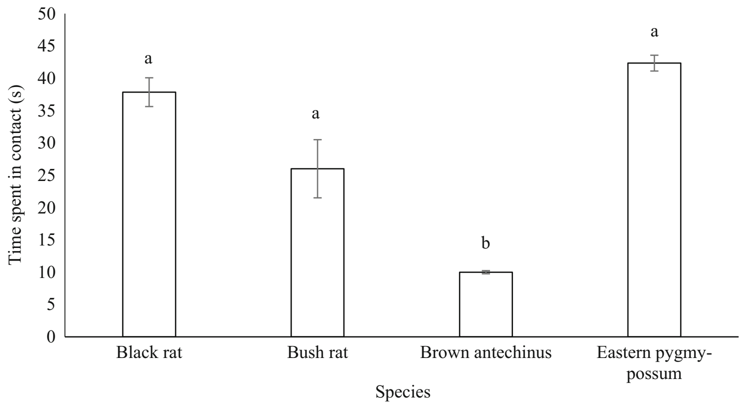
Fig. 1 Stem diameters of *Banksia ericifolia* inflorescences (n = 240) from five plants according to their distances from the main trunk. The *different symbols* (1–5) represent different plants

Fig. 2 Frequency distribution of stem diameters of inflorescences measured on five *Banksia ericifolia* plants arranged into 5 mm range categories



rats spent similar amounts of time at the artificial inflorescences as bush rats and eastern pygmy-possums, and more time than brown antechinus. We measured the time spent at an artificial inflorescence rather than visit frequency because it shows a strong relationship to pollination efficacy since it increases the probability of pollen transfer (Paton and Turner 1985). The temporal patterns of black rats visiting inflorescences were also similar to that of small native pollinators. However, we found that natives and black rats used inflorescences differently. Black rats spent less time at artificial inflorescences on thinner stems

Fig. 3 The mean (± SE) amount of time that mammal species spent in contact with artificial *Banksia ericifolia* inflorescences per visit. Groups with the same letters are not significantly different



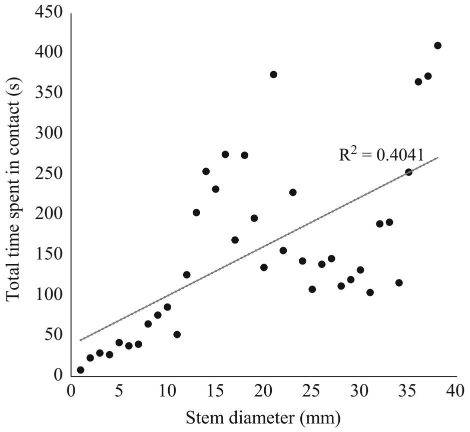


Fig. 4 Sum of the total time that individual black rats spent in contact with artificial *Banksia ericifolia* inflorescences at different stem diameters

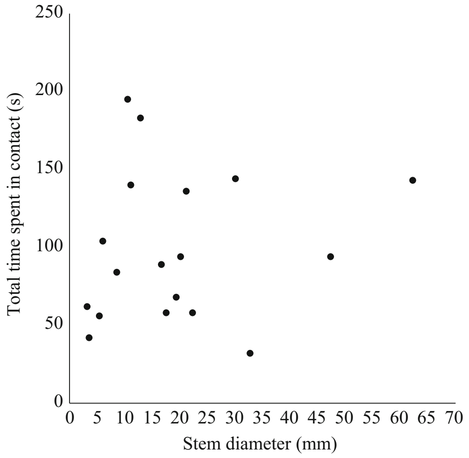


Fig. 5 Sum of the total time that individual native mammals (eastern pygmy-possums, brown antechinus and bush rats) spent in contact with artificial *Banksia ericifolia* inflorescences at different stem diameters

compared to thicker stems, whereas the time spent by native species was not associated with stem thickness. This result supports our hypothesis that alien black rats would be limited in their ability to access some of the inflorescences due to their weight when compared to the lighter native mammals.

Our results support previous pollination experiments with black rats in areas of Sydney Harbour National Park, including North Head. Black rats regularly visited and typically foraged non-destructively on *B. ericifolia* inflorescences, and so have the potential to pollinate these plants (Saul A., unpublished data). Therefore, black rats throughout Sydney's remnant bushland may have replaced the role of lost native pollinators. However, the efficacy of participants in mutualisms is fundamental the success of the relationship (Schupp et al. 2017). Our results suggest that black rats would only partly fulfil the role of lost mammal pollinators. Because black rats spent less time at inflorescences on thin stems, which are on the periphery of plants, *B. ericifolia* plants could experience reduced seed sets in systems with only black rats as the mammalian pollinators.

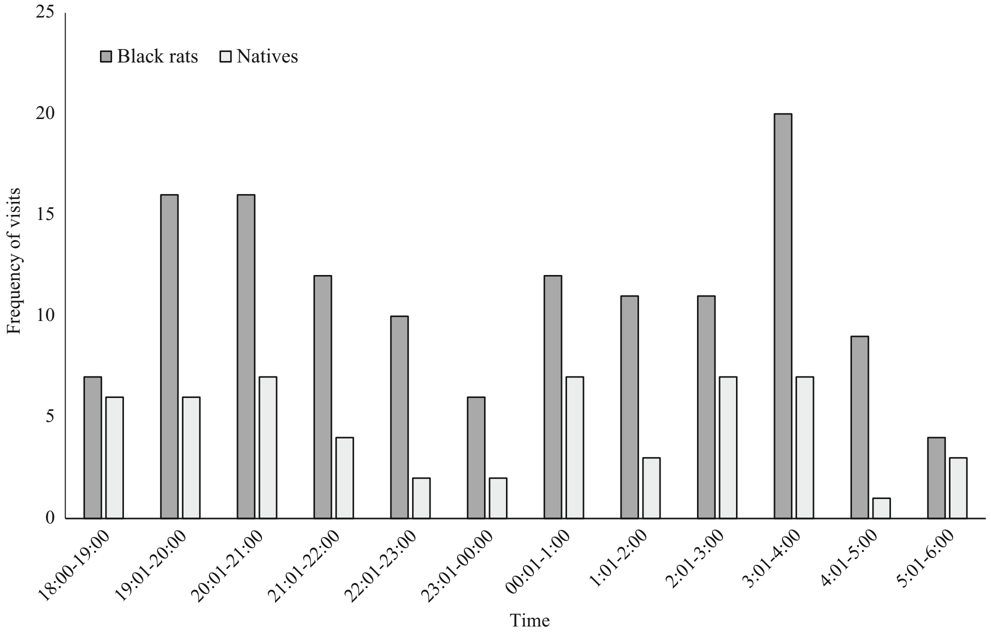


Fig. 6 Frequency of visits by black rats (dark grey) and native pollinators (eastern pygmy-possums, brown antechinus and bush rats; light grey) to artificial *Banksia ericifolia* inflorescences at different times during the night

Although *B. ericifolia* is known to not be self-compatible (Paton and Turner 1985), the relative importance of its potential pollinators has not been clarified due to the difficulties of studying this species. Invertebrates are frequent visitors to *B. ericifolia* inflorescences but are probably not large enough to transfer pollen (Cunningham 1991) or provide the force needed to press it into the stigma (Whelan and Goldingay 1978). Birds are also frequent visitors but their efficacy as pollinators of this species has not been resolved (Paton and Turner 1985), however they do affect pollination of a similar species, *B. spinulosa* (Cunningham 1991). It is possible that native birds, such as honeyeaters and wattlebirds, could provide cross-pollination to the peripheral inflorescences that are not reached by black rats since they are still present at some of Sydney's bushland remnants. Furthermore, as stated earlier, the population dynamics of *B. ericifolia* at our study site are unknown and our results point to the importance of understanding the limits to the benefits provided by aliens before accepting them as functional replacements. The long-term effects of a black rat only system upon *B. ericifolia* health and reproduction should be compared with that from a system with a complete native mammal assemblage.

The extensive use of *B. ericifolia* inflorescences by black rats and native mammals indicate some resource niche overlap that could result in interference (Case and Gilpin 1974) and exploitation competition. Where there is a size difference between competitors, the smaller subordinate party usually avoids interacting with the larger competitor by altering temporal (Kronfeld-Schor and Dayan 2003) and spatial patterns of resource use (Schoener 1983). However, we found no evidence of direct intra- or inter-specific encounters by visiting species to the artificial inflorescences at North Head, although the black rats were the most common visitor, reflecting their high abundance on the headland. Additionally, the temporal use of artificial inflorescences by natives did not appear to vary in response to black rat presence at the resource. Native individuals were observed foraging at the same artificial inflorescence 5 min after a black rat suggesting that space may not be substantially partitioned by natives (Kronfeld-Schor and Dayan 2003). Seasonality in *B. ericifolia* flowering may induce food limitation and potentially result in increased interspecific competition during times of diminished inflorescence availability. However, the headland has a strong diversity of flowering plants and the eight co-occurring *Banksia* species have different flowering seasons.

Black rats at North Head do have negative impacts on native biota such as predation on bird's nests and on skinks (Smith et al. 2016), but our results suggest their role as a pollinator of *B. ericifolia* should be taken into consideration when making management decisions about rodent population control (Davis et al. 2011). Clarification is also needed on the role of black rats in other ecosystem processes, including as potential seed and fungal dispersers, in relation to native counterparts, whether they be extant and functionally extinct.

However, our results identify that there are limits to the value of using species from outside their natural range as an ecological replacement for locally extinct native species (Seddon et al. 2014a). Recent literature has questioned the need for reintroductions in areas where entrenched alien species provided similar services as extirpated natives (Corlett 2016) while others have suggested that restoring ecosystem functions after extinction events may require introductions of functionally similar species. Our findings support the notion that in many circumstances the services provided by aliens and natives may not fully overlap partly so because of the alien's novelty in the system. In our system, reintroducing endemic pollinators such as the eastern pygmy-possum and brown antechinus, which are not limited by stem size, is needed to fully restore the ecological process of mammal pollination in spite of abundant black rat pollinators. We suggest that in many other systems, such subtle mismatches that can exist between aliens and their host environment will limit an alien species ability to fully provide appropriate ecosystem services equivalent to their native counterparts.

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