Investigating the impact of potential increased competition with common brushtail possums (Trichosurus vulpecula) in the decline of bush rats (Rattus fuscipes) in Booderee National Park

Aurelie Moffatt Kanishka

March 2024

A thesis submitted for the degree of Doctor of Philosophy of
The Australian National University

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. To the best of the author’s knowledge, it contains no material previously published or written by another person, except where due reference is made in the text.

Aurelie Moffatt Kanishka

March 2024

Acknowledgments

I am enormously grateful to my primary supervisor David Lindenmayer for his continuous support and guidance. I would also like to thank my supervisory panel. I would like to thank Natasha Robinson and Chris Dickman for their support in project conception, delivery, and writing. I'd like to thank Nick Dexter for his knowledge about Booderee National Park, and for sharing his specific insights about my study system. And, I'd also like to thank John Evans, who joined my panel mid-way through, but has been valuable support for the statistical analyses of my later chapters. I'd like to thank Wade Blanchet, who was originally on my panel and helped me immensely with the statistical analysis for Chapter Three, which has now been published.

I also received specific support for certain parts of my project, and I'd like to thank and acknowledge the people who supported me in this. Firstly, Chris MacGregor, who has been involved from the beginning, and gave me a great deal of support in the field, from helping me set up and test my experiments to saving me when I got in trouble. Secondly, Tyrone Lavery, stepped in to support me in my writing, both in improving my skills and being an emotional support when I was struggling. Finally, Linda Neaves taught me everything she could about DNA metabarcoding and helped me deal with my problematic samples.

I'd additionally like to acknowledge the people who helped me in the field when it came to collecting data. This includes the volunteers I work with, especially the Sustainable Farms team, who help collect my faecal samples. And also the rangers at Booderee National Park, who helped keep me safe while I was in the field.

I would like to acknowledge that my work was completed on the land of the Wreck Bay Aboriginal Community, who are the custodians of this land. I am immensely grateful that they allowed me to do this research on their lands, and their support in allowing me to do so. I would like to acknowledge the elders past and present of this group. I would also like to acknowledge that the other parts of the research took place on Ngunnawal and Ngambri land, where I have also lived for the past four years. I'd like to acknowledge their elders past and present.

I would also like to acknowledge the funding bodies who helped with this research. Firstly, the National Environmental Science Program funded the field equipment for Chapter 4. Secondly, the Holsworth Wildlife Research Endowment funded the DNA extraction costs for Chapter 5.

Finally, I’d like to thank my friends and family who have provided a great of emotional support during this project. Including Tash, Harry, and Murraya who were also up for a coffee and chat. My amazing office mates, Jordann, Jenna, and Mac, who I leaned on at difficult times and was also able to joke around with. My friends back in Adelaide were always excited about all of my progress, even if they didn’t understand what I was talking about. And finally, my mum, Rebecca, dad, Sunie, brother, Jahan, and sister-in-law, Larissa, who I leaned on for emotional support and were always around to celebrate my successes. Especially my mum, who was always their support me through my emotional ups and downs, and I wouldn’t have been able to do this without.

This research is supported by an Australian Government Research Training Program (RTP) Scholarship.

Abstract

Environmental change influences the composition and abundance of species within ecosystems. Changes in ecosystem dynamics can lead to disruptions to species interactions, resulting in unforeseen consequences, and risk of species loss. Competition is one such interaction that plays an important role in the maintenance and structuring of ecosystems but is often overlooked in ecosystem change and conservation research.

Changes in ecosystem dynamics can arise via multiple pathways (e.g., novel disturbances and/or species introductions). However, an underappreciated pathway is through well-intended conservation efforts, such as the removal of invasive predators, that can result in unintended negative outcomes. In Booderee National Park, located on the south coast of New South Wales, Australia, there has been an effective and ongoing fox-baiting program for more than 20 years. This program has been linked to population increases of the common brushtail possum *Trichosurus vulpecula*, a native species. During the same period, a significant decline of native small mammals, including the bush rat *Rattus fuscipes*, has been detected.

The objective of this thesis is to investigate whether increased competition with the common brushtail possum has contributed to the decline of bush rats in Booderee National Park. To achieve this, I used multiple methods to quantify the association between the two species and attempt to characterise the mechanism(s) of competition underpinning this association. In doing so I addressed the following aims: (1) quantify changes in the co-occurrence of co-occurrence of common brushtail possums and bush rats over time, (2) document evidence of competitive interactions through experimental manipulation of supplementary food sources, and (3) determine if there is a significant overlap in the diets of the species.

To tackle the first aim (Chapter 3), I analysed 17 years of mammal trapping to examine the co-occurrence of bush rats and common brushtail possums. The model revealed a negative association between the two species' abundances, however time since fire had a greater influence on bush rat populations. For the second aim (Chapter 4), I used camera traps to study competitive interactions, finding that heavy possum presence led to reduced bush rat foraging activity and shorter bait consumption periods, indicating temporal avoidance by bush rats. Addressing the third aim (Chapter 5), I employed DNA metabarcoding of faecal samples to assess diet overlap between possums and bush rats. Results showed both species are generalists with overlapping diets, though bush rats exhibited a wider diet range. This flexibility likely aids bush rats in selecting outside of possums' preferred food items, mitigating competition effects.

These findings collectively suggest that possums are contributing to the decline of bush rats in Booderee National Park through a negative, primarily competitive, interaction. This association has arisen from the growth of possum populations following the successful fox baiting program in the park. Without proper management, possum populations can be expected to continue to grow, and this negative interaction will continue to be detrimental to bush rats.

My study demonstrates that conservation actions, such as invasive predator control, can have cascading negative impacts on ecological community composition. The change in the abundance and population growth patterns of a species as a result of reduced predation pressure can destabilise pre-existing interactions. However, many of these interactions are either indirect or difficult to monitor and manage. Careful ecosystem management, including the construction of trophic web maps, is required to predict, mitigate and manage these unexpected consequences.

Table of Contents

List of Tables

List of Figures

Chapter 1 Overall Introduction

Interactions between species together with abiotic forces such as weather and disturbance events are among the factors that influence the structure of ecological communities (Bruno et al., 2003; Irwin et al., 2006; Kissling & Schleuning, 2015; Lavender et al., 2019). These factors include interactions within and across trophic levels (predation), dominance and suppression (competition), commensalism, symbiotic relationships (facilitation, mutualism), and host-parasite relationships (parasitism) (Miele et al., 2019; Périquet et al., 2016; Raffel et al., 2010). A large body of work from the second half of the twentieth century pointed to the importance of competition in shaping patterns of species coexistence, often reducing local species richness in the short term via exclusion but increasing richness over evolutionary timescales via niche partitioning (Chesson, 2000; Diamond & Case, 1986; King & Moors, 1979).

Mechanisms that allow species coexistence include dispersal, ecological differentiation, and environmental cycling (Laroche et al., 2016). Competition is an ecological interaction that can result in both species declines and the maintenance of ecological communities (Chesson, 2018; Spaak et al., 2023). Competition maintains communities by influencing the number of species and individuals within the community, based on the availability of shared resources (Chesson & Kuang, 2008; Spaak et al., 2023). Competition additionally plays a role in how species interact with their resources, through niche segregation via avoidance of aggressive interactions or differential efficiency in the exploitation of shared resources (Godsoe et al., 2015). As an example, Püttker et al. (2019) found that spatial patterns and niche partitioning based on ecological specialisation allowed for coexistence between competing rodent species in fragmented habitats within an Atlantic forest in Brazil.

Worldwide, ecosystems are changing; competitive interactions that once enabled coexistence are being disrupted and are resulting in declines and local extinctions of subordinate species (Lurgi et al., 2018; Zhou et al., 2020). These changes are sometimes linked to new and emerging selective pressures (e.g., changes to fire regimes, and invasive species), and changes in niche availability, which in turn may lead to adaptation, new secondary succession patterns, and changes in species assemblies (Fox, 1987; Traba et al., 2016). However, as ecosystems change, niche availability will often change as well (Scheele et al., 2018), potentially resulting in cascading effects on species occupation and coexistence patterns, especially in animals (Fox, 1982; Gosper et al., 2015). The species-habitat relationship for mammals, and probably other taxa, can be described by the habitat accommodation model, which states that as habitats change, species composition changes with resulting shifts in niche availability (Fox, 1982; Gosper et al., 2015; but cf. Hubbell, 2001). For example, Gosper et al. (2015) found that with fire disturbances, hot-climate specialised ants became more prevalent in open habitats, whereas cold-climate specialised ants became more prevalent in more closed habitats, as more time since fire passed. Alternatively, species may change their habitat preferences to adapt to the changing environment, resulting in two or more species occupying the same niche or sharing overlapping microhabitats (Shaner & Ke, 2022). Research has demonstrated that with increasing niche overlap, as a consequence of individuals changing their niche use or expanding their niche breadth, there will be an increase in interspecific competition (Shaner & Ke, 2022). According to these ideas, when co-occurring species increase the overlap in a shared microhabitat, competition between those species should increase (Furness et al., 2021; Shuai et al., 2016). A prediction from this thinking is that there is a threshold beyond which competition results in declines of the least competitive species (Shuai et al., 2016).

Changes in species composition, such as the introduction or removal of a species from an ecological community, can result in intensified species interactions and trigger trophic cascades, resulting in the decline of some members of that community (Lurgi et al., 2018). For example, amphibian diversity in France has become restricted due to predation from the introduced Marsh frog *Pelophylax ridibundus* (Pille et al., 2021). Similarly, limited resource availability due to drought conditions in California, USA has exacerbated competition between native bumble bees *Bombus* spp. and invasive honeybees *Apis mellifera*, resulting in declines of the former (Thomson, 2016). Competitive release can occur with the loss of a dominant competitor, in a manner similar to mesopredator release following apex predator loss, allowing subordinate competitors to thrive (M'soka et al., 2016; Ruscoe et al., 2011). This can be seen in the rise in the survival of the invasive black rat *Rattus rattus* and house mouse *Mus musculus* after the control of the invasive common brushtail possum *Trichosurus vulpecula* in New Zealand (Ruscoe et al., 2011). It can also be seen in the increased survival of native spotted hyenas *Crocuta crocuta* in Zambia after the significant depletion of co-occurring lion *Panthera leo* populations (M'soka et al., 2016). However, less is known about the trophic cascades that can occur with the loss of competing species (M'soka et al., 2016). In Australia, both native and invasive mammals have been linked to the declines of other mammals, through both predation and competition, although the effects of invasive species are usually considered to be stronger (Woinarski et al., 2015).

In terms of competitive interactions, there are two overarching mechanisms through which these interactions can occur: exploitative and interference competition (King & Moors, 1979). Exploitative competition occurs when one species in a community consumes a resource, depleting its availability for the rest of the community via its efficiency in acquiring that resource

(Ferguson et al., 2013; Kawata, 1997). For example, vertebrate herbivores can be a barrier to ecological restoration because of their efficient grazing habits, which in turn can exclude other herbivore species via both competition for food and the modification of habitat (Barton et al., 2011; Chee & Wintle, 2010). Interference competition can be described as a behavioural interaction, where one species actively limits another species' ability to access a resource, primarily through aggression (King & Moors, 1979; Lindenmayer et al., 2023; Maniscalco et al., 2001). For example, noisy miners *Manorina melanocephala* competitively interfere with other bird species' ability to access flowers and other food resources, mobbing and harassing them when they approach these food resources (Beggs et al., 2020).

Competition in ecological communities is a complex phenomenon and can be difficult to observe and quantify (Hart et al., 2018). While some forms of competition can be categorised by direct, and often aggressive, interactions (Beggs et al., 2020), others are categorised by the limitation in resources (Barton et al., 2011) or mediated by the presence of a third or further species (Westgate et al., 2021). Competitive interactions can lead to avoidance behaviours, with species using indirect and alternative cues such as odour to avoid negative interactions (Coppock et al., 2016). The level of species' ecological specialisation creates another level of complexity (Barnes & Murphy, 2023; Püttker et al., 2019). Generalist species are often found to be more resilient to ecosystem change, but also to be weaker competitors (Lloyd & Vetter, 2019; Treloar et al., 2021). This is primarily because generalist species have a wider range of resources they can exploit than specialists and can switch their use of resources in relation to what is available within an ecosystem (Treloar et al., 2021). However, competition between generalist pairs of species has rarely been studied, and therefore, we do not know to what extent generalists can share resources before being impacted by competition (Barnes & Murphy, 2023).

The complexity of defining competition makes the goal of accurately measuring competition difficult in practice (Hart et al., 2018). Some common methods of uncovering competition involve experiments where the densities of putative competitor species are manipulated, both in the field and within the laboratory (Dickman, 1988; Karlsson et al., 2018). While these experiments can be used to observe the effects of competition, in many cases such experiments involve disturbances to shared resources or the environment, so the level of competition found may not translate to the actual level of competition that prevails naturally in the absence of manipulations (Ferry et al., 2020; Karlsson et al., 2018). Many studies therefore measure patterns of co-occurrence of ecologically similar species as an alternative and interpret competition from any negative associations that may be uncovered (O'Reilly-Nugent et al., 2020). However, these studies are limited by their correlative nature. Another method often used is to measure patterns and overlap of resource use and interpret competitive potential from these patterns (Spaak et al., 2023; Wang et al., 2023).

All methods of field experimentation and monitoring can be expensive, which in some circumstances can limit their effectiveness, especially if putative competitor species are not correctly identified (Likens & Lindenmayer, 2018; Morant et al., 2020). One method of tackling these issues is through the creation of conceptual maps and trophic food webs, as these can be used to model and monitor known and pre-existing interactions between species, and then use these to predict the impacts of ecosystem change (Endrédi et al., 2018; Greenville et al., 2017). In this thesis, my method of tackling the complexity of accurately measuring competition takes the idea of using a conceptual map to predict interactions between putatively competing generalist species, and then using multiple methods of measuring and interpreting potential competition and discussing the combined resulting patterns in light of competition theory.

1.1 The study system

It has been found, during some conservation and management efforts, that ignoring species' interactions can lead to unintended, negative effects, such as mesopredator release or competitive release (Lazenby et al., 2015; Ruscoe et al., 2011). For example, in Booderee National Park (BNP), control of the invasive red fox *Vulpes vulpes* – ostensibly to protect native prey species and conserve natural values – has led to an increase in the abundance of macropods and common brushtail possums *Trichosurus vulpecula* (hereafter 'possum'), commensurate with declines in bush rats *Rattus fuscipes* and other small mammals (Dexter et al., 2012; Lindenmayer et al., 2018). The increased grazing from macropods has, additionally, led to changes in vegetation in BNP (Dexter et al., 2013). There has also been a loss of biodiversity which is suspected to be linked to the increase in abundance of macropods (Lindenmayer et al., 2018). However, despite the extensive research that has been conducted to date in BNP (Dexter et al., 2013; Lindenmayer et al., 2018), there are no clear answers to why the park's biodiversity is changing so dramatically.

There is a large amount of anecdotal evidence, but relatively little direct empirical evidence, for the ability of possums to outcompete other species in certain habitats in Australia. Possums have adapted to many different environments (i.e., urban environments), and have become invasive in New Zealand (Adams et al., 2013, 2014; Glen et al., 2012; Moorhouse et al., 2003; Rouco et al., 2017). In contrast, in other habitats, for example in arid regions, possums are threatened and have been lost from most of their previous range (McDonald et al., 2015). Possums have a flexible and generalist diet (Herath et al., 2021). While the species is commonly described as a folivore, it will also consume any available high-nutrient foods (e.g., fruits, seeds, leftovers from bins in urban areas, and some prey animals) (Cruz et al., 2012; Gloury & Handasyde, 2016). Possums are also known to occupy and use multiple hollow trees, which are often shared between multiple individuals (Cowan, 1989; Youngentob et al., 2012). In habitats where hollow resources are limited, possums have been shown to aggressively, and competitively, exclude other species, such as greater gliders *Petauroides volans* (Youngentob et al., 2012).

Bush rats have an omnivorous, generalist diet (Stokes et al., 2009). Bush rats tend to occupy habitats with dense ground cover, especially when there are perceived predator cues, as these habitats offer protection (Strauß et al., 2008). However, they are found in a variety of habitats and occupy almost all habitat types in BNP. The home range of bush rats varies between 0.1 ha and 7.8 ha, depending on the environmental conditions, and varies between populations (Callander, 2018). Bush rats have been shown to be competitively vulnerable, especially to aggressive competitors such as swamp rats *Rattus lutreolus* and use olfactory cues to avoid aggressive encounters (Heavener et al., 2014; Maitz & Dickman, 2001). They also exhibit competitor naivety towards novel competitors, such as the invasive black rat *Rattus rattus*, to which they appear to be competitively vulnerable (Heavener et al., 2014; Stokes et al., 2009). Since fox control at BNP, bush rat numbers have declined, and their detection rate is also reducing (Lindenmayer et al., 2018). Similar declines in bush rats have also been found in Western Australia, with reports likewise linking the declines to increases in the abundance of common brushtail possums (Wayne et al., 2015).

Bush rats are terrestrial and ground-dwelling and usually nest in burrows at or below ground level (Callander, 2018). Possums, in comparison, preferably nest in trees, usually at least a metre above ground, but can ground-den in a hollow log or at the base of a tree if suitable tree hollows are absent (Cowan, 1989). An increase in the population numbers of possums, such as is occurring in BNP, could force some possums to use ground-level dens simply because of the limited availability of their preferred arboreal dens. With both bush rats and possums active at ground level, they might potentially share microhabitats and associated food resources. As both species are ecological generalists, more information is required about the species' particular diets within BNP to determine if they share food resources, and whether an overlap in these resources is preventing bush rats from accessing enough food (Herath et al., 2021; Vernes et al., 2015). As possums preferentially consume resources with the greatest nutrient content (Herath et al., 2021), they may be reducing the availability of high-nutrient-content foods for bush rats through exploitative competition (Kawata, 1997; Vernes et al., 2015). Another hypothesis is that, if the two species are sharing more space and resources, there is a greater opportunity for aggressive interactions, leading to interference competition (Lindenmayer et al., 2023; Maniscalco et al., 2001).

The objective of my project is to investigate whether competition between a dominant, abundant species is causing declines of native, naturally co-occurring species. I have used common brushtail possums and bush rats as model co-occurring species. I investigated whether competition is occurring, and if so, by what mechanism. My prediction is that increased competition with possums, as a result of increases in their population size, is contributing significantly to the decline of bush rats in BNP.

The reason for assuming that possums will be the dominant species in competition is based on previous research demonstrating that body size differences lead to asymmetric competition, with larger animals usually being competitively dominant (Rayan & Linkie, 2016; Thompson & Fox, 1993). The size difference between possums and bush rats is pronounced: Common brushtail possums usually exceed 2 kg, whereas bush rats average ~100 g (Callander, 2018; Cruz et al., 2012). One hypothesis is that possums will competitively interfere with bush rats, through aggressive interactions or intimidation. However, another hypothesis is that possums are accessing and consuming resources before bush rats and are thus the more efficient foragers of the two species. Either hypothesis will be influenced by the degree of overlap in the resources the two species prefer (Case & Gilpin, 1974; Villsen et al., 2022).

1.2 Aims and objectives

A major general outcome of this project will be to determine the nature and outcome of interactions between two species of ecologically generalist mammals that appear likely to be in competition. A specific outcome will be to determine whether possums negatively impact another Australian native species, specifically the bush rat. To determine whether competitive interactions between possums and bush rats are causing the latter species to decline, the project has the following aims. These are to:

1. Quantify changes in the abundances of co-occurring common brushtail possums and bush rats over time in Booderee National Park.

2. Document evidence of competitive interactions through experimental manipulation of supplementary food sources.

3. Describe the diets of common brushtail possums and bush rats and quantify the degree of overlap in their diets.

1.3 Thesis structure

In chapter two, I will review how competition has been addressed in previous animal conservation research. This chapter is under revision with *Conservation Science and Practice* for publication. In chapter three, I analysed the association between the abundance of bush rats and common brushtail possums in Booderee National Park using a co-occurrence model. This model is based on data from 14 years of annual monitoring. This chapter was published in *PLoS ONE*. In chapter four, using a manipulated experimental design, I investigated the foraging behaviours of bush rats and possums in BNP. This chapter aimed to investigate if bush rat foraging behaviour changed in relation to possum activity. This chapter is under revision with *Animal Behaviour*. In chapter five, I investigated the diet ranges of bush rats and possums using DNA metabarcoding. I have additionally quantified the overlap in the species' diets based on these diet ranges. This chapter has been submitted to *Ecology and Evolution*. In the final chapter, I will present a brief, overall discussion of the results of chapters three, four and five, and how they have addressed my overall aims for this thesis. Chapters two to five have been prepared for publication separately, and therefore, this is some repetition in the study area description (and associated maps), and an overlap in the references cited.

1.4 References

Adams, A. L., Dickinson, K. J. M., Robertson, B. C., & van Heezik, Y. (2013). Predicting Summer Site Occupancy for an Invasive Species, the Common Brushtail Possum (*Trichosurus vulpecula*), in an Urban Environment. *PLoS One; San Francisco*, *8*(3), e58422. http://dx.doi.org.virtual.anu.edu.au/10.1371/journal.pone.0058422

Adams, A. L., Recio, M. R., Robertson, B. C., Dickinson, K. J. M., & van Heezik, Y. (2014). Understanding home range behaviour and resource selection of invasive common brushtail possums (*Trichosurus vulpecula*) in urban environments. *Biological Invasions*, *16*(9), 1791–1804. https://doi.org/10.1007/s10530-013-0627-4

Barnes, E. E., & Murphy, S. M. (2023). Bottom-up and top-down pressures mediate competition between two generalist insects. *Ecology*, *104*(3), e3957. https://doi.org/10.1002/ecy.3957

Barton, P. S., Manning, A. D., Gibb, H., Wood, J. T., Lindenmayer, D. B., & Cunningham, S. A. (2011). Experimental reduction of native vertebrate grazing and addition of logs benefit beetle diversity at multiple scales. *Journal of Applied Ecology*, *48*(4), 943–951. JSTOR.

Beggs, R., Pierson, J., Tulloch, A. I. T., Blanchard, W., Westgate, M., & Lindenmayer, D. (2020). An empirical test of the mechanistic underpinnings of interference competition. *Oikos*, *129*(1), 93–105. https://doi.org/10.1111/oik.06583

Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, *18*(3), 119–125. https://doi.org/10.1016/S0169-5347(02)00045-9

Callander, M. (2018). *Translocation and reintroduction of native bush rats (Rattus fuscipes) into Sydney Harbour National Park: Restoring ecosystem function*. https://researchdirect.westernsydney.edu.au/islandora/object/uws%3A47378/

Case, T. J., & Gilpin, M. E. (1974). Interference competition and niche theory. *Proceedings of the National Academy of Sciences of the United States of America*, *71*(8), 3073–3077. https://doi.org/10.1073/pnas.71.8.3073

Chee, Y. E., & Wintle, B. A. (2010). Linking modelling, monitoring and management: An integrated approach to controlling overabundant wildlife. *Journal of Applied Ecology*, *47*(6), 1169–1178. https://doi.org/10.1111/j.1365-2664.2010.01877.x

Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366.

Chesson, P. (2018). Updates on mechanisms of maintenance of species diversity. *Journal of Ecology*, *106*(5), 1773–1794. https://doi.org/10.1111/1365-2745.13035

Chesson, P., & Kuang, J. J. (2008). The interaction between predation and competition. *Nature; London*, *456*(7219), 235–238. http://dx.doi.org.virtual.anu.edu.au/10.1038/nature07248

Coppock, A. G., Gardiner, N. M., & Jones, G. P. (2016). Sniffing out the competition? Juvenile coral reef damselfishes use chemical cues to distinguish the presence of conspecific and heterospecific aggregations. *Behavioural Processes*, *125*, 43–50. Scopus. https://doi.org/10.1016/j.beproc.2016.02.001

Cowan, P. E. (1989). Denning Habits of Common Brushtail Possums, *Trichosurus vulpecula*, in New Zealand Lowland Forest. *Wildlife Research*, *16*(1), 63–78. https://doi.org/10.1071/wr9890063

Cruz, J., Sutherland, D. R., Martin, G. R., & Leung, L. K.-P. (2012). Are smaller subspecies of common brushtail possums more omnivorous than larger ones? *Austral Ecology*, *37*(8), 893–902. https://doi.org/10.1111/j.1442-9993.2011.02346.x

Dexter, N., Hudson, M., James, S., MacGregor, C., & Lindenmayer, D. B. (2013). Unintended Consequences of Invasive Predator Control in an Australian Forest: Overabundant Wallabies and Vegetation Change. *PLOS ONE*, *8*(8), e69087. https://doi.org/10.1371/journal.pone.0069087

Dexter, N., Ramsey, D. S. L., MacGregor, C., & Lindenmayer, D. (2012). Predicting Ecosystem Wide Impacts of Wallaby Management Using a Fuzzy Cognitive Map. *Ecosystems*, *15*(8), 1363–1379. JSTOR.

Diamond, J. M., & Case, T. J. (1986). *Community Ecology*. Harper & Row.

Dickman, C. R. (1988). Body Size, Prey Size, and Community Structure in Insectivorous Mammals. *Ecology*, *69*(3), 569–580. https://doi.org/10.2307/1941006

Endrédi, A., Senánszky, V., Libralato, S., & Jordán, F. (2018). Food web dynamics in trophic hierarchies. *Ecological Modelling*, *368*, 94–103. https://doi.org/10.1016/j.ecolmodel.2017.11.015

Ferguson, N., White, C. R., & Marshall, D. J. (2013). Competition in benthic marine invertebrates: The unrecognized role of exploitative competition for oxygen. *Ecology*, *94*(1), 126–135.

Ferry, N., Cordonnier, M., Hulot, F. D., Dakwa, F., Sebele, L., Dray, S., Fritz, H., & Valeix, M. (2020). Heterogeneity of water physico-chemical characteristics in artificially pumped waterholes: Do African herbivores drink at the same locations and does it lead to interference competition? *Journal of Arid Environments*, *173*, 104014. https://doi.org/10.1016/j.jaridenv.2019.104014

Fox, B. J. (1982). Fire and Mammalian Secondary Succession in an Australian Coastal Heath. *Ecology*, *63*(5), 1332–1341. https://doi.org/10.2307/1938861

Fox, B. J. (1987). Species assembly and the evolution of community structure. *Evolutionary Ecology*, *1*(3), 201–213. https://doi.org/10.1007/BF02067551

Furness, E. N., Garwood, R. J., Mannion, P. D., & Sutton, M. D. (2021). Productivity, niche availability, species richness, and extinction risk: Untangling relationships using individual-based simulations. *Ecology and Evolution*, *11*(13), 8923–8940. https://doi.org/10.1002/ece3.7730

Glen, A. S., Byrom, A. E., Pech, R. P., Cruz, J., Schwab, A., Sweetapple, P. J., Yockney, I., Nugent, G., Coleman, M., & Whitford, J. (2012). Ecology of brushtail possums in a New Zealand dryland ecosystem. *New Zealand Journal of Ecology; Christchurch*, *36*(1), 29–37.

Gloury, A. M., & Handasyde, K. A. (2016). Comparative dietary ecology of two congeneric marsupial folivores. *Austral Ecology*, *41*(4), 355–366. https://doi.org/10.1111/aec.12320

Godsoe, W., Murray, R., & Plank, M. J. (2015). The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography*, *38*(11), 1071–1079. https://doi.org/10.1111/ecog.01134

Gosper, C. R., Pettit, M. J., Andersen, A. N., Yates, C. J., & Prober, S. M. (2015). Multi-century dynamics of ant communities following fire in Mediterranean-climate woodlands: Are changes congruent with vegetation succession? *Forest Ecology and Management*, *342*, 30–38. https://doi.org/10.1016/j.foreco.2015.01.006

Greenville, A. C., Wardle, G. M., & Dickman, C. R. (2017). Desert mammal populations are limited by introduced predators rather than future climate change. *Royal Society Open Science*, *4*(11), 170384. https://doi.org/10.1098/rsos.170384

Hart, S. P., Freckleton, R. P., & Levine, J. M. (2018). How to quantify competitive ability. *Journal of Ecology*, *106*(5), 1902–1909. https://doi.org/10.1111/1365-2745.12954

Heavener, S. J., Carthey, A. J. R., & Banks, P. B. (2014). Competitive naïveté between a highly successful invader and a functionally similar native species. *Oecologia*, *175*(1), 73–84. https://doi.org/10.1007/s00442-013-2874-6

Herath, A. P. H. M., Wat, K. K. Y., Banks, P. B., & McArthur, C. (2021). Animal personality drives individual dietary specialisation across multiple dimensions in a mammalian herbivore. *Functional Ecology*, *35*(10), 2253–2265. https://doi.org/10.1111/1365-2435.13893

Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*. Princeton University Press. https://www.jstor.org/stable/j.ctt7rj8w

Irwin, R. E., III, A. E. E. D. B., & Losos, E. J. B. (2006). The Consequences of Direct versus Indirect Species Interactions to Selection on Traits: Pollination and Nectar Robbing in Ipomopsis aggregata. *The American Naturalist*, *167*(3), 315–328. JSTOR. https://doi.org/10.1086/499377

Karlsson, M. F., de Souza, E. O., Ayelo, P. M., Zannou, J. A., Mègnigbèto, G. S. B., & Bokonon-Ganta, A. H. (2018). Interspecific competition between egg parasitoids: Native *Fopius caudatus* and exotic *Fopius arisanus*, in *Ceratitis cosyra*. *Biological Control*, *117*, 172–181. https://doi.org/10.1016/j.biocontrol.2017.11.010

Kawata, M. (1997). Exploitative competition and ecological effective abundance. *Ecological Modelling*, *94*(2), 125–137. https://doi.org/10.1016/S0304-3800(96)00008-7

King, C. M., & Moors, P. J. (1979). On Co-Existence, Foraging Strategy and the Biogeography of Weasels and Stoats (*Mustela nivalis* and *M. erminea*) in Britain. *Oecologia*, *39*(2), 129–150. JSTOR.

Kissling, W. D., & Schleuning, M. (2015). Multispecies interactions across trophic levels at macroscales: Retrospective and future directions. *Ecography*, *38*(4), 346–357. https://doi.org/10.1111/ecog.00819

Laroche, F., Jarne, P., Perrot, T., & Massol, F. (2016). The evolution of the competition–dispersal trade-off affects α- and β-diversity in a heterogeneous metacommunity. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1829). https://doi.org/10.1098/rspb.2016.0548

Lavender, T. M., Schamp, B. S., Arnott, S. E., & Rusak, J. A. (2019). A comparative evaluation of five common pairwise tests of species association. *Ecology*, *100*(4), e02640. https://doi.org/10.1002/ecy.2640

Lazenby, B. T., Mooney, N. J., & Dickman, C. R. (2015). Detecting species interactions using remote cameras: Effects on small mammals of predators, conspecifics, and climate. *Ecosphere; Washington*, *6*(12), 1–18. http://dx.doi.org.virtual.anu.edu.au/10.1890/ES14-00522.1

Likens, G., & Lindenmayer, D. (2018). *Effective Ecological Monitoring*. Csiro Publishing.

Lindenmayer, D. B., Blanchard, W., Evans, M. J., Beggs, R., Lavery, T., Florance, D., Crane, C., Smith, D., Siegrist, A., Lang, E., & Scheele, B. C. (2023). Context dependency in interference competition among birds in an endangered woodland ecosystem. *Diversity and Distributions*, *29*(4), 556–571. https://doi.org/10.1111/ddi.13680

Lindenmayer, D. B., Wood, J., MacGregor, C., Foster, C., Scheele, B., Tulloch, A., Barton, P., Banks, S., Robinson, N., Dexter, N., O'Loughlin, L. S., & Legge, S. (2018). Conservation conundrums and the challenges of managing unexplained declines of multiple species. *Biological Conservation*, *221*, 279–292. https://doi.org/10.1016/j.biocon.2018.03.007

Lloyd, K. J., & Vetter, S. (2019). Generalist trophic ecology in a changing habitat: The case of the four-striped mouse in a woody-encroached savannah. *African Journal of Ecology*, *57*(3), 371–381. https://doi.org/10.1111/aje.12613

Lurgi, M., Ritchie, E. G., & Fordham, D. A. (2018). Eradicating abundant invasive prey could cause unexpected and varied biodiversity outcomes: The importance of multispecies interactions. *Journal of Applied Ecology*, *55*(5), 2396–2407. https://doi.org/10.1111/1365-2664.13188

Maitz, W. E., & Dickman, C. R. (2001). Competition and habitat use in native Australian Rattus: Is competition intense, or important? *Oecologia*, *128*(4), 526–538. https://doi.org/10.1007/s004420100689

Maniscalco, J. M., Ostrand, W. D., Suryan, R. M., & Irons, D. B. (2001). Passive interference competition by glaucous-winged gulls on Black-Legged Kittiwakes: A cost of feeding in flocks. *The Condor; Waco*, *103*(3), 616–619.

McDonald, P. J., Luck, G. W., Dickman, C. R., Ward, S. J., & Crowther, M. S. (2015). Using multiple-source occurrence data to identify patterns and drivers of decline in arid-dwelling Australian marsupials. *Ecography*, *38*(11), 1090–1100. https://doi.org/10.1111/ecog.01212

Miele, V., Guill, C., Ramos-Jiliberto, R., & Kéfi, S. (2019). Non-trophic interactions strengthen the diversity-functioning relationship in an ecological bioenergetic network model. *PLoS Computational Biology*, *15*(8). Scopus. https://doi.org/10.1371/journal.pcbi.1007269

Moorhouse, R., Greene, T., Dilks, P., Powlesland, R., Moran, L., Taylor, G., Jones, A., Knegtmans, J., Wills, D., Pryde, M., Fraser, I., August, A., & August, C. (2003). Control of introduced mammalian predators improves kaka *Nestor meridionalis* breeding success: Reversing the decline of a threatened New Zealand parrot. *Biological Conservation*, *110*(1), 33–44. https://doi.org/10.1016/S0006-3207(02)00173-8

Morant, J., González-Oreja, J. A., Martínez, J. E., López-López, P., & Zuberogoitia, I. (2020). Applying economic and ecological criteria to design cost-effective monitoring for elusive species. *Ecological Indicators*, *115*, 106366. https://doi.org/10.1016/j.ecolind.2020.106366

M'soka, J., Creel, S., Becker, M. S., & Droge, E. (2016). Spotted hyaena survival and density in a lion depleted ecosystem: The effects of prey availability, humans and competition between large carnivores in African savannahs. *Biological Conservation*, *201*, 348–355. https://doi.org/10.1016/j.biocon.2016.07.011

O'Reilly-Nugent, A., Wandrag, E. M., Catford, J. A., Gruber, B., Driscoll, D., & Duncan, R. P. (2020). Measuring competitive impact: Joint-species modelling of invaded plant communities. *Journal of Ecology*, *108*(2), 449–459. https://doi.org/10.1111/1365-2745.13280

Périquet, S., Mapendere, C., Revilla, E., Banda, J., Macdonald, D. W., Loveridge, A. J., & Fritz, H. (2016). A potential role for interference competition with lions in den selection and attendance by spotted hyaenas. *Mammalian Biology*, *81*(3), 227–234. https://doi.org/10.1016/j.mambio.2015.10.005

Pille, F., Pinto, L., & Denoël, M. (2021). Predation Pressure of Invasive Marsh Frogs: A Threat to Native Amphibians? *Diversity*, *13*(11), Article 11. https://doi.org/10.3390/d13110595

Püttker, T., Barros, C. S., Pinotti, B. T., Bueno, A. A., & Pardini, R. (2019). Co-occurrence patterns of rodents at multiple spatial scales: Competitive release of generalists following habitat loss? *Journal of Mammalogy*, *100*(4), 1229–1242. https://doi.org/10.1093/jmammal/gyz083

Raffel, T. R., Hoverman, J. T., Halstead, N. T., Michel, P. J., & Rohr, J. R. (2010). Parasitism in a community context: Trait-mediated interactions with competition and predation. *Ecology*, *91*(7), 1900–1907. https://doi.org/10.1890/09-1697.1

Rayan, D. M., & Linkie, M. (2016). Managing conservation flagship species in competition: Tiger, leopard and dhole in Malaysia. *Biological Conservation*, *204*, 360–366. https://doi.org/10.1016/j.biocon.2016.11.009

Rouco, C., Norbury, G. L., & Anderson, D. P. (2017). Movements and habitat preferences of pests help to improve population control: The case of common brushtail possums in a

New Zealand dryland ecosystem. *Pest Management Science*, *73*(2), 287–294. https://doi.org/10.1002/ps.4252

Ruscoe, W. A., Ramsey, D. S. L., Pech, R. P., Sweetapple, P. J., Yockney, I., Barron, M. C., Perry, M., Nugent, G., Carran, R., Warne, R., Brausch, C., & Duncan, R. P. (2011). Unexpected consequences of control: Competitive vs. predator release in a four-species assemblage of invasive mammals. *Ecology Letters*, *14*(10), 1035–1042. https://doi.org/10.1111/j.1461-0248.2011.01673.x

Scheele, B. C., Foster, C. N., Banks, S. C., & Lindenmayer, D. B. (2018). The Role of Biotic Interactions in the Niche Reduction Hypothesis: A Reply to Doherty and Driscoll. *Trends in Ecology & Evolution*, *33*(3), 148–149. https://doi.org/10.1016/j.tree.2017.12.001

Shaner, P.-J. L., & Ke, L. (2022). Niche overlap in rodents increases with competition but not ecological opportunity: A role of inter-individual difference. *Journal of Animal Ecology*, *91*(8), 1679–1692. https://doi.org/10.1111/1365-2656.13750

Shuai, L.-Y., Song, Y.-L., Kotler, B. P., Embar, K., & Zeng, Z.-G. (2016). Foraging behaviour in East Asian desert rodents and its implications on coexistence. *Israel Journal of Ecology and Evolution*, *62*(3–4), 171–177. https://doi.org/10.1080/15659801.2015.1045279

Spaak, J. W., Millet, R., Ke, P.-J., Letten, A. D., & De Laender, F. (2023). The effect of non-linear competitive interactions on quantifying niche and fitness differences. *Theoretical Ecology*, *16*(2), 161–170. Scopus. https://doi.org/10.1007/s12080-023-00560-6

Stokes, V. L., Banks, P. B., Pech, R. P., & Spratt, D. M. (2009). Competition in an Invaded Rodent Community Reveals Black Rats as a Threat to Native Bush Rats in Littoral Rainforest of South-Eastern Australia. *Journal of Applied Ecology*, *46*(6), 1239–1247. JSTOR.

Strauß, A., Solmsdorff, K. Y., Pech, R., & Jacob, J. (2008). Rats on the run: Removal of alien terrestrial predators affects bush rat behaviour. *Behavioral Ecology and Sociobiology*, *62*(10), 1551–1558. https://doi.org/10.1007/s00265-008-0584-6

Thompson, P., & Fox, B. J. (1993). Asymmetric Competition in Australian Heathland Rodents: A Reciprocal Removal Experiment Demonstrating the Influence of Size-Class Structure. *Oikos*, *67*(2), 264–278. https://doi.org/10.2307/3545471

Thomson, D. M. (2016). Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecology Letters*, *19*(10), 1247–1255. https://doi.org/10.1111/ele.12659

Traba, J., Casals, P., Broto, F., Camprodon, J., Giralt, D., Guixé, D., Mechergui, R., Rios, A., Sales, S., Taull, M., Ammari, Y., Solano, D., & Bota, G. (2016). Coexistence and habitat partitioning at micro- and macro-scales of rodent species in a North African desert (Bou-Hedma National Park, Tunisia). *Journal of Arid Environments*, *131*, 46–58. https://doi.org/10.1016/j.jaridenv.2016.04.002

Treloar, S., Lohr, C., Hopkins, A. J. M., & Davis, R. A. (2021). Rapid population expansion of Boodie (Burrowing Bettong, *Bettongia lesueur*) creates potential for resource competition with Mala (Rufous Hare-wallaby, *Lagorchestes hirsutus*). *Ecological Management & Restoration*, *22*(S1), 54–57. https://doi.org/10.1111/emr.12471

Vernes, K., Cooper, T., & Green, S. (2015). Seasonal fungal diets of small mammals in an Australian temperate forest ecosystem. *Fungal Ecology*, *18*, 107–114. https://doi.org/10.1016/j.funeco.2015.09.015

Villsen, K., Corse, E., Archambaud-Suard, G., Héran, K., Meglécz, E., Ereskovsky, A. V., Chappaz, R., & Dubut, V. (2022). Diet Metabarcoding Reveals Extensive Dietary Overlap between Two Benthic Stream Fishes (*Zingel asper* and *Cottus gobio*) and Provides Insights into Their Coexistence. *Diversity*, *14*(5), Article 5. https://doi.org/10.3390/d14050412

Wang, D., Hu, X., Li, M., Liu, J., Tang, M., Liu, W., Zhan, J., Xu, Y., & Zhang, W. (2023). Diet composition and interspecific niche of Taohongling Sika deer (*Cervus nippon kopschi*) and its sympatric Reeve's muntjac (*Muntiacus reevesi*) and Chinese hare (*Lepus sinensis*) in winter (Animalia, Mammalia). *ZooKeys*, *1149*, 17–36. https://doi.org/10.3897/zookeys.1149.96936

Wayne, A. F., Maxwell, M. A., Ward, C. G., Vellios, C. V., Wilson, I., Wayne, J. C., & Williams, M. R. (2015). Sudden and rapid decline of the abundant marsupial *Bettongia penicillata* in Australia. *Oryx; Cambridge*, *49*(1), 175–185. http://dx.doi.org.virtual.anu.edu.au/10.1017/S0030605313000677

Westgate, M. J., Crane, M., Florance, D., & Lindenmayer, D. B. (2021). Synergistic impacts of aggressive species on small birds in a fragmented landscape. *Journal of Applied Ecology*, *58*(4), 825–835. https://doi.org/10.1111/1365-2664.13838

Woinarski, J. C. Z., Burbidge, A. A., & Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(15), 4531–4540. https://doi.org/10.1073/pnas.1417301112

Youngentob, K. N., Yoon, H.-J., Coggan, N., & Lindenmayer, D. B. (2012). Edge effects influence competition dynamics: A case study of four sympatric arboreal marsupials. *Biological Conservation*, *155*, 68–76. https://doi.org/10.1016/j.biocon.2012.05.015

Zhou, J., Zhou, L., & Xu, W. (2020). Diversity of wintering waterbirds enhanced by restoring aquatic vegetation at Shengjin Lake, China. *Science of The Total Environment*, *737*, 140190. https://doi.org/10.1016/j.scitotenv.2020.140190

Chapter 2 A global systematic review of the influence of competition on the outcomes of fauna conservation interventions

2.1 Abstract

Ecosystems typically exhibit resilience to disturbances, yet excessive pressure can disrupt species interactions, resulting in biodiversity loss. Conservation interventions strive to safeguard ecosystems and reinstate vital ecological functions. Competition between animals plays a pivotal role in ecosystem persistence and dynamics, but its significance is often underestimated in conservation research.

We conducted a global review that analysed 147 articles, focusing on the impact of competitive interactions between animals on conservation interventions. We found a tendency for researchers to retrospectively interpret observed patterns of interactions as competitive. Negative outcomes, such as species declines, were frequently associated with competitive interactions. Despite efforts to predict outcomes using characteristics of the competition process, we found no consistent patterns of outcomes based on these characteristics.

Our findings suggest the considerable influence that competition may have on conservation outcomes, emphasizing a need for proactive consideration of competition dynamics as part of planning conservation interventions. By integrating animal competition into conservation planning, monitoring, and mitigation efforts, unexpected negative impacts can be minimised, fostering more effective conservation outcomes.

2.2 Introduction

Competition, predation, mutualism, and webs of indirect interactions among multiple animal species are well known to structure natural ecological communities (Verhoef & Morin, 2010) and could be expected to influence communities following interventions that manipulate species abundances or composition for conservation purposes. However, Heinen et al. (2020) argued that the conservation literature has mostly overlooked species interactions, especially competitive interactions. Competition is a powerful form of species interaction that may influence the fitness of competing individuals and can shape the structure and composition of ecological communities via its effects on the regulation and maintenance of species diversity (Chesson & Kuang, 2008; Spaak et al., 2023). In undisturbed ecosystems, competitive interactions often result in long-term species co-existence and play a role in maintaining species populations rather than contributing to species declines, especially when species-specific ecological differences and environmental heterogeneity are accounted for (Castillo-Alvino & Marvá, 2020; Chesson, 1994, 2000, 2018).

Competition between animals often takes the form of competition for food or space which can, in turn, influence animal foraging and reproductive decisions, and lead to subordinate species or individuals abandoning areas they previously occupied (Ferguson et al., 2013; Kumeh & Omulo, 2019). Competition can occur both between and within species, with both forms often occurring simultaneously (Kassinis et al., 2024). Therefore, competition can influence patterns of species occurrence and abundance by reducing access to shared resources (Ferguson et al., 2013; Maniscalco et al., 2001). This effect can arise from direct aggression where a dominant individual reduces access to resources by a subordinate individual (known as encounter or interference competition) (Beggs et al., 2019; Lindenmayer et al., 2023; Maniscalco et al., 2001), or through the depletion of a resource by a dominant individual that limits the amount of that resource that is available for other individuals and species (known as resource, scramble or exploitative competition) (Ferguson et al., 2013; Sale, 1982).

Ultimately, all forms of competition limit the ability of subordinate species to persist, with potential subsequent effects at the level of the ecosystem (Ferguson et al., 2013; Lindenmayer et al., 2023). However, competition can be extremely difficult to observe and document and often involves quantifying combinations of different characteristics, including the mechanism of competition (Hart et al., 2018). Some forms of competition are indirect and mediated by the presence of a third species (Westgate et al., 2021). For example, apparent competition occurs when two species avoid shared space due to a shared predator (Ferguson et al., 2013; Kuhnen et al., 2017). Even in the case of direct interactions, such as those seen in interference competition, aggressive encounters are rarely observed and avoidance of dominant individuals by subordinate individuals may arise from cues such as odour (Coppock et al., 2016). Consequently, some studies have deduced competition using field experiments (Dickman, 1988), indirect inferences from models (e.g., joint-species distribution models), or inverse numerical or distributional patterns (Fox & Pople, 1984; O'Reilly-Nugent et al., 2020). Because of this difficulty in quantifying and measuring/monitoring competition, we predict this interaction is often overlooked, including in conservation interventions.

Environmental change can reduce the availability of shared resources, shift competitive balances, and lead to losses and declines of less competitive species and the collapse of ecosystem functioning (Sandor et al., 2022; Valiente-Banuet et al., 2015). Due to these effects, competition is often predicted to have negative impacts on ecosystems, and as such is described as a negative interaction with deleterious outcomes for competitors (Chesson, 2018). For example, avian communities in alpine regions of Europe are expected to shift dramatically, with increasingly negative competitive interactions predicted to occur (Brambilla et al., 2020). However, as mentioned above, some of the effects of competition are difficult to predict, such as wood frogs *Rana sylvatica* in the USA avoiding previously strong competitive effects through their metamorphosis phase occurring earlier than predicted (Rollins & Benard, 2020). We predict that with ongoing environmental change, the importance of understanding traits that foreshadow negative outcomes will become increasingly important. This is because, under changing conditions, such as those arising from climate change, competition is likely to shift in otherwise difficult-to-predict ways (Rollins & Benard, 2020).

Similar to the effects of environmental change, some conservation interventions can alter the presence and density of species and resources within ecosystems, and this can lead to alterations in the frequency and intensity of interactions between competing species, especially among animals (Heinen et al., 2020; Nie et al., 2019). Competitive interactions can, in turn, influence conservation interventions resulting in unexpected and detrimental outcomes, often for other species within the ecosystem. For example, the introduction of non-native honeybees *Apis mellifera* to urban areas in Paris, France, to promote pollination and honey production, failed to recognise the potential for negative impacts on native pollinators through competition, with evidence that these actions reduced pollinator diversity and perversely limited efficient pollination (Ropars et al., 2019). Likewise, rewilding-focused restoration or reintroduction attempts have been reported to fail due to competitive or predator-prey interactions between animals that have been translocated and those already present in the rewilding sites (Baker et al., 2017; Navarro et al., 2023; Nogués-Bravo et al., 2016).

In light of the above, the potential influence of competition on the outcomes of conservation interventions is a significant research gap. We aimed to address this gap by systematically reviewing published articles on conservation interventions in ecosystems that interpreted competition as a potential factor that influenced the intended outcomes of the intervention. By ‘conservation intervention’ we refer to any management actions taken in an ecosystem that have the goal of protecting and/or restoring species and/or habitat, regardless of the efficacy of the approaches used (Table 2-1). We have included passive actions, which we define as ‘designating protections’ without directly interfering with animals or habitats, such as designating protected areas or changing policies. We include passive actions as these can have flow-on effects on ecosystem dynamics through the restriction of activities (e.g. hunting, fishing, habitat removal). We also include active actions, which we define as directly managing or interfering with animals and/or habitat, including species introductions, attempted eradications (e.g., of invasive species or pathogens), or changes to habitats (e.g., restoration and creation of artificial habitats). Laboratory, zoo, and captive studies were included in our review if the purpose was related to conservation in the wild. Additionally, by 'post-intervention ecosystems' we refer to the state of the ecosystem after the conservation intervention has been implemented.

Table 2-1. A list of the categories of conservation interventions, and the definitions used for each category. The intervention refers to the types of management actions taken in ecosystems with the goal of protecting/restoring animals and habitats. The activity level refers to the level of direct influence the intervention has on the target animals or habitats, with active interventions directly altering the target, and passive interventions influencing aspects surrounding the target.

Intervention	Activity Level	Description
Artificial Habitat	Active	Artificial additions to habitats (e.g., feeding stations, nest boxes) or addition of species to controlled habitats (e.g., zoos)
Biological Control	Active	Addition of a species, or group of species, to a habitat to control pests (most examples are insects)
Introduction	Active	Introduction of a species to habitat for the protection of that species (e.g., translocations, reintroductions)
Eradication	Active	Removals or reductions of species within a habitat (e.g., removals of invasive species, culls of overabundant native species)
Protected Area	Passive	An area with defined borders that has been set aside for the protection of wildlife within it, with specific restrictions to human activity within the defined area (e.g., marine protected areas, nature reserves)
Protected Species	Passive/Active	Multiple targeted actions taken to protect species within a habitat other than intervening directly with the species itself (e.g., restoration actions focused on the requirements of the target species)
Policy	Passive	Changes to policies (e.g., harvesting rules) with the goal of protecting species
Restoration	Active	Changes to a habitat with the goal of returning it to a functional and productive state to the benefit of all native and or target animal species inside the habitat (e.g., revegetation, removal of invasive plants, removal of infrastructure/pollutants)

We asked: "To what degree is competition considered as a factor that may influence the outcomes of animal conservation?" We used this question to generate and then test three predictions: (1) researchers are more likely to invoke competition as a *post hoc* interpretation of observed patterns in post-intervention ecosystems than consider it *a priori* with no influence from intervention type, (2) researchers will record negative outcomes from putative competitive interactions in post-intervention ecosystems with no influence from intervention type, and (3) different characteristics of the competition process (i.e., mechanisms, intra- versus interspecific, trophic guild of interactants, and identity of the shared resource) can be used to predict the effects of competition resulting from interventions.

2.3 Methods

We conducted a systematic review to assess the extent to which competition has been considered in assessing the outcomes of conservation interventions. Our focus was on whether competition between animal species has been perceived to influence the outcomes of such interventions. We focused on literature published in English to track, across time, how competition has been addressed. All types of conservation interventions were considered (Table 2-1), including passive actions such as the implementation of protected areas or changes to policies, so we could compare how competition has been addressed by the various approaches.

We used the ScienceDirect database to identify literature that considered competition in post-intervention ecosystems. The search terms were: (‘interference competition’ OR ‘exploitative competition’) and (restor OR recover OR reintrod) and (manag OR reserv OR protect OR monitor) not (plant OR DNA OR model). The terms ‘interference’ and ‘exploitative’ were used to specify competition in ecological terms. The terms ‘restor’, ‘recover’ and ‘reintrod’ were used to specify that we were investigating conservation research. The terms ‘manag’, ‘reserv’, ‘protect’ and ‘monitor’ were further used to specify and include multiple forms of conservation interventions and management actions. Some of the specific terms, such as ‘reserv’, ‘reintrod’ and ‘restor’ were chosen as they describe the management actions we were targeting. However, upon reviewing the articles, we found a greater range of distinct conservation interventions and have subsequently included them in our review. The excluded terms were to limit the search output so that the results were focused on animal competition in observational and experimental studies. Models, while often useful for predicting the outcomes of interventions, were excluded due to their predictive and non-empirical nature (Baker et al., 2017). These search terms produced 6000 articles, many of which were from disciplines outside ecology (e.g., economics, sociology, anthropology). To further refine the focus of our review, we used a three-step selection process to decide which studies were relevant. Step one aimed to filter titles that were unrelated to ecological topics, and those that were intentionally excluded based on our search terms. Step two involved screening the abstracts of the remaining studies using a set of four a priori selection criteria based on ‘yes or no’ questions, to objectively determine which articles should be included. The four questions were:

(1) Does the study mention competitive interactions? (2) Does the study involve a conservation intervention? (3) Is it an animal-focused study? And (4) Does the study have an experimental or observational design? We excluded any article eliciting a 'no' response to any of the options within the selection criteria questions. These criteria should remove any articles that take a theoretical or mathematical approach to studying competition theory. Finally, the full body of text of the remaining articles was rescreened against the four selection criteria questions. The first two steps were completed using the 'sysrev' package ver. 0.4.9002 (Bozada et al., 2021) in R version 4.4.1 (R Core Team, 2021), the latter two following reading of the articles by the lead author (AK).

Using a questionnaire developed for this review (Appendix A.1), we collected data from the 147 articles identified in our selection process. This was done using two ranking scales created for this review. The first scale ranked the degree to which observed patterns of interactions in a post-intervention ecosystem were interpreted as competition. A value of 1 was applied to studies where competition was a possible (but unlikely) interpretation (i.e., mentioned in a single paragraph of the Discussion, or purposely controlled making it less likely to account for observed patterns). A value of 2 was applied to studies where competition was a likely interpretation of patterns, but there were other interpretations considered just as likely. A value of 3 was applied to studies where competition was considered the most likely interpretation of observed patterns (i.e., pre-investigation, recorded as investigated, or post-investigation, recorded as a conclusion).

The second scale ranked the strength and direction of the effects of competition on the intended outcomes of the conservation intervention within the ecosystem and ranged from negative to positive outcomes. The 'outcome' was interpreted either from a combined effect of the competing species on the ecosystem or a reflection of the species the researchers were focusing on, and depended on how researchers reported this information (see Appendix A.2). For this, scale, a value of -2 was applied to articles where competition had a major negative outcome (often corresponding to major declines in species abundance or the loss of species in the ecosystem). A value of -1 was applied to articles where competition had notable but minor negative outcomes (often corresponding to recorded declines or displacement). A value of 0 was applied to articles where competition had a neutral outcome (often corresponding to species co-existing). A value of 1 was applied to articles where competition had a notable but minor positive outcome (often corresponding to recorded increases in short-term abundance). Finally, a value of 2 was applied to articles where competition had a major positive outcome (often corresponding to target species increasing in abundance).

We also collected information about selected characteristics of the competition process; the mechanism of competition (i.e., interference, exploitative, apparent), whether it was interspecific versus intraspecific, the resource being competed for, and the trophic guild of the interacting species. In cases where any of these characteristics were not reported in the article, we used ‘NA’ to specify that the information was missing. We used trophic guild to describe the broad feeding behaviours of the species within a given study (Denny et al., 2018; Jacquot et al., 2017). We also collected additional descriptive information on how and when the studies took place (i.e., location, duration, and volume of data collected).

We analysed the data collected using the scales described above, the interventions, and the characteristics of the competition process using the base ver. 4.1.0 and glmmTMB ver. 1.1.7 (Brooks et al., 2017) packages in R (R Core Team, 2021). We analysed the categorical data from the first prediction using chi-squared tests to assess how researchers interpreted patterns of interactions. For the second prediction, where we assessed the outcomes of competition within the literature, we analysed the mean of the scale results using a simple one-sample t-test. We also used generalised linear mixed models (GLMMs) to compare the association between the means of the two scales, as the response variables, and the intervention type for the first two predictions. Finally, to assess our third prediction, which was to assess the association between the characteristics of the competition process and outcomes of competition, we used GLMMs for the second scale as the response variable against information collected on the selected characteristics, within a single model.

2.4 Results

We found 147 articles that considered competition between animal species in ecosystems subject to conservation interventions. These articles spanned five decades (1977-2021), with most articles being produced between 2010 and 2020. Most studies were conducted in the USA (n = 17), followed by Australia (n = 13) and Spain (n = 10), with the other 107 articles from 55 different countries. In total, 18 major taxa were studied, with most articles investigating mammals (35.6%), and other articles investigating birds, fish, arthropods, or multiple taxa (Appendix A.3). In terms of the conservation interventions (Table 2-1), most focused on protected areas (n = 74), then species introductions (n = 21), followed by use of artificial habitats (n = 15), protection of focal species (n = 11), restoration (n = 8), biological control (n = 7), attempted eradications (n = 6), with the least number of strategies employing changes to policies (n = 5).

2.4.1 Prediction 1: consideration given to competition

Our first prediction was that competition would be a minor consideration in formulating post-intervention research and more likely to be invoked as a *post hoc* explanation of results. We tested this by tallying articles where competition was investigated, and by using the scale of consideration given to competition that we assigned to each article. Competition was investigated in 53 (36%) of the articles and was introduced as a conclusion in 91 (62%) of the articles (Fig 2-1a). Additionally, three articles statistically or experimentally controlled for competition before investigation (2%) ($\chi^2_2 = 79.51$, $p < 0.001$) (Fig 2-1a).

Based on the results from the first scale, the average result (m = 1.95) indicated that competition was often one of several potential interpretations of the patterns of interactions observed in post-intervention ecosystems. However, most articles interpreted these patterns to be either less likely arising from competition (scale = 1, n = 57) or for competition to have been the main driver (scale = 3, n = 51). There were no statistically significant differences between intervention types (all p-values were > 0.05) (Fig 2-1b).

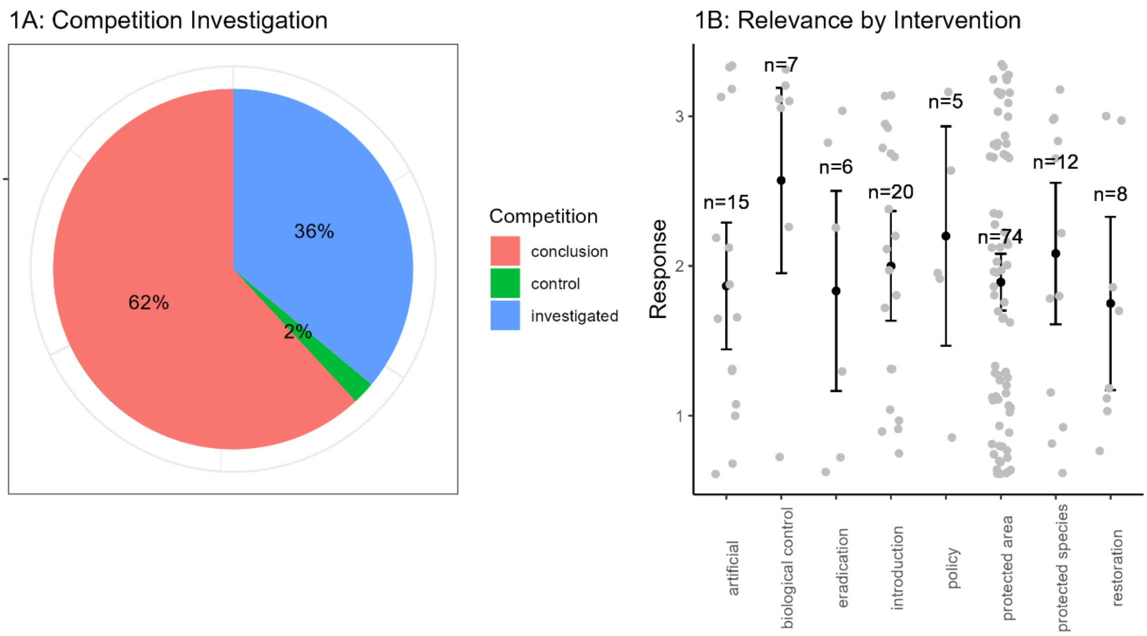


Figure 2-1. Consideration given by researchers to competition as a factor influencing outcomes in post-intervention ecosystems. *Fig 1A* shows the percentage of articles that either investigated competition or interpreted the results of an outcome of competition; note that 2% (n = 3) of articles controlled for competition. *Fig 1B* shows how likely researchers were to interpret interactions as competition based on intervention type using the estimated mean from a generalised linear mixed model of the results from

the first scale against intervention type. Sample sizes and raw data points are shown, with error bars corresponding to the 95% confidence intervals. The results of the generalised linear mixed model show no statistical differences between intervention types.

2.4.2 Prediction 2: results of the outcomes of competition

Our second prediction was that competition would be interpreted as having had a negative outcome on species persistence in post-intervention ecosystems. Our results revealed that the average outcome of competition was interpreted as mildly negative (m = -0.60), with most articles suggesting that competition would result in species declines (36.1%) or displacements (31.3%) (t_{146} = -7.36, $p < 0.001$) (Fig 2-2a). Additionally, there was a negative association between the scale of outcomes and the scale of how likely patterns of interactions were interpreted as having resulted from competition (Fig 2-3). None of the differences between the outcomes by intervention were statistically significant (all p-values were > 0.05) (Fig 2-2b).

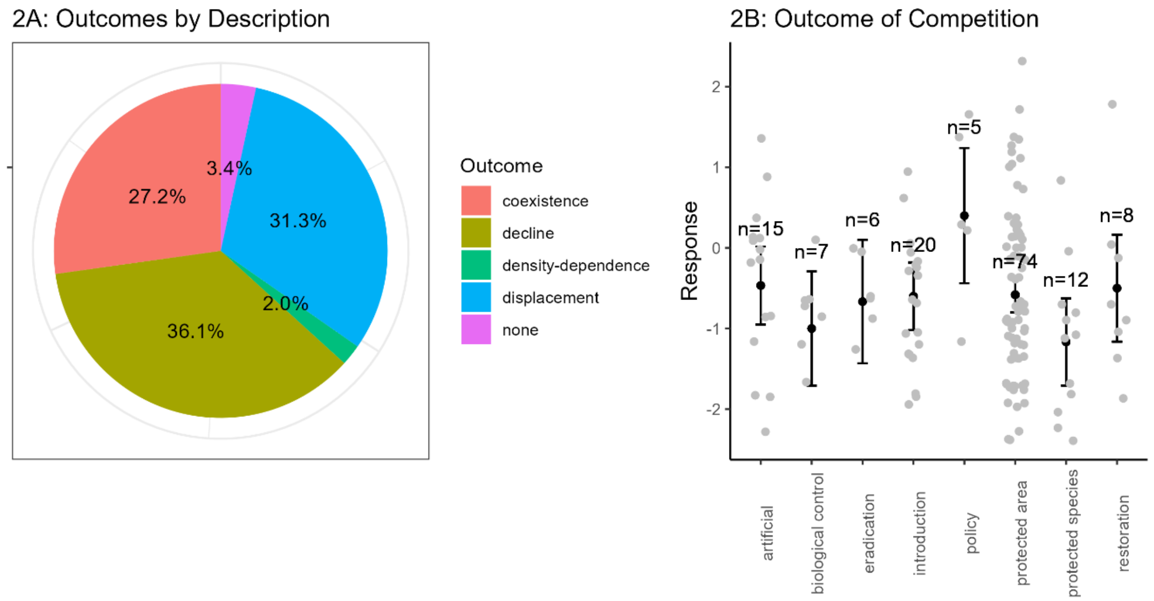


Figure 2-2. Perceptions of researchers on the outcomes of competition in post-intervention ecosystems. *Fig 2A* shows different types of outcomes as they were reported by researchers in the articles. *Fig 2B* shows the scale outcomes, from negative to positive, by intervention type, using estimated means from a generalised linear mixed model of the results of the second scale against intervention type. Sample sizes and raw data points are shown, with error bars corresponding to the 95% confidence intervals. The results of the generalised linear mixed model show no statistical differences between intervention types.

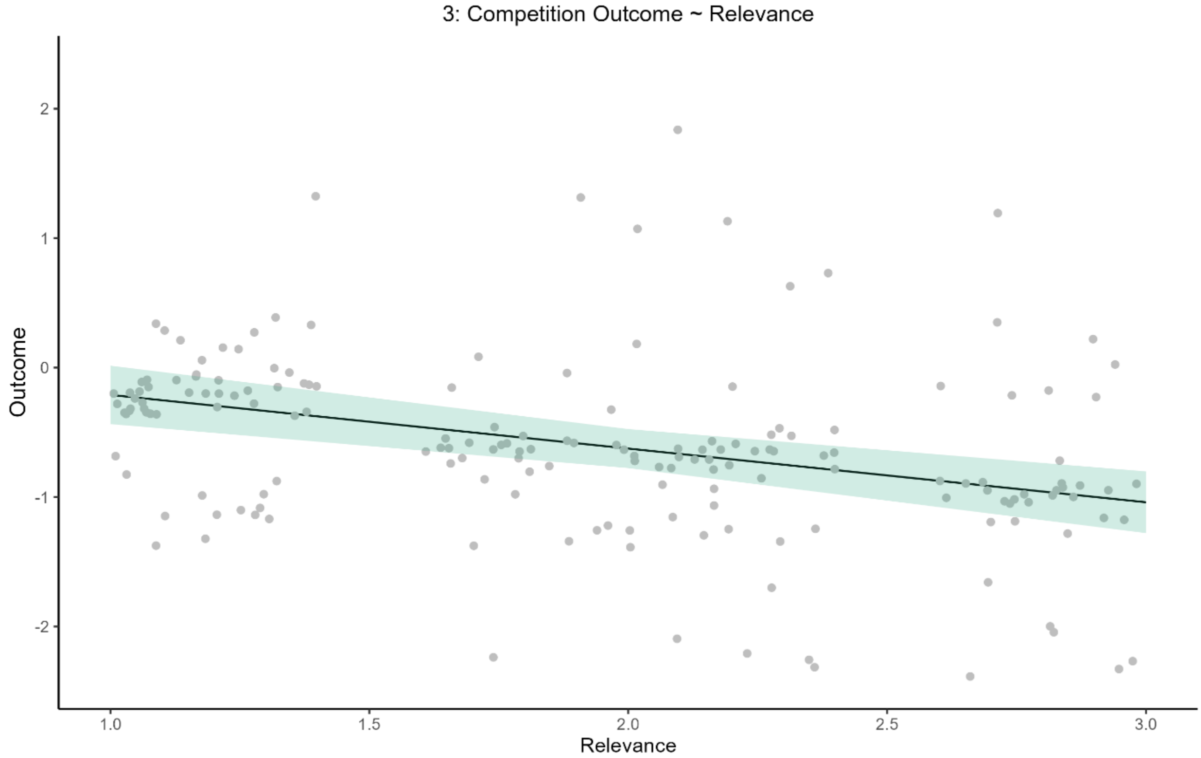


Figure 2-3. The association between the scaled ranking for how much patterns of interactions were interpreted as competition and the scaled (from negative to positive) outcome of competition in post-intervention ecosystems, which was analysed using a generalised linear mixed model (n = 147). The results depict a statistically significant negative linear relationship, with raw data points shown and the green-shaded area representing the 95% confidence intervals.

2.4.3 Prediction 3: association between features of competing species and competition outcomes

Our third prediction was that we could identify differences between characteristics of the competition process that are associated with negative post-intervention outcomes and use these differences to predict different outcomes of competition. Only one characteristic was significantly different from others within the same grouping, although this characteristic also displayed a large amount of error: members of the omnivore trophic guild were associated with significantly more negative post-intervention outcomes compared to species in other trophic guilds ($m = -0.566$, $p = 0.032$) (Fig 2-4).

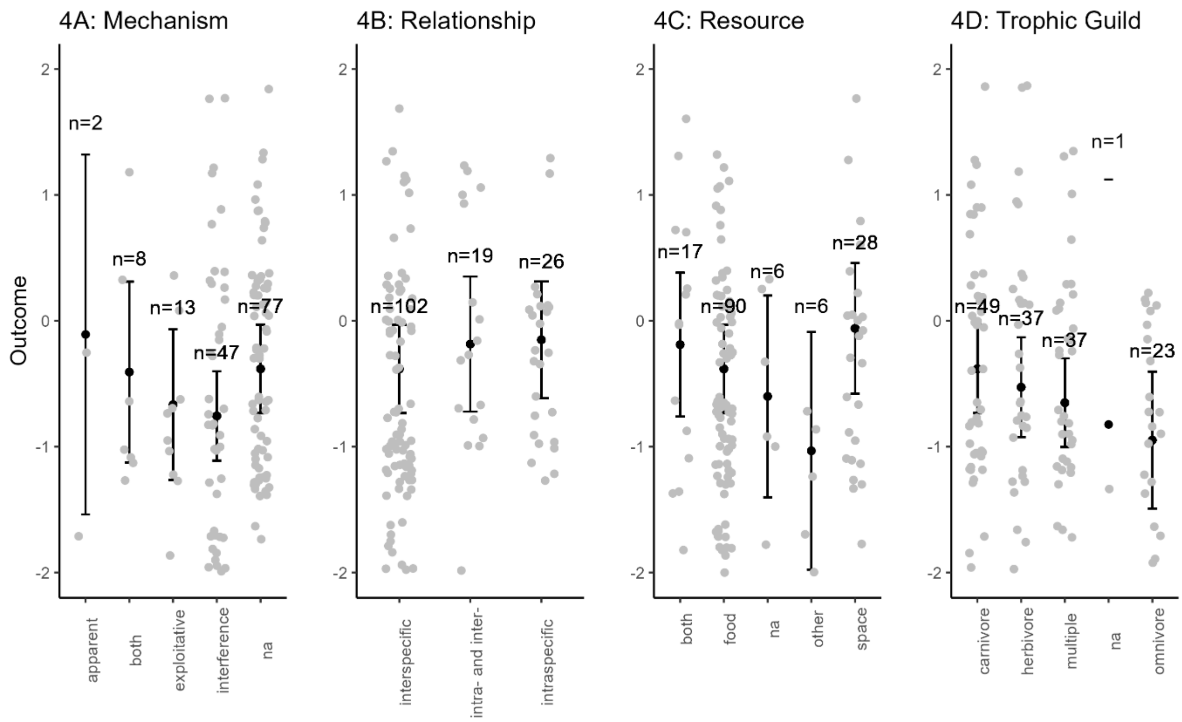


Figure 2-4. The estimated means from a generalised linear mixed model of the outcome of competition against characteristics of the competition process, with sample sizes, raw data points and error bars corresponding to the 95% confidence intervals shown. *Fig 4A*; there is no statistical difference between mechanisms of competition. *Fig 4B;* there is no statistical difference between the different competitive relationships within and between species (interspecific vs. intraspecific). *Fig 4C;* there is no statistical difference between the main resources competed for. *Fig 4D;* there is a statistical difference between the trophic guild of interactants, with omnivores having statistically more negative outcomes than members of other guilds (m = -0.566, p = 0.032).

2.5 Discussion

2.5.1 Prediction 1: consideration of competition in post-intervention ecosystems

Our results partially support our first prediction and show that competition was more likely to be perceived after a conservation intervention than in the planning or investigative phases. However, while competition was often introduced as a *post hoc* explanation of results, it was just as likely for competition to be posited as a major interpretation as it was to be a minor interpretation. Our inference from these results is that competition is seldom measured in post-intervention monitoring, nor considered in pre-intervention planning. This could reflect the difficulty of observing and measuring competition and the need to infer its effects using indirect cues. This is despite advances in technology (e.g., remote wildlife cameras) that have allowed for a greater breadth of data collection and interpretation of species interactions (O'Reilly-Nugent et al., 2020). For example, avoidance behaviours, such as giant pandas *Ailuropoda melanoleuca* spatially avoiding wild boar *Sus scrofa* in China, are often interpreted as a sign of interspecific competition even if the animals are not observed to interact directly (Nie et al., 2019). Similarly, occupancy-type models, presence-absence data, and patterns of spatial and temporal avoidance are regularly used to infer changes in levels of competition, and for wildlife, this is often interpreted from data captured by remote camera traps (Astete et al., 2017).

The extent to which patterns of interactions were interpreted as competition in published articles was often based on a researcher's or manager's expectations that competition would occur, which may have related to how well the researchers understood their study system (Geary et al., 2019). In many cases, the expected competition level accurately represented what was found, as it was based on previous insights recorded during monitoring that could be interpreted as competition (Geary et al., 2019; Wolfenden et al., 2015). For example, in Mauritius, the native pink pigeon *Nesoenas mayeri*, a protected species, and the introduced Madagascan turtle dove *Nesoenas picturata* were observed to have similar calls during monitoring to assess protection efforts for the former species (Wolfenden et al., 2015). As a result of this observation, researchers used call playback experiments to measure whether pink pigeons responded to the calls of turtle doves in the same way as they did to conspecific calls. The results showed signal jamming, a form of competition where the male pink pigeon treated areas occupied by turtle doves as occupied by conspecific competitors for mates, thereby reducing the reproductive output of pink pigeons and impeding their recovery (Wolfenden et al., 2015). However, issues arise in situations where competition is not predicted to influence post-intervention conservation outcomes, and therefore isn't measured but is later found to have a significant impact. As an example, monitoring of herbivores within the Gobi Gurvan National Park in southern Mongolia, which is set aside, in part, for the protection of vegetation and rare endemic species, unexpectedly recorded high numbers of livestock (Retzer et al., 2006). The associated high levels of competition for grazing space will likely have long-lasting implications for endemic wildlife and human-wildlife conflict but were not factored into the monitoring program (Retzer et al., 2006).

Researchers, for the most part, did not differ in how much they interpreted patterns of interactions as competition depending on the type of intervention implemented. Interactions observed in biological control interventions were more often interpreted as competition as they are often tested explicitly prior to the release of the control agents (Fig 2-1) (Mace & Mills, 2017; Momanyi et al., 2006). An example of this is documented by Momanyi *et al*. (2006), who tested the effects of an introduced biological control species, the parasitoid *Diadegma semiclausum*, prior to its release, to assess its suitability as a control agent for a crop pest, the diamondback moth *Plutella xylostella*, compared to indigenous parasitoids. They found that this introduced parasitoid was a more successful control agent but also that it would lead to the near-complete displacement of local indigenous parasitoid species (such as *Oomyzus sokolowskii*) through competition (Momanyi et al., 2006).

2.5.2 Prediction 2: the outcomes of competition influence conservation interventions

Our prediction that competition would have predominantly negative influences on post-intervention ecosystems was supported. However, some articles demonstrated the positive influences of competition on intervention outcomes. One interpretation of this overall result is that conservation interventions can directly influence the outcomes of competitive interactions, both in positive and negative ways. For example, efforts to protect the Audouin's gull *Larus audouinii* in the most productive wetland in the Ebro Delta in Spain had both positive and negative outcomes (Oro et al., 2009). The intervention was successful for the target species; however, intervention efforts also led to a decrease in overall bird diversity as a result of increasing levels of competition between Audouin's gull and other dominant gulls, leading to the displacement of smaller seabirds. In this case, major declines or losses of species were avoided by the existence of nearby alternative, but poorer-quality, nesting sites (Oro et al., 2009).

Articles that gave greater consideration to the role of competition in conservation interventions were also more likely to identify negative outcomes as a result (Fig 2-3). We consider two likely explanations for this result. First, clear or strong negative effects of competition are more likely to be noticed and discussed as a major study conclusion. Guillemain, Fritz & Duncan (2002) found strong evidence of displacement of young and naïve dabbling ducks *Anas* spp. in protected wetlands in France, which was clearly linked to intraguild interference competition, and resulted in the younger ducks losing the protection of conservation land tenure. Second, explicit measurement of competition increases the likelihood that negative effects will be encountered and documented. For example, investigations into spatial avoidance of competition by giant pandas found that they avoided better-quality habitats in protected areas to reduce encounters with other medium-sized mammals (Liu et al., 2020).

Competition outcomes did not differ depending on the type of conservation intervention (Fig 2-2b). Policy-based interventions were the only interventions, on average, to have positive outcomes, but also had the fewest examples (n = 5). Spitzer et al. (2021) documented policy changes that utilised the density-dependent aspects of competition to control moose *Alces alces* populations by promoting the protection of key vegetation and herbivore populations. Conversely, interventions focused on protecting key species often had more negative outcomes. The directed protection of wolves *Canis lupus* in Italy in the late 1900s was met with many challenges, including continuing competition for both food and mates with feral domestic dogs *Canis familiaris* (Boitani, 1992).

2.5.3 Prediction 3: can we predict the outcomes of competition?

Our third prediction, that the outcomes of some characteristics of the competition process would be measurably different from other characteristics, was largely unsupported. Understanding which species traits and other aspects of the competition process (such as the number of species involved in interactions) are associated with more or less negative post-intervention outcomes may become increasingly important as the effects of environmental change become more detrimental (Rollins & Benard, 2020). This is because competition is likely to have more unexpected and negative outcomes with these changes (Rollins & Benard, 2020). Therefore, theoretically, we want to be able to predict the future outcomes of competition on conservation interventions based on the differences in how characteristics are currently associated with competitive outcomes. However, our results revealed only one characteristic that was statistically more negative than others, and that was membership in the trophic guild of ‘omnivores’. It is possible that omnivores, as dietary generalists, would be at a competitive disadvantage in obtaining food if co-occurring with foragers that specialise in exploiting food types such as green plants or animal prey (Barnes & Murphy, 2023). However, the large variance around the mean for this trait suggests that it would not be a reliable predictor of competition outcomes (Fig 2-4). Additionally, as we could not determine whether the authors were discussing “true” or “relative” omnivores, we cannot determine the importance of omnivory for competitive species interactions (Gillespie, 2017). For example, the successful breeding of the omnivorous ferruginous duck *Aythya nyroca* in north-eastern Algeria is impacted primarily by interspecific competition for nesting space rather than competition for food (Loucif et al., 2021).

Some trends that we had expected to find were not significant, such as interspecific competition having greater negative effects than intraspecific competition as it is more likely to result in species declines (Fig 2-4) (Bronstein & Loya, 2014). This trend was observed in some articles, such as the study by Bronstein & Loya (2014), which found that interspecific competition dictated the presence and exclusion of coral species, whereas intraspecific competition affected the growth of individual corals. However, even in this case, the results showed that both forms of competition had negative effects, and the differences in strength between them were not significant (Bronstein & Loya, 2014).

Some characteristics were not consistently associated with either a positive or negative outcome after a conservation intervention. Two articles addressing the same characteristic (for example, interference competition) would often have opposite outcomes, even when both examples had undergone the same conservation intervention. Santosa et al. (2012) found that co-existence between leaf monkeys *Presbytis rubicunda* and white-bearded gibbons *Hylobates albibarbis* in the Cabang Panti Research Station in west Kalimantan likely resulted from avoidance of interference competition through dietary and spatial segregation tactics, which were dependent on the availability of resources, and did not substantially disadvantage either species. In contrast, Liu et al. (2020) found that, within a panda-specified protected area, competition between giant pandas and cattle displaced pandas into poor-quality habitats. Such disparate outcomes may be a result of one situation where the species have either co-existed or co-evolved over long periods, therefore leading to neutral to positive outcomes in their association, compared to another situation involving a native species and a recently introduced competitor species (Liu et al., 2020; Santosa et al., 2012).

Our analyses indicate that it would be difficult to use the assessed characteristics of competing species and other characteristics of the competition process to predict future outcomes of conservation interventions. One reason for this is that these characteristics were not well reported in the literature. Many articles did not mention mechanisms of competition, the trophic guild of the interactants, or other potentially important information (Hart et al., 2018). For example, researchers did not always consider the mechanism of competition to be important, and therefore it was often not mentioned. Additionally, different combinations of the characteristics we assessed can produce different outcomes, demonstrating how individualist and situational the outcomes of competitive interactions can be. For example, in studies of interspecific competition, an article describing exploitative competition may find that it drives species declines (Lioy et al., 2016), while another that focuses on interference competition may find coexistence (Santosa et al., 2012).

2.5.4 Management Recommendations

Despite competition often producing negative outcomes for species in ecosystems and being a key factor in structuring ecological communities, it is rarely considered a process to be monitored in conservation interventions. This suggests that the outcomes of conservation will often be unpredictable, as found by Oro et al. (2009). We suggest some key approaches to avoid or reduce unforeseen and potentially perverse consequences. For example, monitoring and research prior to the implementation of conservation interventions may reveal the most likely potential impacts of a change in an ecological community or even the broader ecosystem from active interventions, and can also create a baseline measure to monitor any variations after the implementation of passive interventions, such as by assessing the historical associations of species (e.g., co-occurrence analysis) (Geary et al., 2019; Heinen et al., 2020; Rayan & Linkie, 2016). Several articles in this review used co-occurrence analysis as a way of measuring occupancy in place of observing competition, especially within predator guilds (Rayan & Linkie, 2016; Steinmetz et al., 2011; Tian et al., 2019). For example, in Malaysia, tigers *Panthera tigris*, leopards *Panthera pardus*, and dholes *Cuon alpinus* co-occur to different degrees depending on the level of active protection they receive in reserves, with dholes not co-existing with the other two species within a reserve with a higher degree of restriction in human activity, potentially to avoid higher risk of competition and/or intraguild predation (Rayan & Linkie, 2016).

Investigations of trophic food webs provide another method for modelling ecological associations using historical and current data from managed ecosystems, but they also often include both direct and indirect interactions among species that can complicate interpretation (Endrédi et al., 2018). However, the role of competition in the maintenance of trophic food webs, while potentially important, has been under-investigated (Endrédi et al., 2018; Scoleri et al., 2020). Competition can influence the densities of species in different trophic levels, especially in predator guilds, which can have flow-on effects for species in lower trophic levels, such as prey species (Endrédi et al., 2018). Given the information on the nature and direction of ecological relationships they provide, trophic webs could be used profitably to direct conservation efforts. Bamber *et al.* (2020), for example, demonstrated that restored populations of pine martens *Martes martes* could control invasive grey squirrel *Sciurus carolinensis* populations in the United Kingdom by utilising top-down trophic effects. However, trophic food webs require large amounts of information to construct and monitor (Baker et al., 2017; Endrédi et al., 2018). In long-term managed areas, trophic webs can be constructed using long-term abundance time series and pre-existing knowledge of interactions (Baker et al., 2017). In poorly managed or newly established reserves, this depth of knowledge is lacking, making trophic food webs difficult to construct (Endrédi et al., 2018). However, emerging machine learning approaches such as random forest analysis provide means by which interactions can be predicted even in the absence of complete empirical data and may prove useful in generating trophic webs that can reliably predict the outcomes of conservation interventions (Llewelyn et al., 2023).

Predictive modelling using other approaches can also be used to forecast outcomes and assist in planning conservation interventions (Baker et al., 2017; Balme et al., 2009; Bode et al., 2015). For example, Bode et al. (2015) demonstrated, using dynamic control theory and predictive modelling, that predator-prey-ordered eradication schedules could be used to optimally eradicate invasive species from islands. In contrast, Mace & Mills (2017) found that in conservation-based biological control projects, it is far more difficult to predict the future and ongoing effectiveness of controls due to seasonal changes in density dependence. The lack of consistent knowledge of the different characteristics of the competition process, and their effects, makes the task of ongoing effective conservation more difficult. In the case of post-intervention ecosystems, as noted above, competition is both difficult and expensive to monitor (Balme et al., 2009; Bode et al., 2015; Hart et al., 2018). Therefore, we recommend that competitive interactions be considered and managed in post-intervention ecosystems if early monitoring shows species of conservation concern to be declining unexpectedly or with no other directly observable cause.

2.6 Conclusions

(1) Competition between animals is rarely monitored due to the difficulty of defining what is meant by competition, and the fact that it is hard to directly measure. Therefore, researchers often must rely on indirect methods, such as modelling and measuring co-occurrence to detect it.

(2) In cases where competition has highly negative and observable effects, for example, species becoming locally extinct or declining significantly, competition is much more likely to be directly investigated or managed in conservation interventions.

(3) One of the difficulties in identifying competition is that there are many influences on it, such as the type of resources and characteristics of species involved (e.g., the trophic guild they belong to). Apart from a weak result from omnivores, we did not detect any associated patterns that would allow researchers and managers to reliably predict the outcomes of competition in advance.

(4) Given the difficulties and associated costs of measuring and monitoring competition, we recommend that researchers use methods such as creating trophic food webs, random forest analysis, or other predictive models prior to conservation interventions being implemented. This will allow managers to identify competition as a likely factor if species begin declining with no other directly observable cause, and to have proactive plans in place for confirming and mitigating the effects of such competition.

2.7 References

Astete, S., Marinho-Filho, J., Kajin, M., Penido, G., Zimbres, B., Sollmann, R., Jácomo, A. T. A., Tôrres, N. M., & Silveira, L. (2017). Forced neighbours: Coexistence between jaguars and pumas in a harsh environment. *Journal of Arid Environments*, *146*, 27–34. https://doi.org/10.1016/j.jaridenv.2017.07.005

Baker, C. M., Gordon, A., & Bode, M. (2017). Ensemble ecosystem modelling for predicting ecosystem response to predator reintroduction. *Conservation Biology*, *31*(2), 376–384. https://doi.org/10.1111/cobi.12798

Balme, G. A., Slotow, R., & Hunter, L. T. B. (2009). Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biological Conservation*, *142*(11), 2681–2690. https://doi.org/10.1016/j.biocon.2009.06.020

Bamber, J. A., Shuttleworth, C. M., Hayward, M. W., & Everest, D. J. (2020). Reinstating trophic cascades as an applied conservation tool to protect forest ecosystems from invasive grey squirrels (*Sciurus carolinensis*). *Food Webs*, *25*, e00164. https://doi.org/10.1016/j.fooweb.2020.e00164

Barnes, E. E., & Murphy, S. M. (2023). Bottom-up and top-down pressures mediate competition between two generalist insects. *Ecology*, *104*(3), e3957. https://doi.org/10.1002/ecy.3957

Beggs, R., Pierson, J., Tulloch, A. I. T., Blanchard, W., Westgate, M. J., & Lindenmayer, D. (2019). An experimental test of a compensatory nest predation model following lethal control of an overabundant native species. *Biological Conservation*, *231*, 122–132. https://doi.org/10.1016/j.biocon.2019.01.003

Bode, M., Baker, C. M., & Plein, M. (2015). Eradicating down the food chain: Optimal multispecies eradication schedules for a commonly encountered invaded island ecosystem. *Journal of Applied Ecology*, *52*(3), 571–579. https://doi.org/10.1111/1365-2664.12429

Boitani, L. (1992). Wolf research and conservation in Italy. *The Study and Management of Small Populations*, *61*(2), 125–132. https://doi.org/10.1016/0006-3207(92)91102-X

Bozada, T., Borden, J., Workman, J., Del Cid, M., Malinowski, J., & Luechtefeld, T. (2021). Sysrev: A FAIR Platform for Data Curation and Systematic Evidence Review. *Frontiers in Artificial Intelligence*, *4*. https://www.frontiersin.org/articles/10.3389/frai.2021.685298

Brambilla, M., Scridel, D., Bazzi, G., Ilahiane, L., Iemma, A., Pedrini, P., Bassi, E., Bionda, R., Marchesi, L., Genero, F., Teufelbauer, N., Probst, R., Vrezec, A., Kmecl, P., Mihelič, T., Bogliani, G., Schmid, H., Assandri, G., Pontarini, R., … Chamberlain, D. (2020). Species interactions and climate change: How the disruption of species co-occurrence will impact on an avian forest guild. *Global Change Biology*, *26*(3), 1212–1224. https://doi.org/10.1111/gcb.14953

Bronstein, O., & Loya, Y. (2014). Echinoid community structure and rates of herbivory and bioerosion on exposed and sheltered reefs. *Journal of Experimental Marine Biology and Ecology*, *456*, 8–17. https://doi.org/10.1016/j.jembe.2014.03.003

Brooks, M. E., Kristensen, K., Benthem, K. J. van, Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378–400.

Castillo-Alvino, H., & Marvá, M. (2020). The competition model with Holling type II competitive response to interfering time. *Journal of Biological Dynamics*, *14*(1), 222–244. https://doi.org/10.1080/17513758.2020.1742392

Chesson, P. (1994). Multispecies Competition in Variable Environments. *Theoretical Population Biology*, *45*(3), 227–276. https://doi.org/10.1006/tpbi.1994.1013

Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366.

Chesson, P. (2018). Updates on mechanisms of maintenance of species diversity. *Journal of Ecology*, *106*(5), 1773–1794. https://doi.org/10.1111/1365-2745.13035

Chesson, P., & Kuang, J. J. (2008). The interaction between predation and competition. *Nature; London*, *456*(7219), 235–238. http://dx.doi.org.virtual.anu.edu.au/10.1038/nature07248

Coppock, A. G., Gardiner, N. M., & Jones, G. P. (2016). Sniffing out the competition? Juvenile coral reef damselfishes use chemical cues to distinguish the presence of conspecific and heterospecific aggregations. *Behavioural Processes*, *125*, 43–50. Scopus. https://doi.org/10.1016/j.beproc.2016.02.001

Denny, C. K., Stenhouse, G. B., & Nielsen, S. E. (2018). Scales of selection and perception: Landscape heterogeneity of an important food resource influences habitat use by a large omnivore. *Wildlife Biology*, *2018*(1), wlb.00409. https://doi.org/10.2981/wlb.00409

Dickman, C. R. (1988). Body Size, Prey Size, and Community Structure in Insectivorous Mammals. *Ecology*, *69*(3), 569–580. https://doi.org/10.2307/1941006

Endrédi, A., Senánszky, V., Libralato, S., & Jordán, F. (2018). Food web dynamics in trophic hierarchies. *Ecological Modelling*, *368*, 94–103. https://doi.org/10.1016/j.ecolmodel.2017.11.015

Ferguson, N., White, C. R., & Marshall, D. J. (2013). Competition in benthic marine invertebrates: The unrecognized role of exploitative competition for oxygen. *Ecology*, *94*(1), 126–135.

Fox, B. J., & Pople, A. R. (1984). Experimental confirmation of interspecific competition between native and introduced mice. *Australian Journal of Ecology*, *9*(4), 323–334. https://doi.org/10.1111/j.1442-9993.1984.tb01370.x

Geary, W. L., Nimmo, D. G., Doherty, T. S., Ritchie, E. G., & Tulloch, A. I. T. (2019). Threat webs: Reframing the co-occurrence and interactions of threats to biodiversity. *Journal* *of Applied Ecology*, *56*(8), 1992–1997. Scopus. https://doi.org/10.1111/1365-2664.13427

Gillespie, D. R. (2017). Omnivory – A Flexible Feeding Strategy. In Reference Module in Life Sciences. Elsevier. https://doi.org/10.1016/B978-0-12-809633-8.12260-5

Guillemain, M., Fritz, H., & Duncan, P. (2002). The importance of protected areas as nocturnal feeding grounds for dabbling ducks wintering in western France. *Biological Conservation*, *103*(2), 183–198. https://doi.org/10.1016/S0006-3207(01)00120-3

Hart, S. P., Freckleton, R. P., & Levine, J. M. (2018). How to quantify competitive ability. *Journal of Ecology*, *106*(5), 1902–1909. https://doi.org/10.1111/1365-2745.12954

Heinen, J. H., Rahbek, C., & Borregaard, M. K. (2020). Conservation of species interactions to achieve self-sustaining ecosystems. *Ecography*, *43*(11), 1603–1611. https://doi.org/10.1111/ecog.04980

Jacquot, M., Tixier, P., Flores, O., Muru, D., Massol, F., Derepas, B., Chiroleu, F., & Deguine, J.-P. (2017). Contrasting predation services of predator and omnivore diversity mediated by invasive ants in a tropical agroecosystem. *Basic and Applied Ecology*, *18*, 31–39. https://doi.org/10.1016/j.baae.2016.09.005

Kassinis, N. I., Zotos, S., Charalambidou, I., Roulin, A., & Vogiatzakis, I. N. (2024). Competitive interactions of two sympatric raptors affecting their spatial distribution in an island environment. *Journal of Ornithology*. https://doi.org/10.1007/s10336-023-02124-1

Kuhnen, V. V., de Aguiar, M. A. M., Gonçalves, A. Z., & Setz, E. Z. F. (2017). Realized trophic niche driven by apparent competition: An example with marsupials. *Biotropica*, *49*(6), 832–837. https://doi.org/10.1111/btp.12468

Kumeh, E. M., & Omulo, G. (2019). Youth's access to agricultural land in Sub-Saharan Africa: A missing link in the global land grabbing discourse. *Land Use Policy*, *89*, 104210. https://doi.org/10.1016/j.landusepol.2019.104210

Lindenmayer, D. B., Blanchard, W., Evans, M. J., Beggs, R., Lavery, T., Florance, D., Crane, C., Smith, D., Siegrist, A., Lang, E., & Scheele, B. C. (2023). Context dependency in interference competition among birds in an endangered woodland ecosystem. *Diversity and Distributions*, *29*(4), 556–571. https://doi.org/10.1111/ddi.13680

Lioy, S., Mori, E., Wauters, L. A., & Bertolino, S. (2016). Weight operated see-saw feeding hoppers are not selective for red squirrels when greys are present. *Mammalian Biology*, *81*(4), 365–371. https://doi.org/10.1016/j.mambio.2016.03.008

Liu, Z.-X., Dayananda, B., Jeffree, R. A., Tian, C., Zhang, Y.-Y., Yu, B., Zheng, Y., Jing, Y., Si, P.-Y., & Li, J.-Q. (2020). Giant panda distribution and habitat preference: The influence of sympatric large mammals. *Global Ecology and Conservation*, *24*, e01221. https://doi.org/10.1016/j.gecco.2020.e01221

Llewelyn, J., Strona, G., Dickman, C. R., Greenville, A. C., Wardle, G. M., Lee, M. S. Y., Doherty, S., Shabani, F., Saltré, F., & Bradshaw, C. J. A. (2023). Predicting predator–prey interactions in terrestrial endotherms using random forest. *Ecography*, *2023*(9), e06619. https://doi.org/10.1111/ecog.06619

Loucif, K., Maazi, M. C., Houhamdi, M., & Chenchouni, H. (2021). Nest site selection and breeding ecology of the Ferruginous Duck (*Aythya nyroca*) in Algeria. *Global Ecology and Conservation*, *26*, e01524. https://doi.org/10.1016/j.gecco.2021.e01524

Mace, K. C., & Mills, N. J. (2017). Connecting natural enemy metrics to biological control activity for aphids in California walnuts. *Biological Control*, *106*, 16–26. https://doi.org/10.1016/j.biocontrol.2016.11.009

Maniscalco, J. M., Ostrand, W. D., Suryan, R. M., & Irons, D. B. (2001). Passive interference competition by glaucous-winged gulls on Black-Legged Kittiwakes: A cost of feeding in flocks. *The Condor; Waco*, *103*(3), 616–619.

Momanyi, C., Löhr, B., & Gitonga, L. (2006). Biological impact of the exotic parasitoid, *Diadegma semiclausum* (Hellen), of diamondback moth, *Plutella xylostella* L., in

Kenya. *Biological Control*, *38*(2), 254–263. https://doi.org/10.1016/j.biocontrol.2006.03.003

Navarro, C. J., Carilla, J., Acosta, O. O., Nieto, C., Ovejero, R., & Grau, H. R. (2023). Herbivore rewilding does not promote biodiversity in Argentine Andean peatlands. *Anthropocene*, *42*. Scopus. https://doi.org/10.1016/j.ancene.2023.100382

Nie, Y., Zhou, W., Gao, K., Swaisgood, R. R., & Wei, F. (2019). Seasonal competition between sympatric species for a key resource: Implications for conservation management. *Biological Conservation*, *234*, 1–6. https://doi.org/10.1016/j.biocon.2019.03.013

Nogués-Bravo, D., Simberloff, D., Rahbek, C., & Sanders, N. J. (2016). Rewilding is the new Pandora's box in conservation. *Current Biology*, *26*(3), R87–R91. https://doi.org/10.1016/j.cub.2015.12.044

O'Reilly-Nugent, A., Wandrag, E. M., Catford, J. A., Gruber, B., Driscoll, D., & Duncan, R. P. (2020). Measuring competitive impact: Joint-species modelling of invaded plant communities. *Journal of Ecology*, *108*(2), 449–459. https://doi.org/10.1111/1365-2745.13280

Oro, D., Pérez-Rodríguez, A., Martínez-Vilalta, A., Bertolero, A., Vidal, F., & Genovart, M. (2009). Interference competition in a threatened seabird community: A paradox for a successful conservation. *Biological Conservation*, *142*(8), 1830–1835. https://doi.org/10.1016/j.biocon.2009.03.023

R Core Team. (2021). *R: A Language and Environment for Statistical Computing* [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Rayan, D. M., & Linkie, M. (2016). Managing conservation flagship species in competition: Tiger, leopard and dhole in Malaysia. *Biological Conservation*, *204*, 360–366. https://doi.org/10.1016/j.biocon.2016.11.009

Retzer, V., Nadrowski, K., & Miehe, G. (2006). Variation of precipitation and its effect on phytomass production and consumption by livestock and large wild herbivores along an altitudinal gradient during a drought, South Gobi, Mongolia. *Journal of Arid Environments*, *66*(1), 135–150. https://doi.org/10.1016/j.jaridenv.2005.10.009

Rollins, H. B., & Benard, M. F. (2020). Challenges in predicting the outcome of competition based on climate change-induced phenological and body size shifts. *Oecologia*, *193*(3), 749–759. https://doi.org/10.1007/s00442-020-04705-w

Ropars, L., Dajoz, I., Fontaine, C., Muratet, A., & Geslin, B. (2019). Wild pollinator activity negatively related to honey bee colony densities in urban context. *PLOS ONE*, *14*(9), e0222316. https://doi.org/10.1371/journal.pone.0222316

Sale, P. F. (1982). Stock-Recruit Relationships and Regional Coexistence in a Lottery Competitive System: A Simulation Study. *The American Naturalist*, *120*(2), 139–159. JSTOR.

Sandor, M. E., Elphick, C. S., & Tingley, M. W. (2022). Extinction of biotic interactions due to habitat loss could accelerate the current biodiversity crisis. *Ecological Applications*, *32*(6). Scopus. https://doi.org/10.1002/eap.2608

Santosa, Y., Taqiuddin, Mustari, A. H., & Rahman, D. A. (2012). Cohabitation Study of the Leaf Monkey and Bornean White-Bearded Gibbons in Gunung Palung National Park, West Kalimantan. *HAYATI Journal of Biosciences*, *19*(3), 115–123. https://doi.org/10.4308/hjb.19.3.115

Scoleri, V. P., Johnson, C. N., Vertigan, P., & Jones, M. E. (2020). Conservation trade-offs: Island introduction of a threatened predator suppresses invasive mesopredators but eliminates a seabird colony. *Biological Conservation*, *248*, 108635. https://doi.org/10.1016/j.biocon.2020.108635

Spaak, J. W., Millet, R., Ke, P.-J., Letten, A. D., & De Laender, F. (2023). The effect of non-linear competitive interactions on quantifying niche and fitness differences. *Theoretical Ecology*, *16*(2), 161–170. Scopus. https://doi.org/10.1007/s12080-023-00560-6

Spitzer, R., Coissac, E., Felton, A., Fohringer, C., Juvany, L., Landman, M., Singh, N. J., Taberlet, P., Widemo, F., & P.G.M. Cromsigt, J. (2021). Small shrubs with large importance? Smaller deer may increase the moose-forestry conflict through feeding competition over Vaccinium shrubs in the field layer. *Forest Ecology and Management*, *480*, 118768. https://doi.org/10.1016/j.foreco.2020.118768

Steinmetz, R., Garshelis, D. L., Chutipong, W., & Seuaturien, N. (2011). The Shared Preference Niche of Sympatric Asiatic Black Bears and Sun Bears in a Tropical Forest Mosaic. *PLOS ONE*, *6*(1), e14509. https://doi.org/10.1371/journal.pone.0014509

Tian, C., Liao, P.-C., Dayananda, B., Zhang, Y.-Y., Liu, Z.-X., Li, J.-Q., Yu, B., & Qing, L. (2019). Impacts of livestock grazing, topography and vegetation on distribution of wildlife in Wanglang National Nature Reserve, China. *Global Ecology and Conservation*, *20*, e00726. https://doi.org/10.1016/j.gecco.2019.e00726

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M., & Zamora, R. (2015). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, *29*(3), 299–307. https://doi.org/10.1111/1365-2435.12356

Verhoef, H., & Morin, P. (2010). Community Ecology: Processes, Models and Applications. In *Community Ecology: Processes, Models, and Applications*. https://doi.org/10.1093/acprof:oso/9780199228973.001.0001

Westgate, M. J., Crane, M., Florance, D., & Lindenmayer, D. B. (2021). Synergistic impacts of aggressive species on small birds in a fragmented landscape. *Journal of Applied Ecology*, *58*(4), 825–835. https://doi.org/10.1111/1365-2664.13838

Wolfenden, A., Jones, C. G., Tatayah, V., Züel, N., & de Kort, S. R. (2015). Endangered pink pigeons treat calls of the ubiquitous Madagascan turtle dove as conspecific. *Animal Behaviour*, *99*, 83–88. https://doi.org/10.1016/j.anbehav.2014.10.023

Chapter 3 Environmental variables influence patterns of mammal co-occurrence following introduced predator control

3.1 Note

This chapter was published in *PLOS ONE* in November 2023;

Kanishka, A.M., Blanchard, W., Lavery, T.H., Robinson, N.M., Dexter, N., Dickman, C.R., MacGregor, C., Lindenmayer, D.B., 2023. Environmental variables influence patterns of mammal co-occurrence following introduced predator control. PLOS ONE 18, e0292919. https://doi.org/10.1371/journal.pone.0292919

3.2 Abstract

Co-occurring species often overlap in their use of resources and can interact in complex ways. However, shifts in environmental conditions or resource availability can lead to changes in patterns of species co-occurrence, which may be exacerbated by global escalation of human disturbances to ecosystems, including conservation-directed interventions. We investigated the relative abundance and co-occurrence of two naturally sympatric mammal species following two forms of environmental disturbance: wildfire and introduced predator control. Using 14 years of abundance data from repeat surveys at long-term monitoring sites in south-eastern Australia, we examined the association between a marsupial, the common brushtail possum *Trichosurus vulpecula*, and a co-occurring native rodent, the bush rat *Rattus fuscipes*. We asked: In a fox-controlled environment, are the abundances of common brushtail possums and bush rats affected by environmental disturbance and each other's presence?

Using Bayesian regression models, we tested hypotheses that the abundance of each species would vary with changes in environmental and disturbance variables. Additionally, we tested the hypothesis the negative association between bush rats and common brushtail possums was stronger than the association between bush rats and disturbance. Our analyses revealed that bush rat abundance varied greatly in relation to environmental and disturbance variables, whereas common brushtail possums showed relatively limited variation in response to the same variables. There was a negative association between common brushtail possums and bush rats, but this association was weaker than the initial decline and subsequent recovery of bush rats in response to the time since fire.

Using co-occurrence analysis, we can infer negative relationships in abundance between co-occurring species, but to understand the impacts of such associations, and plan appropriate conservation measures, we require more information on interactions between the species and environmental variables. Co-occurrence can be a powerful and novel method to diagnose threats to communities and understand changes in ecosystem dynamics.

3.3 Introduction

Environmental heterogeneity and inter-species interactions are key factors that influence the composition of ecological communities (Chesson, 2018; Godsoe et al., 2015; Stein et al., 2014). Communities develop through combinations of species associations and species' niche requirements (Stein et al., 2014), with niche availability and diversity often influencing the number and identity of species that co-occur (Furness et al., 2021). Habitats with high environmental heterogeneity can provide a greater diversity of niche spaces and promote high species richness (Stein et al., 2014). Inter-species interactions, such as competition, can similarly influence the assembly of communities and ecological networks and additionally influence population densities and species dominance (Yan & Zhang, 2016).

Species co-occurrence analysis is one approach to examine interactions between species in a community. Temporal and spatial co-occurrence patterns are often the product of a mixture of habitat attributes and inter-specific interactions (positive and negative) (Azeria et al., 2012; Tavella & Cagnolo, 2019). Negative interactions between species are likely to reduce their ability to co-occur. However, mechanisms such as environmental and behavioural segregation can mediate negative interactions, enabling co-occurrence, even between highly competitive species (Freilich et al., 2018; Gause, 1934; Godsoe et al., 2015). For example, the sympatric seabirds, the common murre *Uria aalge* and the razorbill *Alca torda*, partition their overlapping niches using spatial segregation and differences in foraging behaviour (Gulka et al., 2019). Similarly, desert rodents in North Africa use separate microhabitats for grazing and protection from predators, which are mediated by the floristic composition of the vegetation (Traba et al., 2016).

Habitats altered by environmental perturbations can, in turn, affect species' population sizes and ultimately disrupt established patterns of species co-occurrence and community structure. Changes to vegetation structure, for example, have been linked to changes in species diversity (Dexter et al., 2013; Zhou et al., 2020). Alterations in fire regimes and fire severity exemplify such impacts (Flannigan et al., 2013; Tavella & Cagnolo, 2019). Comparisons of burnt and unburnt sites in central Argentina showed that aggressive ant species became more dominant and competitive in burnt sites compared to unburnt sites (Tavella & Cagnolo, 2019).

The addition or removal of species from an ecological community can likewise have unexpected impacts on the abundance of other species and trigger trophic or ecological cascades within these communities (Lurgi et al., 2018). The recolonisation of Alaskan kelp forests by sea otters *Enhydra lutris* resulted in heavy depredation of sea urchins *Strongylocentrotus* spp. This caused urchin population declines that, in turn, released kelp from grazing pressure and led to dramatic changes in the composition of the broader kelp forest community (Estes & Duggins, 1995). Conversely, the reintroduction of Tasmanian devils *Sarcophilus harrisii* to Maria Island, Australia, resulted in the suppression of feral cats *Felis catus* but also the unexpected local extinction of the short-tailed shearwater *Ardenna tenuirostris* due to direct predation by Tasmanian devils (Scoleri et al., 2020).

The removal of predators (native or exotic) is one particular kind of modification that can lead to profound cascading ecosystem impacts, typically via unmediated increases in the abundance of herbivores (Dexter et al., 2013; Estes & Duggins, 1995). The dramatic population growth of large herbivores, such as deer and macropods, when released from predation, can have damaging effects on animal and plant communities through overgrazing, destruction of habitat, and increased competition (Foster et al., 2016; Iida et al., 2018). For example, increases in the abundance of Sika deer *Cervus nippon* in Japan altered the composition of dung beetle communities, in turn leading to cascading effects on plant growth, pollination, and ecosystem function (Iida et al., 2018).

By monitoring patterns of co-occurrence following predator removal, particularly selected pairwise relationships, we can make inferences about the ecological roles of predators, prey interactions, and cascading impacts on their environments (Freilich et al., 2018). As many interactions within ecological systems are difficult to observe and extensive datasets are often required to track them, co-occurrence patterns in communities with relatively few species can provide a simpler method of inferring these interactions and allow opportunities to initially observe the effects of environmental change. For example, co-occurrence was higher between two Neotropical marsupials *Didelphis aurita* and *Metachirus nudicaudatus* in the Brazilian Atlantic rainforest in the absence of top predators, which also altered their use of their habitat and resources (Kuhnen et al., 2017). Despite the importance of associations between co-occurring species for the maintenance of ecosystem integrity and functioning, how these associations change in relation to environmental change has received relatively limited attention.

In Australia, control of the introduced red fox *Vulpes vulpes*, a common predator of both common brushtail possums and bush rats (Banks, 1999; Dexter et al., 2007; Roberts et al., 2006), occurs over millions of hectares each year to achieve both conservation and agricultural production objectives (Saunders et al., 2010). Fox control has been conducted in Booderee National Park, south-eastern Australia, over the past 20 years, and the increase in abundance of common brushtail possums *Trichosurus vulpecula* during the same period is presumed to be a response to this (Lindenmayer et al., 2018). In contrast, the bush rat *Rattus fuscipes* has declined, but the drivers of this change remain unclear (Lindenmayer et al., 2018). Booderee National Park also has been subjected to several wildfires during this time, with significant effects on vegetation and temporal activity patterns of small vertebrates (Foster et al., 2016; Lindenmayer et al., 2008). Common brushtail possums and bush rats naturally co-occur and overlap in their potential diets and patterns of day-to-day activity (Callander, 2018; Cruz et al., 2012). A better understanding of associations between bush rats and common brushtail possums might enable us to identify the drivers of potential decline in the former species and the wider implications of invasive predator control (Fig 3-1).

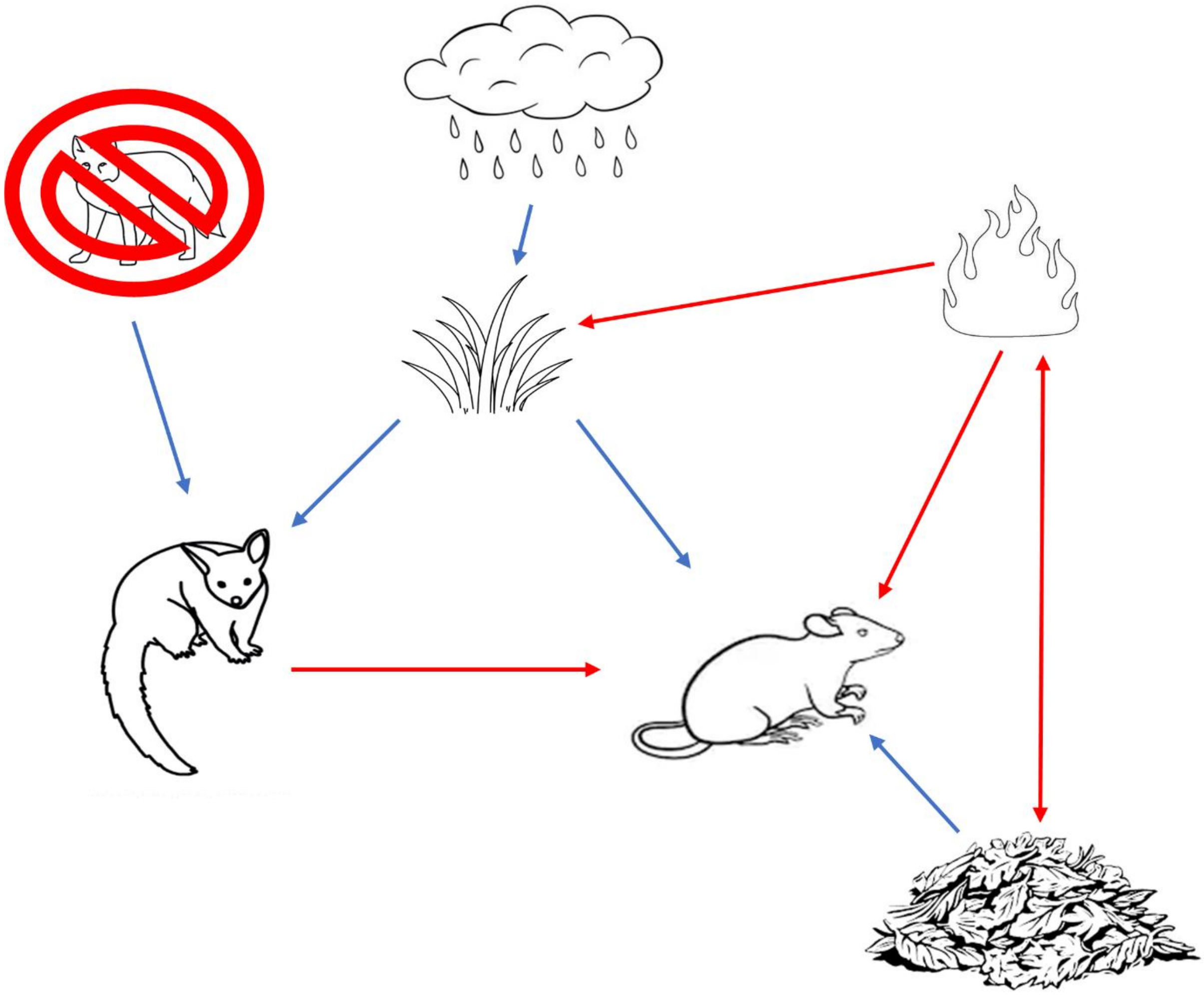


Figure 3-1. Conceptual diagram of our predicted ecosystem. Conceptual diagram of our predictions for how common brushtail possums and bush rats are affected by factors operating within Booderee National Park. Blue lines represent positive relationships, and red lines represent negative relationships. Understorey cover is represented with the image of grass, and leaf litter with the image of a pile of leaves.

We asked: 'In a fox-controlled environment, are the abundances of common brushtail possums and bush rats affected both by environmental disturbance and each other's presence?' Based on this question, we explored the patterns of occurrence of common brushtail possums and bush rats in response to each other and from the effects of wildfire disturbance using Bayesian regression models by addressing the following hypotheses:

1. Bush rat and common brushtail possum abundances change with variations in environmental conditions and disturbance

2. Bush rat abundance is negatively associated with an increase in common brushtail possum abundance

3. The association with common brushtail possums has a greater effect on bush rat abundance than the association with time since fire disturbance

We have adopted a correlative method (rather than a causative approach) to investigate these patterns. We did not specifically seek to identify the drivers that caused the changes in species abundance that we observed.

3.4 Methods

3.4.1 Ethics statement

This study was conducted in strict accordance with the recommendations in the *Australian Code for the Care and Use of Animals for Scientific Purposes*. The protocol was approved by the Animal Experimentation Ethics Committee at the Australian National University (Protocol Number: A2021_52).

3.4.2 Species information

The bush rat is a small, ground-dwelling rodent that ranges from 80 g to 200 g in weight (Callander, 2018). It prefers habitats with wet, moderately complex vegetation, has a small home range (0.1-0.4 ha), and has limited dispersal ability (Callander, 2018; Fordyce et al., 2016; Strauß et al., 2008).

The common brushtail possum is a medium-sized partly arboreal marsupial, ranging in size from 1.5 kg to 3.5 kg (Harper, 2006). It dens in hollows and feeds in the canopy and on the ground (Cruz et al., 2012; Isaac et al., 2008). Common brushtail possums show a preference for forest and woodland habitats (Cruz et al., 2012; Isaac et al., 2008). This is due to the prevalence of trees with denning hollows in those habitats (Cruz et al., 2012; Isaac et al., 2008). It has a relatively large home range, with past research suggesting a variation of 1.7 ha to 12.9 ha dependent on habitat conditions (Ball et al., 2005).

Both the bush rat and common brushtail possum are nocturnal, generalist omnivores, with a substantial potential overlap in their diets, consuming a large variety of plant matter, fungi, and invertebrates (Callander, 2018; Cruz et al., 2012).

3.4.3 Study location

We used data from long-term annual monitoring that commenced in 2003 in Booderee National Park (BNP), Jervis Bay Territory, south-eastern Australia. BNP is on Indigenous land and is jointly managed by the Wreck Bay Aboriginal Community and Parks Australia. The 6600 ha park has a temperate climate, with an average annual rainfall of 1213 mm, spread evenly across the year (BOM, 2021). Average temperatures range from 18.6-25.1°C in summer (January) to 9.9-16.1°C in winter (July) (BOM, 2021). BNP supports a range of vegetation types such as heathlands, wetlands, forests, and woodlands. Two major fires have occurred in BNP over the past 20 years (in 2003 and 2017), with each burning approximately half of the park. A fox baiting program has been in place in BNP since 1999 and was intensified in 2003 to reduce the deleterious impact of this introduced predator on native prey species (Dexter et al., 2013).

3.4.4 Data collection

We surveyed small and medium-sized mammals annually each summer for 14 years at 109 permanent sites starting in 2003, with another 20 sites added in 2008. The sites were surveyed along 100 m transects with 2 large (30 x 30 x 60 cm) cage traps at the beginning and end of transects, small (20 x 20 x 50 cm) cage traps every 20 m between the large cage traps, and 10 Elliott traps (10 x 10 x 30 cm; Elliott Scientific Equipment, Upwey, Victoria) every 10 m (Fig 3-2) (Lindenmayer et al., 2008, 2016). Approximately 50% of the sites were surveyed each year (with the other 50% being surveyed the next year), depending on weather conditions (Lindenmayer et al., 2016). We recorded the number of individuals of both species caught at each site in a given year.

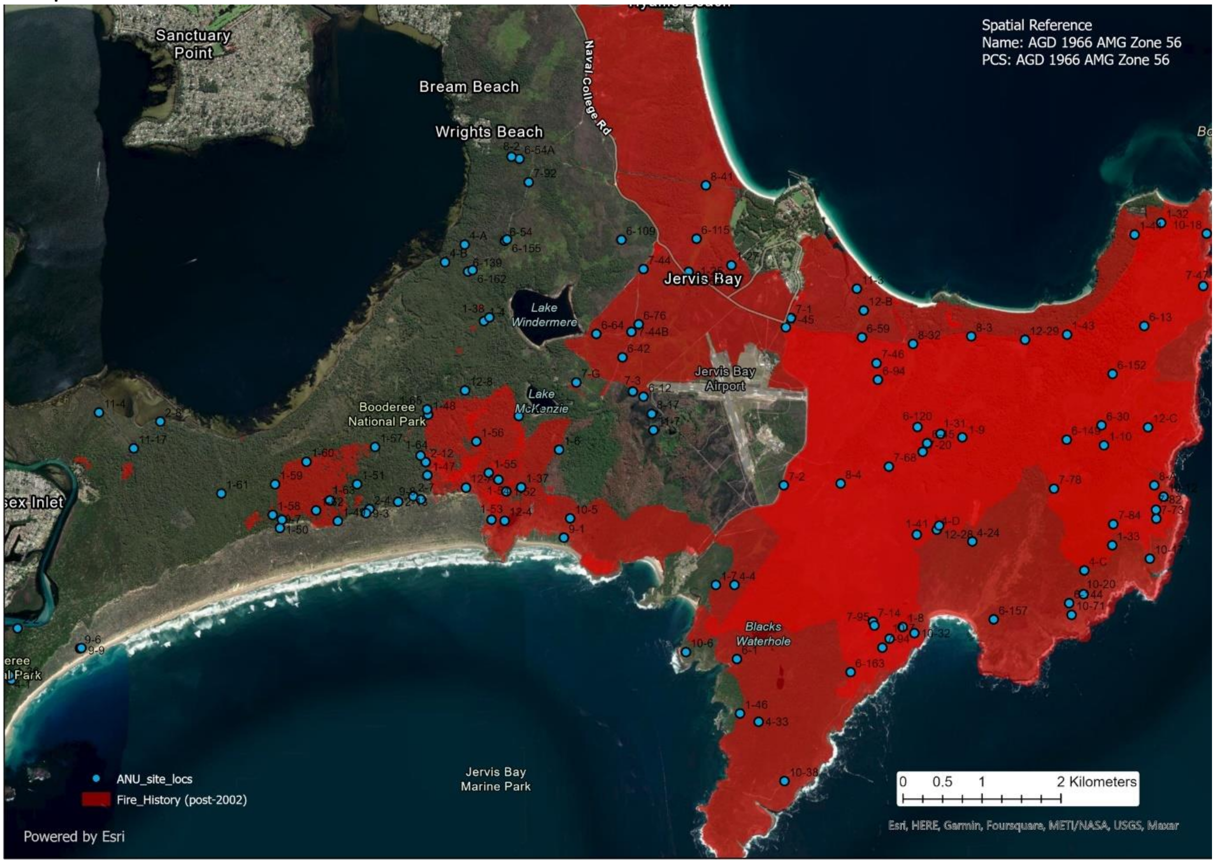


Figure 3-2. Locations of trapping sites at Booderee National Park, Jervis Bay Territory, south-eastern Australia. All green, vegetated areas are within the boundary of BNP. The red polygon represents areas of the park that were burnt after 2002, with the largest area burnt in December 2003. This map was developed using an ArcGIS Pro base map, 20 July 2023, Powered by Esri (Esri, 2022) (Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community) (url: https://cdn.arcgis.com/sharing/rest/content/items/30d6b8271e1849cd9c3042060001f425/resources/styles/root.json).

We collected data on environmental and disturbance variables at each of our 129 sites. These data included visual estimates of the percentage of understorey and leaf litter cover in four 1 x 1 m subplots within 20 x 20 m survey plots during semi-annual vegetation surveys (Lindenmayer et al., 2008). We selected understorey and leaf litter as representative variables of the primary bush rat habitat, which are also components of the common brushtail possum habitat (Callander, 2018; Cruz et al., 2012). We constructed a predictive model to fill the data gaps for those years when sites were not surveyed (see Macgregor et al., 2020). We used monthly rainfall averages collected at the nearby Point Perpendicular weather station for the trapping period at each site (BOM, 2021). We transformed both the rainfall and vegetation variables into quadratic functions using the poly() function in R (R Core Team, 2021).

We used data on fire occurrence recorded on-ground since 2003, and fire history data collected by Booderee National Park over the past 50 years (Foster et al., 2017), specifically the number of years since the last fire at a site. To minimise possible inaccuracies stemming from incorrect fire dates, or the occurrence of unreported fires, we grouped the number of years since fire into 10-year blocks (i.e., 0-10, 11-20, 21-30, 30+ years).

3.4.5 Statistical analysis

We used Bayesian regression models with a hurdle step to test the response of species abundances to the selected variables (i.e., bush rat and possum abundance, years since fire, vegetation variables, and rainfall) using the brms package ver. 2.16.3 (Bürkner, 2017, 2018; Feng, 2021) implemented in R (R Core Team, 2021). These regression models employed Markov Chain Monte Carlo simulations, with four chains and a warm-up of 1000 iterations before sampling another 1000 iterations. We assessed model convergence by ensuring all Rhat values were <1.1 (Bürkner, 2017, 2018). The hurdle step consisted of two components: the first modelled the presence/absence of the response variable, and the second, conditional on the species being present, modelled the conditional abundance using a zero-truncated Poisson (Feng, 2021). We combined these two components in an analysis of unconditional abundance (Feng, 2021).

We created a regression model with bush rats as the response variable, and a regression model with common brushtail possums as the response variable. Both regression models included time, understorey cover, leaf litter cover and rainfall as covariates within the conditional abundance component. These variables were included to assess the variation in bush rat and common brushtail possum abundances with environmental variables (H1). Years since fire was included in the conditional abundance and hurdle step of both regression models as an explanatory variable, as it is a prominent disturbance within BNP, and past research has indicated that fire has a significant effect on small vertebrate populations (Arthur et al., 2012). The other species was also input into the conditional abundance and hurdle step of both regression models (i.e., common brushtail possums into the bush rat model, bush rats into the common brushtail possum model) as an explanatory variable to assess the co-occurrence effect between species (H2). We also included the site as a random effect and used the log of the number of Elliott traps as a control for the bush rat models, and the number of open cage traps as a control for the common brushtail possum models. The control variables account for varying trapping efforts and were selected based on the main trap type that captures the relevant species (i.e., Elliott traps for bush rats, and cage traps for common brushtail possums).

We performed a model selection procedure for both regression models, based on the selection for explanatory variables only, which was across 10 variations of each model. We chose not to perform model selection on the covariates (i.e., the environmental variables) as we were testing variation in species abundance in relation to environmental fluctuations and did not predict significant changes in abundance in relation to these fluctuations. Using model selection, we assessed the relevancy of our exploratory variables to changes in species abundance (H3). The chosen model was the most parsimonious, which was based on the simplest model which was within 2 leave-one-out cross-validation (LOOIC) scores of the best fitting model.

We created ten variations of the regression models for each species and assessed the fit of each variation using LOOIC (Tables 3-1 and 3-2) (Vehtari et al., 2017). LOOIC estimates the out-of-sample predictive fit by measuring the predictive accuracy for each data point using a variation of the expected log pointwise predictive density equation (Vehtari et al., 2017). LOOIC was selected as the appropriate method over other model selection methods as it is informative and was created for Bayesian models (Burnham & Anderson, 2002; Vehtari et al., 2017).

Table 3-1. The bush rat model variations, and associated leave-one cross-validation (LOOIC) scores, are presented in order of best fit. The delta score (ΔLOOIC) in the final column represents the overall change in the LOOIC score from the best-fitting model. The model variations are presented with the first line of variables inputted to model condition abundance (starting with hu =) inputted into the hurdle step. Common brushtail possums (written as *T. vulpecula*) were inputted in the model using either abundance (represented with (A)) or the presence/absence (represented with (PA)). Model 4 (where common brushtail possums were only inputted into the conditional abundance step) was the most parsimonious model and therefore used in this study.

Model	Variables	LOOIC	ΔLOOIC
Model 6	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + *T.vulpecula*(A) + Elliotts	7322.674	0
	hu = Year + Years Since Fire + *T.vulpecula*(PA) + Elliotts		
Model 2	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + *T.vulpecula*(A) + Elliotts	7323.115	0.441
	hu = Year + Years Since Fire + *T.vulpecula*(A) + Elliotts		
Model 4	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + *T.vulpecula*(A) + Elliotts	7323.418	0.744
	hu = Year + Years Since Fire + Elliotts		
Model 9	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + *T.vulpecula*(A) + Elliotts	7332.744	10.07
	hu = Year + *T.vulpecula*(A) + Elliotts		
Model 8	Year + Rainfall + Understorey + Leaf Litter + *T.vulpecula*(A) + Elliotts	7341.191	18.517
	hu = Year + Years Since Fire + *T.vulpecula*(A) + Elliotts		
Model 3	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + Elliotts	7344.454	21.78
	hu = Year + Years Since Fire + *T.vulpecula*(A) + Elliotts		
Model 5	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + Elliotts	7346.091	23.417
	hu = Year + Years Since Fire + Elliotts		
Model 10	Year + Rainfall + Understorey + Leaf Litter + *T.vulpecula*(A) + Elliotts	7349.877	27.203
	hu = Year + *T.vulpecula*(A) + Elliotts		
Model 7	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + Elliotts	7350.136	27.462
	hu = Year + Years Since Fire + *T.vulpecula*(PA) + Elliotts		
Model 1	Year + Rainfall + Understorey + Leaf Litter + Elliotts	7371.065	48.391
	hu = Year + Elliotts		
Null Model	1	8826.685	1504.01
	hu = 1		

Table 3-2. The common brushtail possum model variations, and the associated leave-one-out cross-validation (LOOIC) scores, are presented in order of best fit. The delta score (ΔLOOIC) in the final column represents the overall change in the LOOIC score from the best-fitting model. The model variations are presented with the first line variables inputted to model conditional abundance, and the second line (starting with hu =) inputted into the hurdle step. Bush rats (written as *R. fuscipes*) were inputted into the model using either abundance (represented as (A)) or presence/absence (represented as (PA)). Model 10 (which modelled bush rats and common brushtail possums in both the conditional abundance and hurdle step but did not model years since fire) was selected as the most parsimonious model and therefore used in this study.

Model	**Variables**	**LOOIC**	**∆LOOIC**
Model 8	Year + Rainfall + Understorey + Leaf Litter + *R.fuscipes*(A) + Elliotts	1695.8	0
	hu = Year + Years Since Fire + *R.fuscipes*(A) + Elliotts		
Model 4	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + *R.fuscipes*(A) + Elliotts	1697.407	1.607
	hu = Year + Years Since Fire + Elliotts		
Model 10	Year + Rainfall + Understorey + Leaf Litter + *R.fuscipes*(A) + Elliotts	1697.537	1.737
	hu = Year + *R.fuscipes*(A) + Elliotts		
Model 6	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + *R.fuscipes*(A) + Elliotts	1699.235	3.435
	hu = Year + Years Since Fire + *R.fuscipes*(PA) + Elliotts		
Model 9	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + *R.fuscipes*(A) + Elliotts	1699.804	4.004
	hu = Year + *R.fuscipes*(A) + Elliotts		
Model 2	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + *R.fuscipes*(A) + Elliotts	1700.491	4.691
	hu = Year + Years Since Fire + *R.fuscipes*(A) + Elliotts		
Model 5	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + Elliotts	1704.973	9.173
	hu = Year + Years Since Fire + Elliotts		
Model 3	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + Elliotts	1706.319	10.519
	hu = Year + Years Since Fire + *R.fuscipes*(A) + Elliotts		
Model 7	Year + Rainfall + Understorey + Leaf Litter + Years Since Fire + Elliotts	1707.678	11.878
	hu = Year + Years Since Fire + *R.fuscipes*(PA) + Elliotts		
Model 1	Year + Rainfall + Understorey + Leaf Litter + Elliotts	1709.066	13.266
	hu = Year + Elliotts		
Null Model	1	1765.325	69.525
	hu = 1		

3.5 Results

Of the ten bush rat models fitted, the most parsimonious model (Model 4) included an association with years since fire in both the hurdle step and in conditional abundance, while also demonstrating an association with common brushtail possums in conditional abundance (i.e., the change in abundance when species are present; Table 3-1). Of the ten common brushtail possum model variations fitted, the most parsimonious model (Model 10) included an association with bush rats in both the hurdle step and in conditional abundance but did not contain an association with years since fire (Table 3-2).

Our first hypothesis (H1) was that bush rat and common brushtail possum abundances would vary with changes in environmental and disturbance variables. We found that bush rat presence and abundance decreased over time (Table 3-3), whereas common brushtail possum presence increased over time, but abundance did not (Table 3-4). The lowest abundance of bush rats was in sites characterised by high and low percentages of leaf litter cover, approximately 50% understorey cover, in periods with high rainfall (Table 3-3). In contrast, the abundance of common brushtail possums did not vary significantly in response to the selected environmental variables, and they also demonstrated large variability (Table 3-4). Bush rat presence and abundance were lowest in the first ten years following a fire with subsequent increases in the following year blocks (Fig 3-2, Table 3-3). Conversely, years since fire was found to not be a relevant variable for common brushtail possums, based on the LOOIC scores.

Table 3-3. The results of the Bayesian regression for bush rat model 4 (which was selected as the most parsimonious model using the LOOIC score). m represents the posterior mean, SE represents the posterior standard error, and the lower and upper 95% CIs represent the lower and upper ranges of the 95% credible interval. 30+ years since fire is not presented in the table because it is assumed not to have a significant effect compared to the other years-since-fire categories (Bürkner, 2017). The results of the environmental variables (rainfall, understorey, and leaf litter cover) are quadratic effects, with the subscript "lower" representing the lower limits of the estimated value, and "upper" representing the upper limits of the estimated value. The results of the hurdle effects represent the probability that there are zero bush rats.

Variable	m	SE	Lower 95% CI	Upper 95% CI
Conditional Abundance				
Year	-0.09	0.01	-0.10	-0.08
$Rainfall_{lower}$	-2.58	0.48	-3.53	-1.65
$Rainfall_{upper}$	0.33	0.48	-0.61	1.25
$Understorey_{lower}$	-3.91	1.30	-6.53	-1.40
$Understorey_{upper}$	4.68	1.05	2.57	6.73
Leaf $Litter_{lower}$	0.66	1.82	-2.85	4.28
Leaf $Litter_{upper}$	-10.33	1.22	-12.75	-7.89
Years since $fire_{0-10}$	-0.41	0.12	-0.65	-0.17
Years since $fire_{11-20}$	-0.15	0.11	-0.37	0.07
Years since $fire_{21-30}$	-0.13	0.09	-0.31	0.04
T. vulpecula	-0.08	0.02	-0.11	-0.05
Elliott	0.66	0.04	0.59	0.74
Hurdle effects				
Year	0.21	0.02	0.16	0.26
Years since $fire_{0-10}$	1.29	0.48	0.36	2.26
Years since $fire_{11-20}$	0.44	0.49	-0.50	1.45
Years since $fire_{21-30}$	-0.73	0.81	-2.41	0.78
Elliott	-1.07	0.24	-1.56	-0.60

Table 3-4. The results of the Bayesian regression for common brushtail possum model 10 (which was selected as the most parsimonious model using the LOOIC scores). m represents the posterior mean, SE represents the posterior standard error, and the lower and upper 95% CIs represent the lower and upper ranges of the 95% credible interval. The results of the environmental variables (rainfall, understorey, and leaf litter cover) are quadratic effects, with the subscript “lower” representing the lower limits of the estimated value, and “upper” representing the upper limits of the estimated value. The results of the hurdle effects represent the probability that there are zero common brushtail possums.

Variable	**m**	**SE**	**Lower 95% CI**	**Upper 95% CI**
Conditional abundance				
Year	0.01	0.02	-0.04	0.05
$\text{Rainfall}_{\text{lower}}$	0.97	2.44	-3.85	5.73
$\text{Rainfall}_{\text{upper}}$	-1.13	2.90	-6.90	4.48
$\text{Understorey}_{\text{lower}}$	-12.03	4.69	-21.15	-2.89
$\text{Understorey}_{\text{upper}}$	-3.55	4.02	-11.50	4.35
$\text{Leaf Litter}_{\text{lower}}$	-5.10	5.64	-15.69	6.02
$\text{Leaf Litter}_{\text{upper}}$	4.56	3.44	-2.31	11.38
R. fuscipes	-0.06	0.02	-0.10	-0.02
Cages	0.03	0.01	0.01	0.04
Hurdle				
Year	-0.17	0.03	-0.23	-0.12
R. fuscipes	0.01	0.02	-0.03	0.06
Cages	-0.04	0.01	-0.06	-0.01

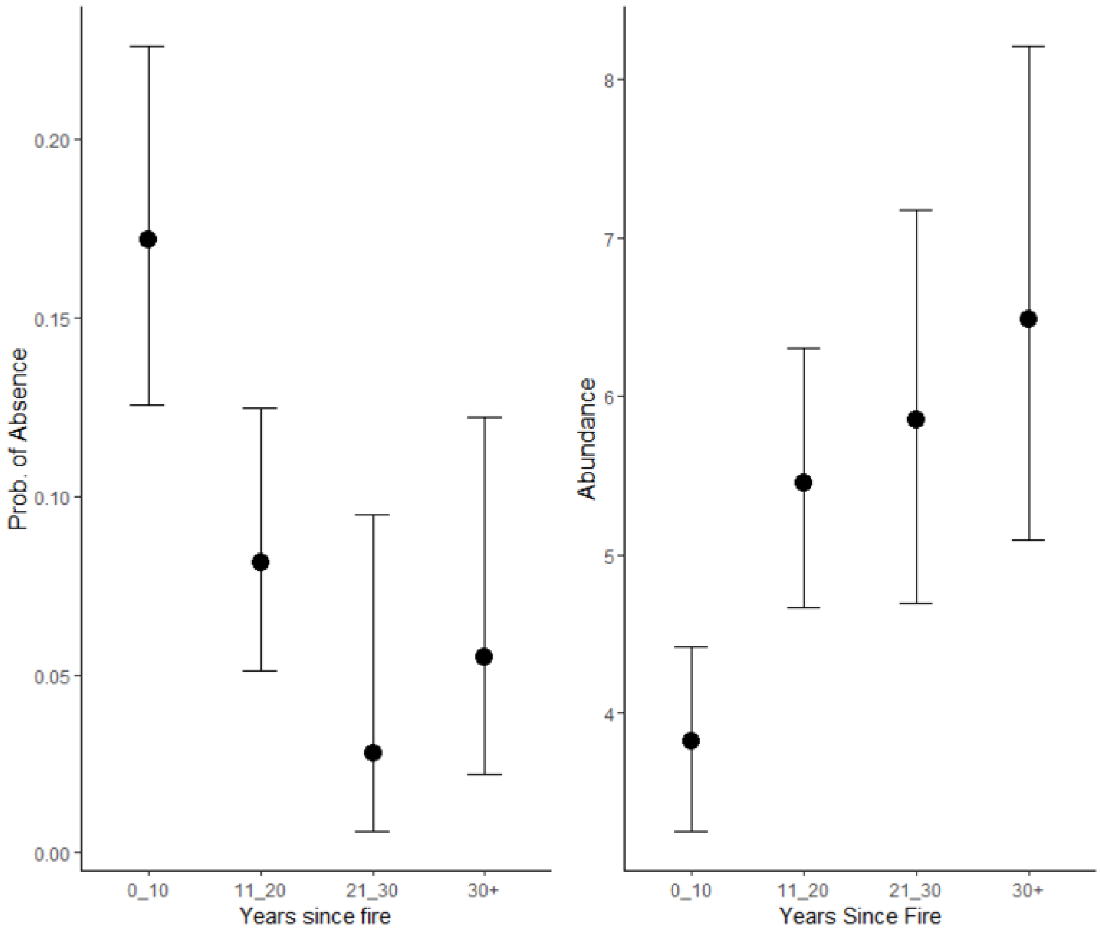


Figure 3-3. The associated change in the absence and abundance of bush rats in response to years since fire. The figure on the left shows the change in the probability of bush rats being absent, with data taken from the hurdle step of the model. The figure on the right shows the change in the unconditional abundance. Error bars represent the 95% credible intervals.

Our second hypothesis (H2) was that bush rat abundance would be negatively associated with an increase in common brushtail possum abundance. Our model demonstrated that in response to the increasing abundance of common brushtail possums, bush rat abundance declined (Fig 3-4, Table 3-3). In the common brushtail possum model, our results demonstrated a similar negative association between common brushtail possums and bush rats (Table 3-4, Appendix B.3).

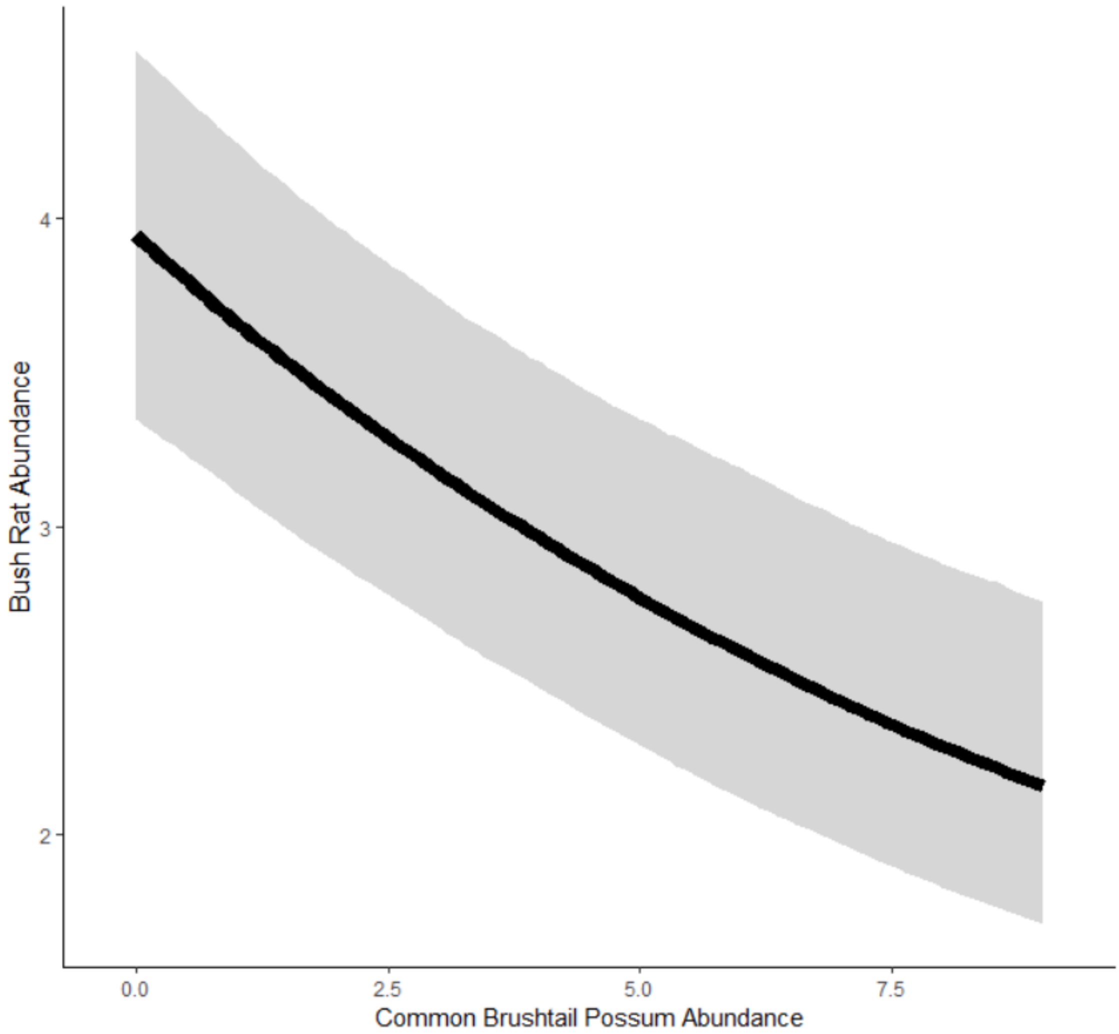


Figure 3-4. The unconditional change in the abundance of bush rats in response to the increasing abundance of common brushtail possums. The shaded regions represent the 95% credible intervals.

Our third hypothesis (H3) was that the association between bush rats and common brushtail possums would be more relevant than the association between bush rats and years since fire. Using the LOOIC scores, the model containing years since fire only was a better fit to our data than the model containing common brushtail possums only (Table 3-2).

3.6 Discussion

Species interactions and associations play important roles in influencing temporal and spatial co-occurrence and can ultimately shape the assembly of biotic communities (Azeria et al., 2012; Chesson, 2018). However, alterations to the environment can cause fundamental shifts in these associations and interactions with flow-on effects for the presence and abundance of individual species (Estes & Duggins, 1995; Flannigan et al., 2013). In this study, we predicted that an increased abundance of common brushtail possums would be associated with the decline of bush rats in Booderee National Park. To investigate this, we constructed three hypotheses about links between changes in environmental conditions and species abundances. We first investigated the role that changes in environmental conditions have on the abundance of bush rats and common brushtail possums (H1), with our results demonstrating that environmental conditions and the time since fire have large effects on the abundance of bush rats but not that of common brushtail possums.

We then investigated the strength of a negative association between common brushtail possums and bush rats (H2) and compared this association with that of the influence of time since fire (H3). Our results demonstrate that an increase in the abundance of common brushtail possums was associated with a reduction in bush rat abundance, with this relationship being observed in both bush rat and common brushtail possum models. However, our results did not support our third hypothesis. The decline of bush rats was better explained by our model containing years since fire only compared to our model containing common brushtail possums only. Collectively, our results suggest that while a negative association between common brushtail possums and bush rats exists, the decline of bush rats might be better explained by the influences of environmental and disturbance variables than by any interactions between the two species.

The negative association between common brushtail possums and bush rats could stem from two possible scenarios. First, the abundances of bush rats and common brushtail possums may be unrelated, with each shaped by individual species' habitat and/or condition preferences (MacKenzie et al., 2004; Steen et al., 2014). A common misstep with co-occurrence models is to assume that the associations between species are indicative of a species interaction when the models could be producing signals from how species are interacting differently or similarly to environmental conditions (Blanchet et al., 2020). Our results do show that understorey cover and time since fire are both strong indicators of variations in bush rat abundance, while only understorey cover was a weak indicator for common brushtail possums (Tables 3-3 and 3-4). Furthermore, research has demonstrated that disturbances like fire affect the two species to different extents. Bush rats have been recorded to be severely restricted by fire events and the associated habitat changes (Arthur et al., 2012; Lindenmayer et al., 2008), whereas the effect on common brushtail possums varies between minor negative influence to positive recoveries post-fire (Geary et al., 2023; Lindenmayer et al., 2008). Therefore, despite their extensive co-occurrence and overlap in some food and habitat resources, bush rats and common brushtail possums each most likely exploit different parts of these resource axes, and also exhibit different home range sizes and dispersal abilities (Tables 3-3 and 3-4) (Callander, 2018; Isaac et al., 2008).

Alternatively, a negative correlation between the abundances of common brushtail possum and bush rats could be a result of direct, negative interactions between the two species. While recent research has documented some predatory behaviours in common brushtail possums (Scoleri et al., 2020), we predict this negative relationship to be competitive due to the potential overlaps in habitat use, and the greater body of research documenting common brushtail possums' competitive behaviours (Callander, 2018; Cruz et al., 2012; Ruscoe et al., 2011). Ruscoe and associates (2011) demonstrated that common brushtail possums in New Zealand are competitively dominant to smaller mammals by documenting the competitive release of black rats *Rattus rattus* (a species of the same genus and with a similar trophic role as the bush rat) after the removal of possums. However, in contrast to our study, both these species are exotic to New Zealand. We further argue that the level of co-occurrence and potential competition between bush rats and common brushtail possums is likely mediated by habitat conditions as well as environmental conditions (e.g., wildfire events, and amount of rainfall).

Changes in species composition or relative abundance can have both direct and cascading influences on community structure (Dexter et al., 2013; Lurgi et al., 2018; Yan & Zhang, 2016). Evidence for this has been derived primarily from complete species removals or additions to communities but has also been deduced from studies of overabundance of herbivores (Iida et al., 2018; Lurgi et al., 2018). Introduced species can often increase levels of competition for resources, such as limited nesting hollows by birds, resulting in lower breeding success for native species (Charter et al., 2016). Many Australian mammals have been negatively impacted by introduced competitors (e.g., rabbits, deer) and predators (e.g., feral cats, red foxes), and these impacts have been documented to be among the leading causes of declines (Dexter et al., 2013; Woinarski et al., 2015). Range shifts can likewise increase competitive encounters. For example, the range expansion of barred owls *Strix varia* has increased interference competition with northern spotted owls *Strix occidentalis caurina*, to the latter's disadvantage (Van Lanen et al., 2011).

Our study highlights potential cascading effects from the loss of an introduced predator (Dexter et al., 2013; Estes & Duggins, 1995). The increased abundance of common brushtail possums is presumed to be a response to the deliberate population reduction of the red fox (Dexter et al., 2013). The negative correlation in the abundance of bush rats with common brushtail possums may be the product of resulting increased competition, especially given that common brushtail possums are possibly one of the main mammalian competitors (Cruz et al., 2012;

Ruscoe et al., 2011). Comparable results have been seen in manipulative field experiments whereby excluding a predator like the shorebird *Calidris pusilla* can have effects that cascade down through different trophic levels with implications for community structure (Cheverie et al., 2014).

The fox baiting program in BNP had effects that have cascaded through the park, many of which are not accounted for (Lindenmayer et al., 2018). There is strong evidence that the removal of foxes has allowed common brushtail possum and macropod populations to increase (Dexter et al., 2013; Lindenmayer et al., 2018). There is subsequent evidence that the increased macropod populations have altered vegetation structure, and potentially altered the fire regime (i.e., frequency/intensity), which consequently affects the animal community, as supported by our model (Dexter et al., 2013; Foster et al., 2016). Our model additionally supports the prediction that the declines of small mammals are related to the increase of common brushtail possum, and evidence suggests a similar response would result from increased macropod abundance (Dexter et al., 2013). These results demonstrate that an understanding of interspecific interactions is important for successful conservation. As in our study, interspecific interactions also had an influence on the semi-successful reintroduction of sea otters *Enhydra lutris* to the Canadian Pacific coastline (Fisher et al., 2014). The unsuccessful reintroductions arose from the unforeseen apparent competition with pinnipeds, which occupied areas of good quality foraging habitat to the detriment of otters (Fisher et al., 2014). Conversely, using the information on shared historical occupancy with the pine marten *Martes martes*, the restoration of this predator is being used to recover red squirrel *Sciurus vulgaris* populations through its role in controlling the invasive grey squirrel *Sciurus carolinensis* in the UK (Bamber et al., 2020).

3.7 Conclusion

An increased abundance of common brushtail possums was associated with a reduced abundance of bush rats. Our results indicate that species presence and interactions can have an important influence on species persistence. However, the strength of interactions may either be moderated by environmental effects or be more indicative of the different effects of environmental conditions on the two species and therefore managers must take both into account if the management of populations and ecological communities is to be effective. Furthermore, co-occurrence analysis can highlight unknown and potentially detrimental associations, which can be used as a starting point when diagnosing threats to community assemblages. Using co-occurrence models is one way to identify potential negative relationships between co-occurring species after an environmental change and/or following the population growth of one species. This information should be used to direct investigations into the impacts of such associations, by investigating the direct and indirect interactions between co-occurring species.

3.8 References

Arthur, A. D., Catling, P. C., & Reid, A. (2012). Relative influence of habitat structure, species interactions and rainfall on the post-fire population dynamics of ground-dwelling vertebrates. *Austral Ecology*, *37*(8), 958–970. https://doi.org/10.1111/j.1442-9993.2011.02355.x

Azeria, E. T., Ibarzabal, J., & Hébert, C. (2012). Effects of habitat characteristics and interspecific interactions on co-occurrence patterns of saproxylic beetles breeding in tree boles after forest fire: Null model analyses. *Oecologia*, *168*(4), 1123–1135.

Ball, S. J., Ramsey, D., Nugent, G., Warburton, B., Efford, M., Ball, S. J., Ramsey, D., Nugent, G., Warburton, B., & Efford, M. (2005). A method for estimating wildlife detection probabilities in relation to home-range use: Insights from a field study on the common brushtail possum (*Trichosurus vulpecula*). *Wildlife Research*, *32*(3), 217–227. https://doi.org/10.1071/WR03125

Bamber, J. A., Shuttleworth, C. M., Hayward, M. W., & Everest, D. J. (2020). Reinstating trophic cascades as an applied conservation tool to protect forest ecosystems from invasive grey squirrels (*Sciurus carolinensis*). *Food Webs*, *25*, e00164. https://doi.org/10.1016/j.fooweb.2020.e00164

Banks, P. B. (1999). Predation by introduced foxes on native bush rats in Australia: Do foxes take the doomed surplus? *Journal of Applied Ecology*, *36*(6), 1063–1071. https://doi.org/10.1046/j.1365-2664.1999.00463.x

Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, *23*(7), 1050–1063. Scopus. https://doi.org/10.1111/ele.13525

BOM. (2021). *Climate statistics for Australian locations*. http://www.bom.gov.au/climate/averages/tables/cw_068151.shtml

Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, *80*, 1–28. https://doi.org/10.18637/jss.v080.i01

Bürkner, P.-C. (2018). Advanced Bayesian Multilevel Modeling with the R Package brms. *The R Journal*, *10*(1), 395–411.

Burnham, K. P., & Anderson, D. R. (Eds.). (2002). Formal Inference From More Than One Model: Multimodel Inference (MMI). In *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (pp. 149–205). Springer. https://doi.org/10.1007/978-0-387-22456-5_4

Callander, M. (2018). *Translocation and reintroduction of native bush rats (Rattus fuscipes) into Sydney Harbour National Park: Restoring ecosystem function*. https://researchdirect.westernsydney.edu.au/islandora/object/uws%3A47378/

Charter, M., Izhaki, I., Ben Mocha, Y., & Kark, S. (2016). Nest-site competition between invasive and native cavity nesting birds and its implication for conservation. *Journal of Environmental Management*, *181*, 129–134. https://doi.org/10.1016/j.jenvman.2016.06.021

Chesson, P. (2018). Updates on mechanisms of maintenance of species diversity. *Journal of Ecology*, *106*(5), 1773–1794. https://doi.org/10.1111/1365-2745.13035

Cheverie, A. V., Hamilton, D. J., Coffin, M. R. S., & Barbeau, M. A. (2014). Effects of shorebird predation and snail abundance on an intertidal mudflat community. *Journal of Sea Research*, *92*, 102–114. https://doi.org/10.1016/j.seares.2014.03.011

Cruz, J., Sutherland, D. R., Martin, G. R., & Leung, L. K.-P. (2012). Are smaller subspecies of common brushtail possums more omnivorous than larger ones? *Austral Ecology*, *37*(8), 893–902. https://doi.org/10.1111/j.1442-9993.2011.02346.x

Dexter, N., Hudson, M., James, S., MacGregor, C., & Lindenmayer, D. B. (2013). Unintended Consequences of Invasive Predator Control in an Australian Forest: Overabundant

Wallabies and Vegetation Change. *PLOS ONE*, *8*(8), e69087. https://doi.org/10.1371/journal.pone.0069087

Dexter, N., Meek, P., Moore, S., Hudson, M., & Richardson, H. (2007). Population responses of small and medium sized mammals to fox control at Jervis Bay, southeastern Australia. *Pacific Conservation Biology*, *13*, 283–292. https://doi.org/10.1071/PC070283

Esri. (2022). *ArcGIS Pro 3.0.3* [Computer software]. Esri.

Estes, J. A., & Duggins, D. O. (1995). Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. *Ecological Monographs*, *65*(1), 75–100.

Feng, C. X. (2021). A comparison of zero-inflated and hurdle models for modeling zero-inflated count data. *Journal of Statistical Distributions and Applications*, *8*(1), 8. https://doi.org/10.1186/s40488-021-00121-4

Fisher, J. T., Pasztor, C., Wilson, A., Volpe, J. P., & Anholt, B. R. (2014). Recolonizing sea otters spatially segregate from pinnipeds on the Canadian Pacific coastline: The implications of segregation for species conservation. *Biological Conservation*, *177*, 148–155. https://doi.org/10.1016/j.biocon.2014.06.025

Flannigan, M., Cantin, A. S., de Groot, W. J., Wotton, M., Newbery, A., & Gowman, L. M. (2013). Global wildland fire season severity in the 21st century. *Forest Ecology and Management*, *294*, 54–61. https://doi.org/10.1016/j.foreco.2012.10.022

Fordyce, A., Hradsky, B. A., Ritchie, E. G., & Di Stefano, J. (2016). Fire affects microhabitat selection, movement patterns, and body condition of an Australian rodent (*Rattus fuscipes*). *Journal of Mammalogy*, *97*(1), 102–111.

Foster, C. N., Barton, P. S., Robinson, N. M., MacGregor, C. I., & Lindenmayer, D. B. (2017). Effects of a large wildfire on vegetation structure in a variable fire mosaic. *Ecological Applications*, *27*(8), 2369–2381. https://doi.org/10.1002/eap.1614

Foster, C. N., Barton, P. S., Sato, C. F., Wood, J. T., MacGregor, C. I., & Lindenmayer, D. B. (2016). Herbivory and fire interact to affect forest understory habitat, but not its use by small vertebrates. *Animal Conservation*, *19*(1), 15–25. https://doi.org/10.1111/acv.12210

Freilich, M. A., Wieters, E., Broitman, B. R., Marquet, P. A., & Navarrete, S. A. (2018). Species co-occurrence networks: Can they reveal trophic and non-trophic interactions in ecological communities? *Ecology*, *99*(3), 690–699. https://doi.org/10.1002/ecy.2142

Furness, E. N., Garwood, R. J., Mannion, P. D., & Sutton, M. D. (2021). Productivity, niche availability, species richness, and extinction risk: Untangling relationships using individual-based simulations. *Ecology and Evolution*, *11*(13), 8923–8940. https://doi.org/10.1002/ece3.7730

Gause, G. F. (1934). EXPERIMENTAL ANALYSIS OF VITO VOLTERRA'S MATHEMATICAL THEORY OF THE STRUGGLE FOR EXISTENCE. *Science (New York, N.Y.)*, *79*(2036), 16–17. https://doi.org/10.1126/science.79.2036.16-a

Geary, W. L., Tulloch, A. I. T., Ritchie, E. G., Doherty, T. S., Nimmo, D. G., Maxwell, M. A., & Wayne, A. F. (2023). Identifying historical and future global change drivers that place species recovery at risk. *Global Change Biology*, *29*(11), 2953–2967. https://doi.org/10.1111/gcb.16661

Godsoe, W., Murray, R., & Plank, M. J. (2015). The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography*, *38*(11), 1071–1079. https://doi.org/10.1111/ecog.01134

Gulka, J., Link to external site, this link will open in a new window, Ronconi, R. A., Link to external site, this link will open in a new window, & Davoren, G. K. (2019). Spatial segregation contrasting dietary overlap: Niche partitioning of two sympatric alcids during shifting resource availability. *Marine Biology*, *166*(9), 1–17. http://dx.doi.org/10.1007/s00227-019-3553-x

Harper, M. J. (2006). Home range and den use of common brushtail possums (*Trichosurus vulpecula*) in urban forest remnants. *Wildlife Research*, *32*(8), 681–687. https://doi.org/10.1071/WR04072

Iida, T., Soga, M., & Koike, S. (2018). Large herbivores affect forest ecosystem functions by altering the structure of dung beetle communities. *Acta Oecologica*, *88*, 65–70. https://doi.org/10.1016/j.actao.2018.03.003

Isaac, J. L., Valentine, L. E., & Goodman, B. A. (2008). Demographic responses of an arboreal marsupial, the common brushtail possum (*Trichosurus vulpecula*), to a prescribed fire. *Population Ecology*, *50*(1), 101–109. https://doi.org/10.1007/s10144-007-0057-1

Kuhnen, V. V., de Aguiar, M. A. M., Gonçalves, A. Z., & Setz, E. Z. F. (2017). Realized trophic niche driven by apparent competition: An example with marsupials. *Biotropica*, *49*(6), 832–837. https://doi.org/10.1111/btp.12468

Lindenmayer, D. B., Blanchard, W., MacGregor, C., Barton, P., Banks, S. C., Crane, M., Michael, D., Okada, S., Berry, L., Florance, D., & Gill, M. (2016). Temporal trends in mammal responses to fire reveals the complex effects of fire regime attributes. *Ecological Applications*, *26*(2), 557–573. https://doi.org/10.1890/15-0575

Lindenmayer, D. B., MacGregor, C., Welsh, A., Donnelly, C., Crane, M., Michael, D., Montague-Drake, R., Cunningham, R. B., Brown, D., Fortescue, M., Dexter, N., Hudson, M., Gill, A. M., Lindenmayer, D. B., MacGregor, C., Welsh, A., Donnelly, C., Crane, M., Michael, D., … Gill, A. M. (2008). Contrasting mammal responses to vegetation type and fire. *Wildlife Research*, *35*(5), 395–408. https://doi.org/10.1071/WR07156

Lindenmayer, D. B., Wood, J., MacGregor, C., Foster, C., Scheele, B., Tulloch, A., Barton, P., Banks, S., Robinson, N., Dexter, N., O'Loughlin, L. S., & Legge, S. (2018). Conservation conundrums and the challenges of managing unexplained declines of multiple species. *Biological Conservation*, *221*, 279–292. https://doi.org/10.1016/j.biocon.2018.03.007

Lurgi, M., Ritchie, E. G., & Fordham, D. A. (2018). Eradicating abundant invasive prey could cause unexpected and varied biodiversity outcomes: The importance of multispecies interactions. *Journal of Applied Ecology*, *55*(5), 2396–2407. https://doi.org/10.1111/1365-2664.13188

Macgregor, C., Blanchard, W., Stein, J., & Lindenmayer, D. (2020). Factors influencing the occurrence of the Southern Long-nosed Bandicoot (*Perameles nasuta* Geoffroy) during a population irruption and decline. *Austral Ecology*, *45*. https://doi.org/10.1111/aec.12930

MacKenzie, D. I., Bailey, L. L., & Nichols, James. D. (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*, *73*(3), 546–555. https://doi.org/10.1111/j.0021-8790.2004.00828.x

R Core Team. (2021). *R: A Language and Environment for Statistical Computing* [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Roberts, M. W., Dexter, N., Meek, P. D., Hudson, M., Buttemer, W. A., Roberts, M. W., Dexter, N., Meek, P. D., Hudson, M., & Buttemer, W. A. (2006). Does baiting influence the relative composition of the diet of foxes? *Wildlife Research*, *33*(6), 481–488. https://doi.org/10.1071/WR05009

Ruscoe, W. A., Ramsey, D. S. L., Pech, R. P., Sweetapple, P. J., Yockney, I., Barron, M. C., Perry, M., Nugent, G., Carran, R., Warne, R., Brausch, C., & Duncan, R. P. (2011). Unexpected consequences of control: Competitive vs. predator release in a four-species assemblage of invasive mammals. *Ecology Letters*, *14*(10), 1035–1042. https://doi.org/10.1111/j.1461-0248.2011.01673.x

Saunders, G. R., Gentle, M. N., & Dickman, C. R. (2010). The impacts and management of foxes *Vulpes vulpes* in Australia. *Mammal Review*, *40*(3), 181–211. https://doi.org/10.1111/j.1365-2907.2010.00159.x

Scoleri, V. P., Johnson, C. N., Vertigan, P., & Jones, M. E. (2020). Conservation trade-offs: Island introduction of a threatened predator suppresses invasive mesopredators but eliminates a seabird colony. *Biological Conservation*, *248*, 108635. https://doi.org/10.1016/j.biocon.2020.108635

Steen, D. A., McClure, C. J. W., Brock, J. C., Craig Rudolph, D., Pierce, J. B., Lee, J. R., Jeffrey Humphries, W., Gregory, B. B., Sutton, W. B., Smith, L. L., Baxley, D. L., Stevenson, D. J., & Guyer, C. (2014). Snake co-occurrence patterns are best explained by habitat and hypothesized effects of interspecific interactions. *Journal of Animal Ecology*, *83*(1), 286–295. https://doi.org/10.1111/1365-2656.12121

Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, *17*(7), 866–880. https://doi.org/10.1111/ele.12277

Strauß, A., Solmsdorff, K. Y., Pech, R., & Jacob, J. (2008). Rats on the run: Removal of alien terrestrial predators affects bush rat behaviour. *Behavioral Ecology and Sociobiology*, *62*(10), 1551–1558. https://doi.org/10.1007/s00265-008-0584-6

Tavella, J., & Cagnolo, L. (2019). Does fire disturbance affect ant community structure? Insights from spatial co-occurrence networks. *Oecologia*, *189*(2), 475–486. https://doi.org/10.1007/s00442-018-4320-2

Traba, J., Casals, P., Broto, F., Camprodon, J., Giralt, D., Guixé, D., Mechergui, R., Rios, A., Sales, S., Taull, M., Ammari, Y., Solano, D., & Bota, G. (2016). Coexistence and habitat partitioning at micro- and macro-scales of rodent species in a North African desert (Bou-Hedma National Park, Tunisia). *Journal of Arid Environments*, *131*, 46–58. https://doi.org/10.1016/j.jaridenv.2016.04.002

Van Lanen, N. J., Franklin, A. B., Huyvaert, K. P., Reiser, R. F., & Carlson, P. C. (2011). Who hits and hoots at whom? Potential for interference competition between barred and northern spotted owls. *Biological Conservation*, *144*(9), 2194–2201. https://doi.org/10.1016/j.biocon.2011.05.011

Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, *27*(5), 1413–1432. https://doi.org/10.1007/s11222-016-9696-4

Woinarski, J. C. Z., Burbidge, A. A., & Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(15), 4531–4540. https://doi.org/10.1073/pnas.1417301112

Yan, C., & Zhang, Z. (2016). Interspecific interaction strength influences population density more than carrying capacity in more complex ecological networks. *Ecological Modelling*, *332*, 1–7. https://doi.org/10.1016/j.ecolmodel.2016.03.023

Zhou, J., Zhou, L., & Xu, W. (2020). Diversity of wintering waterbirds enhanced by restoring aquatic vegetation at Shengjin Lake, China. *Science of The Total Environment*, *737*, 140190. https://doi.org/10.1016/j.scitotenv.2020.140190

Chapter 4 The effect of competitor presence on the foraging decisions of small mammals

4.1 Abstract

Competitive interactions between species can have marked effects on the diets and foraging behaviours of the interactants. Dominant competitors can constrain the foraging decisions of subordinate competitors, reducing the individual fitness of subordinates, and potentially driving their populations to low levels. Following a sustained population decline of the bush rat *Rattus fuscipes* in the presence of the speculatively competitively dominant common brushtail possum *Trichosurus vulpecula* at Booderee National Park in south-eastern Australia, we investigated whether possums affected the foraging decisions of bush rats. Using a manipulative feeding experiment, we predicted that bush rats would: (a) increase visits to baited sites where possums had restricted access to the bait, and (b) restrict visits to baited sites where possums had free access. We used camera traps to investigate visitation patterns and time spent foraging at 40 baited sites with two treatments, one that allowed full access by both species (full-access), and the other that attempted to prevent possum access (restricted-access). We also measured additional covariate factors that may influence visitation. Bush rats visited both treatments less when there were more possum visits. We also found that bush rats spent less time eating bait at sites regularly visited by possums, regardless of possums' access level. Our results indicate that negative interactions, such as competition, can restrict the ability of subordinate species to successfully forage, contributing to species declines.

4.2 Introduction

The foraging strategies of animals influence how they interact with their living and non-living environments (Corman et al., 2016; Denny et al., 2018). Foraging strategies include the decisions that individuals must make regularly about what to eat, when and where to locate food, the time spent foraging, and when to depart from a food source (Corman et al., 2016; Denny et al., 2018; Searle et al., 2005). These decisions can, therefore, influence habitat use and the local distributions of animals, as well as how foragers interact with co-occurring species (Barabás et al., 2016; Godsoe et al., 2015; Halliday & Morris, 2013). The influence of predation risk on foraging has been well-studied. Predators seek prey at times and in places where hunting is most likely to be successful (Denny et al., 2021; Pays et al., 2012). Prey species similarly anticipate and reduce the risk of encountering predators by selecting and departing from foraging patches when they perceive it to be safest to do so (Denny et al., 2021; Pays et al., 2012). If the foraging decisions of prey are constrained markedly by the presence of predators, individual fitness can be compromised, and this can translate to declines at the population level (Preisser et al., 2005).

Competition between species may have similarly large effects on individual foraging strategies and their outcomes. While individuals of a prey species may preferentially choose habitats with denser vegetation to avoid predation, this choice may also result in suboptimal foraging due to the presence of a dominant competitor (Halliday & Morris, 2013). For example, honeybees *Apis mellifera* readily forage on energetically profitable lavender flowers when on their own but forego this food source in the presence of bumble bees *Bombus* spp. to avoid aggressive encounters with this larger competitor (Balfour et al., 2015). Aggressive, or interfering, competitors often attack or chase other species from shared resources (King & Moors, 1979). An example is the Australian noisy miner *Manorina melanocephala*, which chases other native birds away from flowers and other profitable food resources (Beggs et al., 2020). Physical characteristics, such as body size, can influence the success of competitors (Rayan & Linkie, 2016). This is evident in many carnivore guilds, such as that comprising tigers *Panthera tigris*, dholes *Cuon alpinus*, and leopards *Panthera pardus*, with the latter two species showing temporal avoidance of the larger, more aggressive tiger (Rayan & Linkie, 2016). Similarly, the dingo *Canis dingo / familiaris* may constrain the place and time of foraging by smaller-bodied domestic cats *Felis catus* and red foxes *Vulpes vulpes* in Australia, through aggressive competition and, in extreme cases, by intraguild killing (Burrows et al., 2003; Moseby et al., 2012).

Avoidance behaviours are a common response to aggressive interactions (Astete et al., 2017; Barrull et al., 2014), especially by individuals of smaller or subordinate species. In situations where predation is unlikely, avoidance is often used as an indicator of interference (Périquet et al., 2016). For example, despite sharing many prey species, snow leopards *Panthera uncia* and common leopards segregate their use of habitats to avoid aggressive encounters (Lovari et al., 2013). These avoidance behaviours reduce the risks of interspecific aggression but can be detrimental, driving increased vulnerability of individuals to other predators, or reducing the quantity or quality of available food resources (Liu et al., 2020; Périquet et al., 2016). For instance, giant pandas *Ailuropoda melanoleuca* use poor-quality habitat and food to avoid exploitative competition with cattle (Liu et al., 2020). Avoidance can be both spatial or temporal, or a combination of both (Wereszczuk & Zalewski, 2015). For example, long-legged buzzards *Buteo rufinus* and short-toed eagles *Circaetus gallicus* in Israel partition shared habitat on multiple scales, including by spatial and temporal segregation of their foraging activity (Friedemann et al., 2016).

Interactions between species and how these affect the decisions made by individual foragers can be studied by direct observation in large or conspicuous species, such as noisy miners (Beggs et al., 2020; Lindenmayer et al., 2023), but for smaller or more cryptic species other methods are needed. The giving-up density (GUD) technique, which measures how long individuals spend at a food resource given certain conditions, is particularly useful in this respect (Brown, 1988; Denny et al., 2021; Hagy et al., 2017). Alternatively, carefully controlled experiments, such as laboratory-based studies or complete removal or addition experiments can be used to investigate interactions, like competition, around manipulated resource availability (Dickman, 2011; Karlsson et al., 2018). Many of these experiments require known or precisely measured levels of resource scarcity, or restriction of access for one or more interactants to an abundant food resource. We use the latter approach here.

In Booderee National Park, in south-eastern Australia, successful control of fox populations has contributed to changes in prey species abundance and composition, including considerable population growth of common brushtail possums *Trichosurus vulpecula* (hereafter ‘possum’) (Dexter et al., 2013; Lindenmayer et al., 2018). Possum foraging behaviour changes in response to how risky food sources are perceived to be, including the risk of predation and the quality of food, and possum foraging activity in Booderee is therefore likely to have expanded in response to fox control (Mella et al., 2015). Research into the impacts of possum population growth has uncovered a link with declines in small mammals, such as bush rats *Rattus fuscipes* (Kanishka et al., 2023; Lindenmayer et al., 2018). As both possums and bush rats are dietary generalists and often forage in similar habitats, we predict that food competition may be a mechanism that shapes this relationship. Here, we expect that bush rats will alter their activity in response to changes in possum activity. This expectation is based on research that some rodents will change their foraging behaviours when co-foraging with competitors for limited resources (Cordero et al., 2024). Possum aggression and behavioural dominance have also been recorded at bait stations elsewhere, exerting dominance over much larger species (Hickling & Day, 2024).

Using a manipulative experimental design, we investigated the potential influence of competition in shaping the foraging activity of these two native mammal species in Booderee National Park. In our proposed scenario, bush rats are the subordinate competitor, while possums are the dominant competitor. Our experiment was designed to investigate avoidance between this putatively dominant and subordinate pair of mammal species and to reveal foraging decisions made by the subordinate species in the presence and absence of the dominant species. We asked the overarching question: Does the presence of common brushtail possums reduce bush rats’ access to, and foraging activity at, sites with shared food resources? We predicted that bush rats would access food resources (bait) less at sites where possums have access, compared to sites where possums do not have access. We tested this prediction by investigating visitation patterns of the species, which we quantified as the number of times individuals visited baited sites and the time length of those visits. We conducted this investigation based on the following predictions:

1. Bush rats will increase visitation to sites where possums have restricted bait access, while possums will decrease visitation to sites with restricted bait access.

2. Bush rats will make fewer, shorter visits with increasing possum presence at full bait-access sites, but not at restricted bait-access sites.

3. Bush rats will spend less time eating with increasing possum presence at full bait-access sites, but not at restricted bait-access sites.

4. Both possums and bush rats will increase the number and length of visits with increasing time since the other species visited.

4.3 Method

4.3.1 Ethical note

This study was conducted in strict accordance with the recommendations in the Australian Code for the Care and Use of Animals for Scientific Purposes. The protocol was approved by the Animal Experimentation Ethics Committee at the Australian National University (Protocol Number: A2021_52). To ensure ethical standards, we performed a pilot study in 2020 to ensure the type of bait used, the garbage bins placed at each site, and wildlife cameras, would cause no harm or distress to the animals within the environment. The holes cut out of the garbage bins were additionally inspected to ensure there were no sharp points on which animals could injure themselves. Cameras were set with no flash to avoid startling animals.

4.3.2 Study location

Our experiment was conducted in March and April 2022 in Booderee National Park (BNP), a 6,000 ha protected area on the south coast of New South Wales, Australia (Fig 4-1). The Park is owned by the Wreck Bay Indigenous Community and is jointly managed by them and Parks Australia. The Park has a temperate climate, with an average rainfall of 1,213 mm (Bureau of Meteorology, 2022). However, due to the La Niña weather system occurring at the time of data collection, the Park experienced higher-than-average rainfall, including partial flooding, which occurred in the weeks prior to the experiment. The temperatures at the time of the experiment ranged from 13.5° to 26.6°C (Bureau of Meteorology, 2022). The Park has a heterogeneous environment, with vegetation types ranging from forests and woodlands to sedgelands and heathlands (Taws, 1998). The Park has experienced several wildfires in the last decades, with the most recent large fire occurring in 2017 (Kanishka et al., 2023).

Figure 4-1. Satellite map of Booderee National Park, Jervis Bay Territory, Australia. All green, vegetated areas are within the boundary of BNP. The blue circles identify the locations of the 40 supplementary feeding (bait) sites used in our experiment, with an identifying name in white next to each location (Esri, 2022).

4.3.3 Experimental setup

We established our experiment at 40 sites across BNP, selecting these by referring to trapping records from the immediate previous five years (Lindenmayer et al., 2008, 2016). The 40 sites were established in places selected from a long-term monitoring program established in 2002, and had annual mammal trapping records, with trapping occurring at each site every other year (Kanishka et al., 2023; Lindenmayer et al., 2008). The criteria for site selection were records of both bush rats and possums being trapped at the same site within the last five years, with preference given to the most recent trapping sessions or sites where both species had been trapped most regularly. We selected only those sites within woodland and forest vegetation types, as both species were caught consistently within these vegetation types.

We placed 60-litre black garbage bins upside down at 40 sites, with an entrance at the base that was modified to create two site conditions: full-access (entrance: 10 x 10 cm), where both species could easily gain access to bait placed inside the bin, and restricted-access (entrance: 5 x 5 cm), where only bush rats could gain easy access to bait. Specifically, the restricted-access sites were designed to prevent possums from accessing bait. To attract animals to enter the bins, we used 100 g of rodent pellets as bait, placed on a ceramic dish in the centre of the bin. We placed remote cameras facing the entrance to each bin on the bottom of a star picket (1 – 2 m above the ground depending on the slope of the ground) 2 metres away from the bin.

Cameras recorded animal activity for 28 days, and we collected data on the amount of bait taken at each site every other day (depending on site accessibility due to weather conditions). We measured the amount of bait taken by both weight (in grams) and visual assessment (as an estimate of percentage taken or spilt), to confirm visitation to the sites. We replenished the baits at least once a week, if more than 20 g was taken or if there was evidence of the bait going mouldy.

4.3.4 Camera data collection

We collected data on bin visitation from the remote cameras. We used two brands of cameras: Boly ScoutGuard Trail Cameras (Boly Media Communications Inc., California, USA) and Bushnell Core DS No Glow Trail Cameras (Bushnell Outdoor Products, Kansas, USA). We set the cameras to take photos only at night when both species were active and to take three photos in succession upon detecting movement, with a minimum of a 10-second gap between sets of photos.

We recorded information for periods when an animal was visible on camera, which we refer to as “visits”. A visit began when the animal was visible on camera and ended when it was seen exiting the site or there were more than five minutes between photos. During visits, we recorded the species’ identity, time of arrival and exits, and a brief description of the activities the animal was performing during this time. We recorded the time lengths of visits by subtracting the time of entrance from the time of exit. We categorised this description into one of three broad activities (Fig 4-2): the species was (1) within the site (i.e., visible on camera, but not interacting with the bait or bin), (2) interacting with the bin (i.e., sniffing/touching it, trying to move it, climbing on top, or entering/exiting the bin), or (3) eating the bait. We identified the activity "eating the bait" in possums when they visibly had their torso in the bin or head in the dish, and in bush rats when they had their head in the dish, or they were facing the camera and visibly holding/chewing on bait (Fig 4-2).

Figure 4-2. Example camera trap images of the categorised activities. (a) Bush rat within the bait site, but not interacting with the bins. (b) Possum within the site, but not interacting with the bins. (c) Bush rat interacting with the bin (specifically entering the bin). (d) Possum interacting with the bin (specifically jumping on top of the bin). (e) Bush rat eating bait, categorised by bush rat being inside the bin, visibly holding bait. (f) Possum eating bait, categorised by torso within the bin, and dish visibly being empty in

subsequent photos. Images (a) and (c) show examples of restricted-access bins, and images (d) and (e) show examples of full-access bins.

To quantify factors in addition to species presence that could affect foraging by bush rats, we collected information on topographic wetness, years since fire, and the broad vegetation type at each site, as well as estimated illumination from moonlight and rainfall each night. We used fire, rainfall and illumination measures as covariates based on previous research demonstrating their effects on small and medium-sized mammals in Australia (Kanishka et al., 2023; Taylor et al., 2023). We also used the covariates topographical wetness and broad vegetation type as 'stand-in', easily measured variables to represent the environmental heterogeneity of the park (Kopecký et al., 2021; Macgregor et al., 2020). Topographic wetness is an estimate of the relative wetness of a catchment and is used as a proxy of soil moisture and habitat productivity (Kopecký et al., 2021). We calculated a topographic wetness index (TWI) across the park for all sites from raster grids using GROCLIM (site productivity) (Xu & Hutchinson, 2011) and extracted using R version 4.4.1 (R Core Team, 2021). We categorised the broad vegetation type based on semi-annual vegetation surveys (Macgregor et al., 2020). The broad vegetation classifications come from long-used definitions within BNP to describe variations in the heterogenous environment, and model their effects (Taws, 1998). We calculated the number of years since the last fire at each site based on historical and on-ground records. We estimated illumination from moonlight, based on the moon phase, from fishing/tide records for the coast of BNP (Tides4Fishing, 2023). We extracted the daily rainfall data from the nearby Point Perpendicular weather station (Bureau of Meteorology, 2022).

4.3.5 Statistical analysis

To examine the effect of common brushtail possums on bush rat foraging activity, we constructed generalised linear mixed models (GLMMs) using the glmmTMB packager ver. 1.0.1 (Brooks et al., 2017) in R ver. 4.4.1 (R Core Team, 2021). Generalised linear mixed models quantify how continuous variables, such as count data, change in response to predictor variables, which can be either categorical or continuous, while taking random and predicted effects into account (Brooks et al., 2017). We used five different response variables (number of bush rat (*RF_count*) and possum (*TV_count*) visits within a night, length of time of bush rat (*RF_time*) and possum (*TV_time*) visits, and length of time bush rats ate bait (*RF_eat*)) (Table 4-1). We included TWI, years since fire, broad vegetation type, illumination, and rainfall as covariates and included sites as a random intercept effect to account for the correlation between repeated measures at the same sites. There was no animal activity at some sites on many nights, yielding zero-count data that could bias our models (Welsh et al., 1996). Therefore, we used zero-inflated models, which address excess zeros by calculating a probability of absence (Welsh et al., 1996) when modelling the number of visits (i.e., count data). The structure of zero-inflated results establishes the “probability of absence” for the response variable, showing a positive result when the response is absent, and a negative result when the response is present (Welsh et al., 1996). We also used the response variables as explanatory variables in the other models, to test associations between foraging activities between the species. The access condition for the sites (either full- or restricted-access) was also used as an explanatory variable. To compare model effects, we scaled all continuous variables to have a mean of zero and a standard deviation of one.

To select the most important variables for each model, we used Akaike’s Information Criterion for small sample sizes (AICc) (Burnham & Anderson, 2002) on all subsets of the five models (Table 4-1) using the dredge function in the MuMIn package ver. 1.43.17 (Bartoń, 2023). We chose the simplest model within two ΔAICc scores of the top-ranked model (Bartoń, 2023; Burnham & Anderson, 2002).

Table 4-1. Variables used in the five GLMMs examining the effect of common brushtail possums (*Trichosurus vulpecula*, TV) on bush rat (*Rattus fuscipes*, RF) foraging activity, including which models the variables were used in. M1-5 represents the model numbers, and the variable with 'response' is the response variable within the corresponding model in that column. The Category column explains whether we expected the variable to have a predicted effect on the response variable ('explanatory'), or if the variable was an indicator of site variation ('covariate'). Only explanatory variables were also used as response variables. The check marks within the model columns represent what variables are present in the full versions of the models, before model selection. The Variation and Type columns explain the data structure of the variable. Models 1 and 3 contain an additional zero-inflated step.

Name	Description	Category	M1	M2	M3	M4	M5	Variation	Type	Details
RF_count	Number of bush rat visits	Explanatory	Response		✓	✓		Temporal	Continuous	Count of the number of visits over a night. Scaled. Interaction with *bin.type*.
RF_time	Time length of bush rat visits	Explanatory		Response	✓	✓		Temporal	Continuous	Length of bush rat visits. Scaled. Interaction with *bin.type*.
TV_count	Number of possum visits	Explanatory	✓	✓	Response		✓	Temporal	Continuous	Count of the number of visits over a night. Scaled. Interaction with *bin.type*.
TV_time	Time length of possum visits	Explanatory	✓	✓		Response	✓	Temporal	Continuous	Length of possum visits. Scaled. Interaction with *bin.type*.
RF_eat_time	Time length of visits where bush rat eats bait	Response					Response	Temporal	Continuous	Time length of a visit where main activity is bush rat eating bait. Scaled. Only as a response variable in Model 5.
Time.Since.Rat	Time since the visit of a bush rat	Explanatory			✓	✓		Temporal	Continuous	Time since the last time the site was visited by a bush

										rat. Scaled. Interaction with *bin.type*.
Time.Since.Possum	Time since the visit of a possum	Explanatory	✓	✓			✓	Temporal	Continuous	Time since the last time the site was visited by a possum. Scaled. Interaction with *bin.type*
Bin.Type	The access type of the site	Explanatory	✓	✓	✓	✓	✓	Spatial	Categorical	Access type of site. Two categories: 1. Full-access 2. Restricted-access Interaction with all explanatory variables (except *first.visit*).
Broad.Veg.Type	The main type of vegetation within the site	Fixed Effect	✓	✓	✓	✓	✓	Spatial	Categorical	Two categories: 1. Forest 2. Woodland
Years.since.fire	Number of years since fire	Fixed Effect	✓	✓	✓	✓	✓	Spatial	Continuous	One value per site, calculated from the date of the last fire. Scaled.
Twi_twi	Topographical wetness index	Fixed Effect	✓	✓	✓	✓	✓	Spatial	Continuous	One value per site, calculated from spatial raster. Scaled.
Illumination	The nightly estimated level of light across the park	Fixed Effect	✓	✓	✓	✓	✓	Temporal	Continuous	One record for each night. Scaled.

Rainfall	Nightly rainfall amount	Fixed Effect	✓	✓	✓	✓	✓	Temporal	Continuous	Recorded the amount of rainfall for each night. Scaled.

4.3.5.1 Prediction One: Visitation differences in bush rats vs possums at restricted vs full-access sites

We evaluated differences in the number and length of visits of bush rats and possums between the two site conditions (full- and restricted access to food). We used a zero-inflated negative binomial error distribution for the zero-inflated models (number of visits, models 1 and 3), and a Gaussian error distribution for the other models (time length of visits, models 2 and 4). To do this, we measured the response in the visitation patterns of both species in the first four models, separately (number of visits and time lengths of visits for each species as response variables, models 1-4, Table 4-1) to the access condition and the covariates (TWI, broad vegetation type, years since fire, illumination, rainfall).

4.3.5.2 Prediction Two: Bush rat responses to possum presence

We evaluated the number and time length of bush rat visits in response to the number and time length of visits by possums between the two site conditions. For this, we used the models with bush rat numbers and bush rat visit time lengths as the response variables. We included two interactions: between the number of possum visits and site-access condition, and between the lengths of time of possum visits and site-access condition.

4.3.5.3 Prediction Three: The effect of possums on bush rats eating bait

We evaluated the time that bush rats spent at sites when their main activity was eating bait, and how this varied in response to the number and time length of possum visits. To do this, we constructed a GLMM where the response variable was the length of time of bush rat visits when eating bait (model 5, Table 4-1). This response variable was created by calculating a subset of the *RF_time* variable (Table 4-1), by only selecting the time length of visits when the activity of bush rats was “eating the bait”. We used a Gaussian error distribution for this model. The explanatory variables were the number and time lengths of possum visits, with an interaction with the site-access condition for both variables.

4.3.5.4 Prediction Four: Time since the last visit

We evaluated the number and time length of bush rats and possums at bait stations in response to the time since the last visit by the other species. To do so, we used the four models used in the first prediction but focused on a new explanatory variable (models 1-4, Table 4-1). The variable was the time since the last visit by a possum for the bush rat models and the time since the last visit by a bush rat for the possum models. We included an interaction with the access condition.

4.4 Results

Our sites were visited by bush rats 1,904 times and by possums 1,045 times over the 28 days of the experiment. The next most common visitors were macropods (n = 173), such as eastern grey kangaroos *Macropus giganteus* and swamp wallabies *Wallabia bicolor*. We also recorded visits from southern long-nosed bandicoots *Perameles nasuta* (n =41) and antechinuses *Antechinus* spp. (n = 38), and occasional visits from birds of various species (n = 5). There were single visits from an echidna *Tachyglossus aculeatus*, a carpet python *Morelia spilota*, and a red fox *Vulpes vulpes*. We were unable to identify 32 of the visitors because they were obscured by vegetation or we only had a partial view of them (e.g., some fur visible, but no distinct features). Overall, we experienced six camera malfunctions; five of these issues were fixed immediately (with only two nights of information lost per incident). One camera stopped recording after Day 11.

4.4.1 Prediction One: Visitation differences in bush rats vs possums at restricted vs full-access sites

Based on the model selection, the most parsimonious versions of models 1-4 included the covariates *rainfall* and *illumination*, but not *years since fire*, *TWI*, and the *Broad Vegetation Type* (Fig 4-3, Appendix C.1). We found no difference in the number or length of visits by either bush rats or possums in response to whether the sites offer full or restricted access to the food resource (bait) (Fig 4-3, Appendix C.2 – 5). There was no significant difference between the restricted and full access sites in any of the visitation metrics (number of visits, and time length of visits) for either bush rats or possums (Fig 4-3, Appendix C.2 – 5). High rainfall was negatively associated with the number of visits (Bush Rat: $m = -0.185$, $p < 0.001$, Possum: $m = -0.052$, $p < 0.001$) and the length of these visits (Bush Rat: $m = -18.561$, $p < 0.001$, Possum: $m = -45.256$, $p < 0.001$). We also found a positive association between rainfall and the probability of species absence for both bush rats and possums, based on the zero-inflation model (Bush Rat: $m = 0.531$, $p < 0.001$, Possum: $m = 1.175$, $p < 0.001$). High illumination from moonlight was negatively associated with the number of bush rat visits ($m = -0.185$, $p < 0.001$) and the probability that rats were present ($m = 0.096$, $p = 0.011$). However, this variable was positively associated with the amount of time bush rats spent at the site ($m = 7.621$, $p < 0.001$) (Fig 4-3). The number of possum visits was positively associated with increasing illumination ($m = 0.075$, $p < 0.001$). However, high illumination was also associated with a higher probability of absence, based on the zero-inflation model ($m = -0.524$, $p < 0.001$). Possums also decreased the amount of time spent at sites with increasing illumination (m = -68.393, $p < 0.001$) (Fig 4-3).

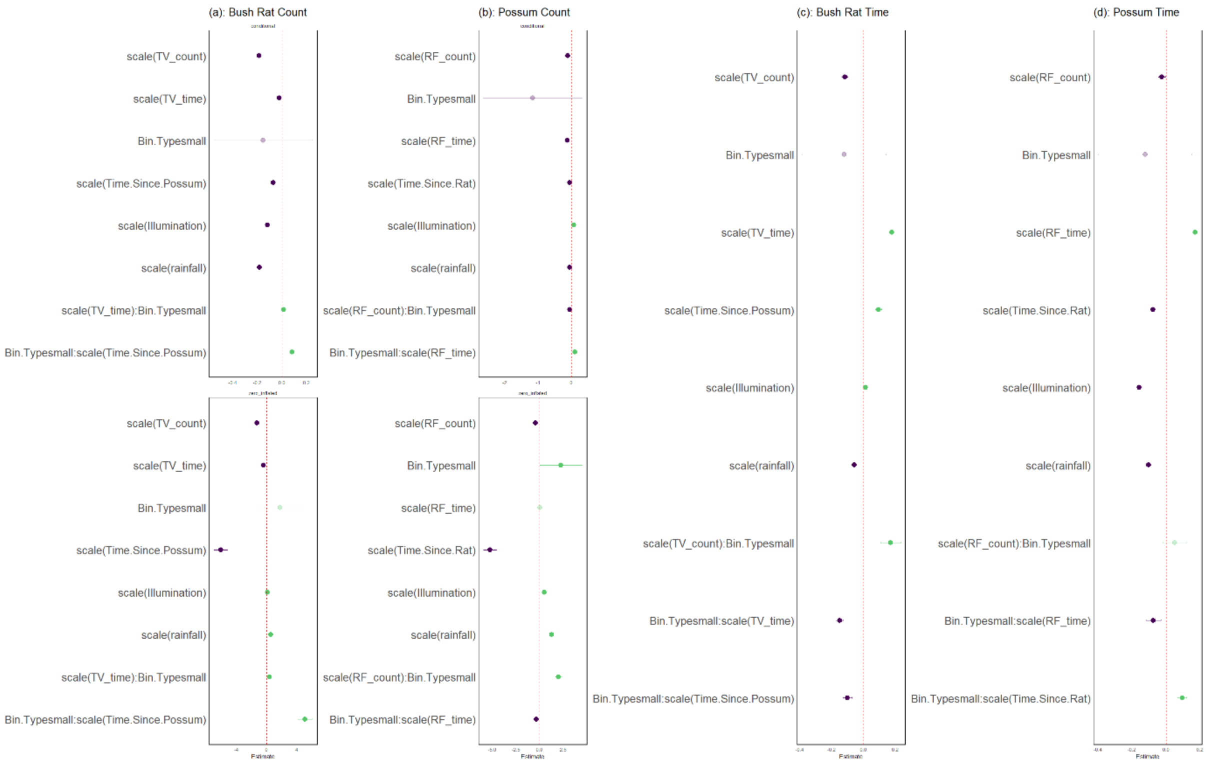


Figure 4-3. Forest plots of the best fitting subsets of models 1 to 4, showing the effect sizes and confidence intervals. Estimates in purple show negative effects and estimates in yellow show positive effects. Error bars are the 95% confidence intervals, and bars that cross the vertical prediction line demonstrate non-significant effects. (a) The results of the number of bush rat visits to bait sites, including the zero-inflation model (model 1). We found predominantly significant results with the exception of the Bin Type, which was non-significant. (b) The results of the number of possum visits to bait sites, including the zero-inflation model (model 3). We found predominantly significant results with the exception of the Bin Type and the time length of the bush rat visit variable (*RF_time*) in the zero-inflation model. (c) The results of the length of time (in seconds) of bush rat visits (model 2). We found predominantly significant results with the exception of the Bin Type. (d) The results of the length of time (in seconds) of possum visits (model 4). We found predominantly significant results with the exception of Bin Type and the interaction between the Bin Type and the number of bush rat visits (*RF_count*).

4.4.2 Prediction Two: Bush rat responses to possum presence

Based on model selection for models 1 and 2, the most parsimonious versions of both models included the possum variables *TV_time* and *Time.Since.Visitation* with an interaction with the *Bin.Type* variable (Fig 4-3). In model one (*RF_count*), the possum variable *TV_count* was included as an independent variable, with no interaction. In model two (*RF_time*), the possum variable *TV_count* was included with an interaction with *Bin.Type* (Fig 4-3). The number of bush rat visits was negatively associated with increasing numbers of possum visits, with no effect of access condition (m = -0.186, $p < 0.001$) (Fig 4-4a). The zero-inflation model showed that the probability of bush rat absence decreased with increasing possum visits (m = -1.262,

$p < 0.001$) (Fig 4-3a). The number of bush rat visits also decreased when possum visits were longer, especially at full-access sites (Fig 4-4b).

Bush rats spent longer at restricted-access bait sites that were visited by many possums, and less time at full-access bait sites that were visited by many possums (Fig 4-4c). The length of time bush rats and possums spent at sites was positively associated, with a more pronounced association at full-access sites (Fig 4-4d).

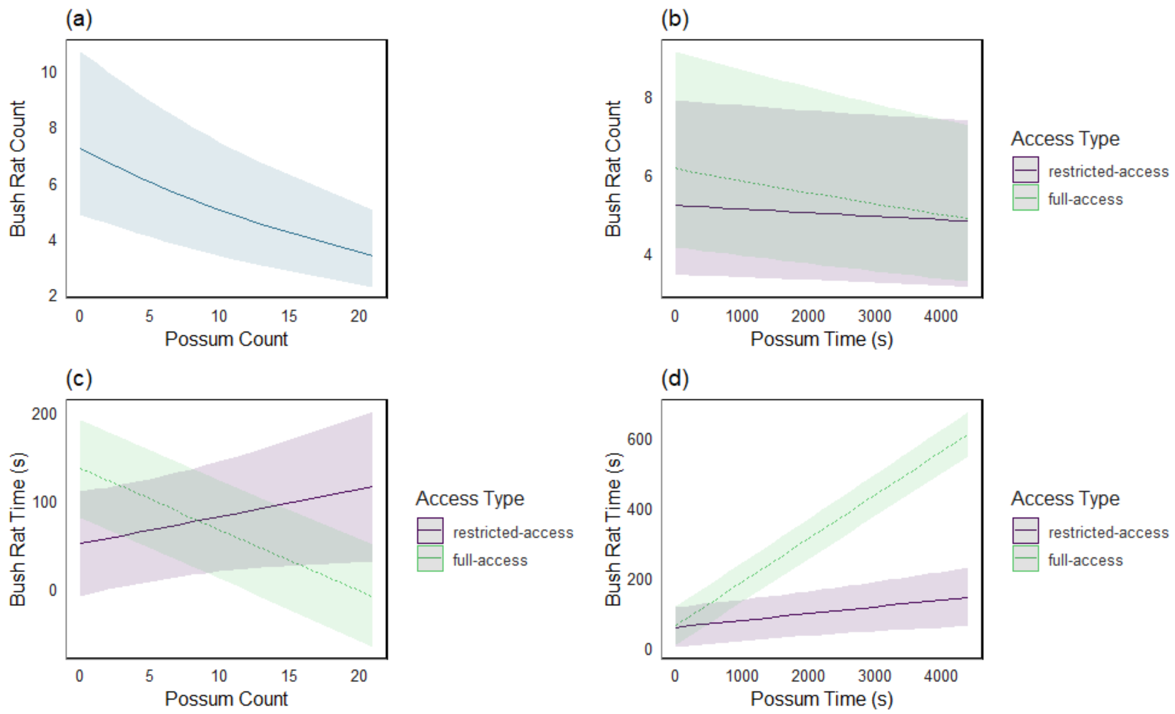


Figure 4-4. Conditional effects of the generalised linear mixed models. (a) The number of bush rat visits significantly decreased as the number of possum visits increased at bait sites. (b) The number of bush rat visits decreased as the length of time (in seconds) of possum visits increased, which was greater at full bait-access sites (in green) compared to restricted bait-access sites (in purple). (c) The length of time (in seconds) of bush rat visits increased as the number of possum visits increased at restricted bait-access sites (in purple) and decreased at full bait-access sites (in green). (d) The length of time (in seconds) of bush rat visits increased as the length of time (in seconds) of possum visits increased, with a greater increase at full bait-access sites (in green) compared to restricted bait-access sites (in purple). The shaded area represents the standard error.

4.4.3 Prediction Three: The effect of possums on bush rats eating bait

Based on the model selection results for model 5 (*RF_eat*), the covariates *rainfall* and *illumination* were found to have an effect, while *Broad.Vegetation.Type*, *years.since.fire* and *TWI* were excluded (Fig 4-3, Appendix C.1). The model also included the possum variables *TV_time* and *Time.Since.Possum* with an interaction with *Bin.Type* and the possum variable *TV_count* without the interaction (Appendix C.6, 7). Bush rat visits when their main activity was eating bait were shorter when more possums visited regardless of access condition (m = -0.075, p < 0.001) (Fig 4-5a). The length of bush rat visits, when they were recorded consuming bait, was positively associated with the overall length of possum visits. This association was more pronounced at full-access sites (Fig 4-5b).

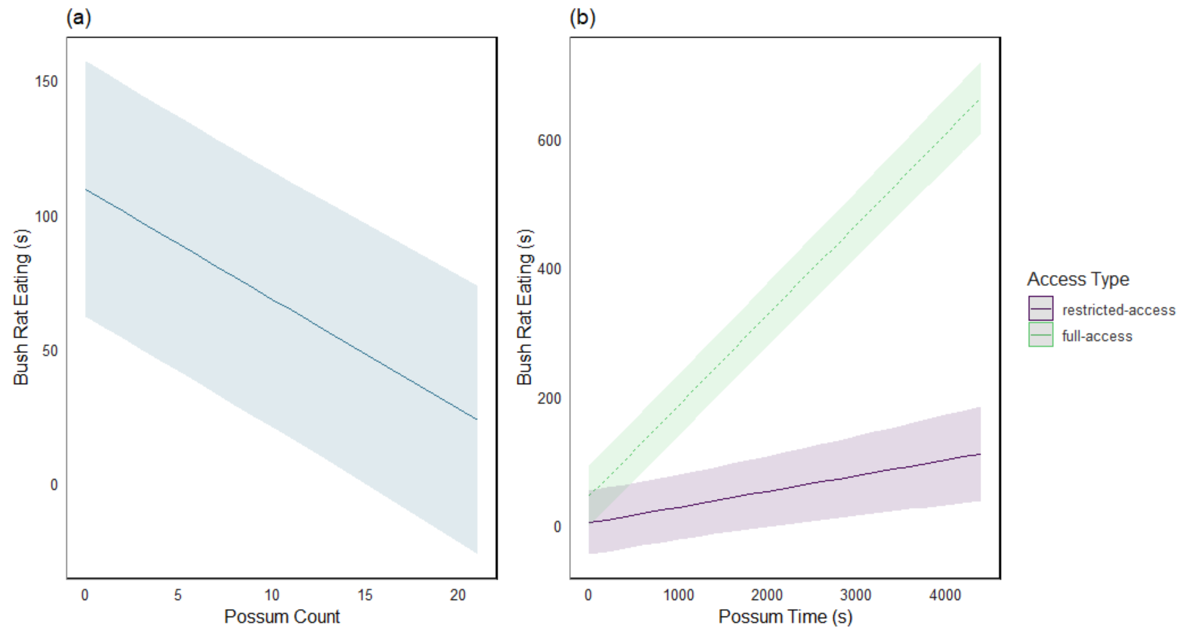


Figure 4-5. The amount of time (in seconds) bush rats spent at a site where their main activity was eating bait, based on the generalised linear mixed model (model 5). (a) the time decreases as the number of possum visits increases. (b) the time increases as the length of time (in seconds) of possum visits increased, which was greater at full bait-access sites (in green) compared to restricted bait-access sites (in purple). The shaded areas correspond to the standard error.

4.4.4 Prediction Four: Time since the last visit

Bush rats slightly increased their number of visits at restricted-access bait sites and decreased their number of visits at full-access bait sites, in response to an increase in the time since a possum visited the site (Fig 4-6a). Possums decreased their number of visits in response to an increase in the time since a bush rat visited, regardless of access type (Fig 4-6b). For bush rats, at full-access sites, the length of bush rat visit time increased with increasing time since a possum visited (Fig 4-6c). At restricted-access sites, overall bush rat visit time was low (Fig 4-6c). The opposite trend can be seen in the length of possums' visits (Fig 4-6d).

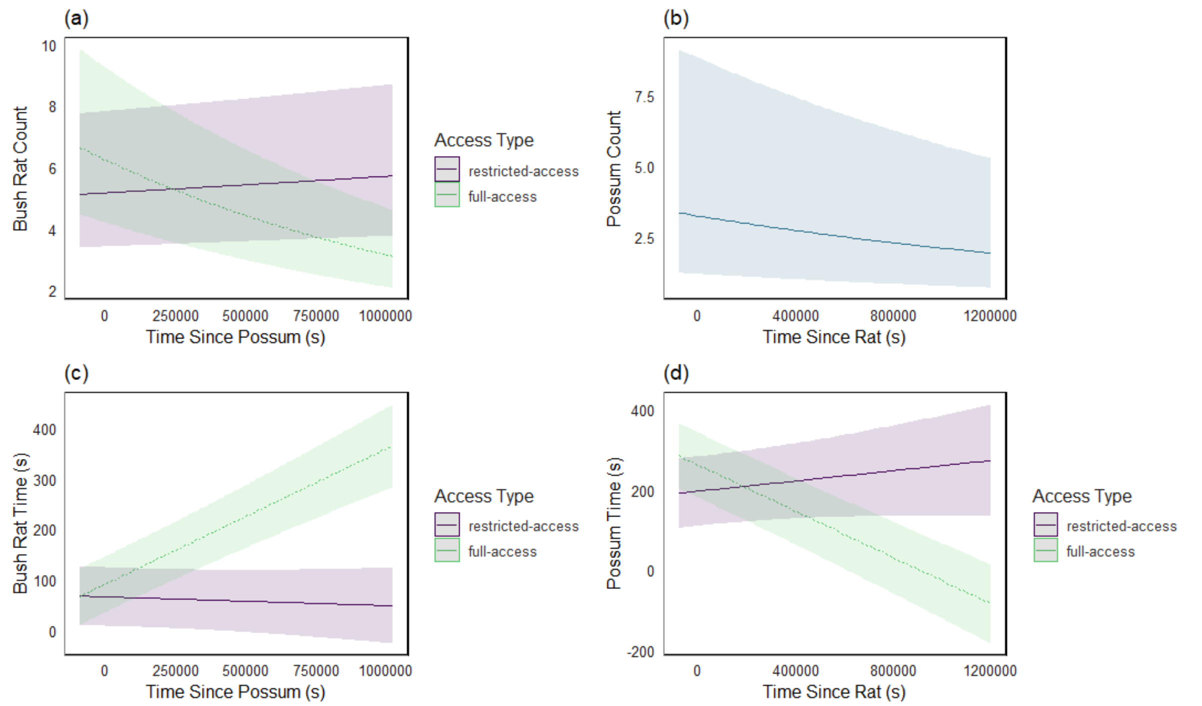


Figure 4-6. Conditional effects in response to the length of time (in seconds) since the other species had visited a site, were modelled using generalised linear mixed models. (a) The number of bush rat visits increased in response to the time since a possum visited (in seconds) at restricted bait-access sites (in purple) and decreased at full bait-access sites (in green). (b) The number of possum visits decreased in response to time since a bush rat visited (in seconds). (c) The time length (in seconds) of bush rat visits increased in response to the time since a possum visited (in seconds) at full bait-access sites (in green) but mildly decreased at restricted bait-access sites (in purple). (d) The time length (in seconds) of possum visits decreased in response to the time since a bush rat visited (in seconds) at full bait-access sites (in green) and increased at restricted bait-access sites (in purple). The shaded area corresponds to the standard error.

4.5 Discussion

Our experiment aimed to investigate whether the presence of common brushtail possums influenced the foraging decisions and activity of bush rats at supplementary feeding sites. We found evidence that bush rats' foraging activity was influenced by the frequency of visitation by possums. In particular, bush rats foraged less frequently and ate bait for shorter periods with increasing numbers of possums (Figs 4-4a and 4-5a).

Foraging decisions play an important role in what and how much food that individuals consume. We aimed to demonstrate two different decision processes the two species could make; exploiting a food source and leaving a foraging patch (Arehart et al., 2023; Baker & Brown, 2014). Many factors influence these decisions including travel time, visibility (e.g., chance of being depredated), food quality and accessibility (e.g., how easily the food is to access and consume), environmental conditions, and the presence of other species in the environment (Arehart et al., 2023; Linley et al., 2020). Our results demonstrate three factors that could be influencing foraging decisions: visibility (i.e., illumination or moonlight), rainfall, and the visitation patterns of other species. However, as all our results are correlative, we cannot determine whether any, or all, of these factors had a causative effect on foraging activity.

4.5.1 Prediction One: Visitation differences in bush rats vs possums at restricted vs full-access sites

The access to bait provided to possums at each of the sites did not influence the visitation patterns of either bush rats or possums. Additionally, site characteristics (years since fire, topographic wetness, vegetation type) did not affect bush rat or possum visitation. Night-time characteristics, such as rainfall and changes in illumination from moonlight, were associated with active foraging nights.

Our data implicates rainfall had a large influence on how long both species spent foraging, with high rainfall influencing the decisions of both species to depart food sources more quickly and visit sites less often. Our study was characterised by high levels of rainfall, with over 700 mm of rain falling in March 2022 (Bureau of Meteorology, 2022). This level of rainfall likely negatively influenced the foraging of all species, with few visits made to the baited sites on nights with the highest rainfall. Some species, especially birds, have been recorded foraging for shorter periods during high rainfall, as factors such as wet feathers can increase the energy required for flight, especially longer-distance travel (De Pascalis et al., 2022). Additionally, rainfall influences the availability of food resources. Williams and Albertson (2006) found that rainfall variability can affect the degradation of grasslands, as well as the variability of grasses, leading to long-term variations in food resource availability. Similarly, in the short term, Chard et al. (2017) found that rainfall increased the bioavailability of invertebrates while decreasing the availability of anthropogenic food sources. The latter effect was observed in our study, as the quality and structure of our baits were impacted by rainfall, and it became mouldy faster when conditions were humid.

Moon phase and the associated illumination is another factor that can influence foraging activity and, in our study, influenced which nights led to greater foraging activity (Linley et al., 2020; Prugh & Golden, 2014). However, the two study species responded differently to high illumination, with possums overall increasing visitation, and bush rats decreasing visitation to bait stations. Previous research has shown that possums use brighter illumination to assist in foraging and predator detection (Śmielak et al., 2023). Alternatively, many small mammals, like the bush rat, will use lower illumination to avoid detection by predators (Taylor et al., 2023). Therefore, the notable differences in response to moonlight in our study may represent how the two species detect and/or avoid predators, although our data cannot provide confirmation of this.

4.5.2 Prediction Two: Bush rat responses to possum presence

We found that possum presence influenced bush rat visitation to bait sites. Bush rats visited sites less often when there was high possum visitation. However, the access given to possums did not influence this visitation. Access type did influence the length of bush rat visits in response to possum visitation, with bush rats spending more time at restricted-access sites when there were more possum visits, and more time at full-access sites when the possums' visits were longer.

The need to forage can lead to increased chances of negative interactions, either by increasing predation risk or increasing encounters with aggressive competitors (Augustine & Springer, 2013; Halliday & Morris, 2013; Mónus & Barta, 2016). Aggression between interacting species can lead to changes in foraging behaviours, including how often a species forages and the sites it preferentially chooses (Beggs et al., 2020). For example, species like the long-legged buzzard *Buteo rufinus* in Cyprus organise their use of space in response to the likelihood of encountering a dominant, larger, or more aggressive competitor, such as the Bonelli's eagle *Aquila fasciata* (Kassinis et al., 2024). Therefore, to reduce the chances of negative outcomes, the ability to detect and avoid aggressive enemies is highly important (Halliday & Morris, 2013; Śmielak et al., 2023). This may lead to a reduction in the number of visits to sites where the aggressive species commonly visit, as we recorded with bush rats. Another way that small mammals do this is by reducing foraging time and effort in habitats that they consider risky, usually demonstrated by higher giving-up densities in more open and uncovered habitats (Denny et al., 2021). Bush rats, specifically, display shorter foraging periods in open habitats, but only when they perceive the presence of an introduced predator (Strauß et al., 2008). Our results indicate that bush rats act as if the full-access sites are riskier habitats, potentially because the restricted-access sites provide an artificial opportunity to hide, whereas the full-access sites do not.

Our results also suggest, unexpectedly, that our study species will spend longer at the same sites. This may suggest a facilitative-like indirect interaction, where either bush rats or possums are using cues from the other to select and spend longer at more suitable sites (Veit & Harrison, 2017). Alternatively, our results may simply be a case of confounding variables that are increasing the suitability of sites, such as the effects of rainfall, with both species responding in similar ways (Denny et al., 2021).

4.5.3 Prediction Three: The effect of possums on bush rats eating bait

We found that bush rat feeding bouts were shorter at sites where possums visited more frequently, suggesting that they chose to depart sooner when the chance of an encounter with a possum was high. Individuals may choose to depart a foraging patch if they perceive that it offers limited benefits or is providing diminishing returns, such as with respect to energy or nutrient availability, or if they perceive that staying in the foraging patch is a risk to their safety (Mella et al., 2018; Shuai et al., 2016). Based on our results, we suggest the latter is more likely. High-quality bait was regularly available, so there should have been no reduction in energetic or nutritional returns for bush rats that continued to forage at bait sites. However, if bush rats perceived possums to visit more frequently, perhaps via previous experience or detection of cues to possum presence, such as olfactory cues (Heavener et al., 2014; Prugh & Golden, 2014), short bouts of eating would provide some foraging benefit while reducing the chance of an encounter with possums. Previous research has found that the duration of rodent foraging at a patch can reflect a trade-off between the impacts of interference competition and the need for safety (Shuai et al., 2016).

4.5.4 Prediction Four: Time since the last visit

Bush rats increased their time at full-access bait stations and decreased their time at restricted-access sites with increasing time since visitation by possums (Fig 4-6). Bush rats visited restricted-access sites more regularly when the duration between possum visits was longer, while they decreased in visit frequency at full-access sites (Fig 4-6). Possums, in general, decreased their visitations with increasing time since a bush rat had visited. These results may indicate that our two study species use cues from each other in locating and selecting easy-to-access food resources. Locating food resources is an energy-consuming task, where species have many factors to consider, such as the nutritional and energetic benefits of the resource, the amount of energy used to travel and search, and the threats posed by other species in the environment (Arehart et al., 2023; Veit & Harrison, 2017). To circumvent such costs, some foragers, such as many sea birds, will follow species with similar diets as a method of locating abundant food sources (Veit & Harrison, 2017). It is possible that possums exhibited similar behaviour with respect to exploiting sites foraged by bush rats, and vice versa, but further research is needed to disentangle the cues that both species use to gain information about the other.

4.5.5 Managing temporal avoidance

Overall, our study demonstrated temporal avoidance of common brushtail possums in the foraging activity of bush rats. Temporal avoidance allows species to segregate the use of resources (such as food) by time periods (Cordero et al., 2024). In our study, we view this segregation as bush rats temporally avoiding supplementary food during periods when possums are present. Regardless of the drivers behind such avoidance behaviours in the subordinate species, these behaviours have costs. Foraging decisions involving avoidance result in energy-consuming actions and missed opportunity costs that can lead to reduced body condition, resulting in lower long-term survival (Corman et al., 2016; Radovics et al., 2023). Avoidance may also result in species selecting and moving into foraging patches with poorer-quality food (Liu et al., 2020). Temporal avoidance can also result in the subordinate species missing out on good quality food resources, as the dominant may consume all available resources (Burgos et al., 2023; Cordero et al., 2024). Additionally, with the changing populations in Booderee National Park, leading to greater numbers of possums, the costs of temporal avoidance are likely to be exacerbated (Kanishka et al., 2023; Lindenmayer et al., 2018). Therefore, in our study, we suggest that increased possum numbers following long-term poison baiting of the red fox in Booderee National Park is likely to have increased the perception of risk from possums by bush rats (Kanishka et al., 2023). This may have contributed to, or exacerbated, the potential avoidance behaviours we observed, in turn contributing to the population decline of bush rats across the study area (Kanishka et al., 2023).

In complex ecosystems with many species, the diversity and availability of plant resources is important as food for consumers and for the opportunities they provide for these species to segregate into different niche spaces; these spaces can create refuge habitats for small mammals that represent enemy-free space (Lees et al., 2022; McCain et al., 2018; Mérő et al., 2015). Given the importance of plant resources and vegetation to mammal species (Casula et al., 2017), we recommend focusing conservation on retaining important vegetation classes and structures (e.g., percentage ground cover, tree availability) to increase food resources, nesting structures, and overall habitat suitability for both species, to provide opportunities for niche segregation. Increasing these resources allows for more foraging opportunities while reducing the chance of run-ins between competing species (Casula et al., 2017; Cordero et al., 2024). For example, in managed forests in Sardinia, a large Mediterranean island, the retention of large trees and rock cover has been found to positively influence small mammal abundance, while also providing protection from antagonistic species, such as wild boar *Sus* spp. (Casula et al., 2017).

4.6 Conclusion

In conclusion, bush rat foraging decisions may be influenced by the presence of common brushtail possums, especially with respect to how long the rats spend consuming food resources. This temporal avoidance of interactions may result in restricted foraging activity. However, while this study reveals negative and very likely competitive interactions between bush rats and possums, it does not uncover the mechanism(s) driving the interaction. To understand this, we recommend further research on the movement and diet of both species and quantification of the availability of relevant food resources in their shared environment.

4.7 References

Arehart, E., Reimer, J. R., & Adler, F. R. (2023). Strategy maps: Generalised giving-up densities for optimal foraging. *Ecology Letters*, *26*(3), 398–410. https://doi.org/10.1111/ele.14160

Astete, S., Marinho-Filho, J., Kajin, M., Penido, G., Zimbres, B., Sollmann, R., Jácomo, A. T. A., Tôrres, N. M., & Silveira, L. (2017). Forced neighbours: Coexistence between jaguars and pumas in a harsh environment. *Journal of Arid Environments*, *146*, 27–34. https://doi.org/10.1016/j.jaridenv.2017.07.005

Augustine, D. J., & Springer, T. L. (2013). Competition and facilitation between a native and a domestic herbivore: Trade-offs between forage quantity and quality. *Ecological Applications*, *23*(4), 850–863. https://doi.org/10.1890/12-0890.1

Baker, M. A. A., & Brown, J. S. (2014). Foraging in space and time structure an African small mammal community. *Oecologia*, *175*(2), 521–535.

Balfour, N. J., Gandy, S., & Ratnieks, F. L. W. (2015). Exploitative competition alters bee foraging and flower choice. *Behavioral Ecology and Sociobiology*, *69*(10), 1731–1738. https://doi.org/10.1007/s00265-015-1985-y

Barabás, G., Michalska-Smith, M. J., & Allesina, S. (2016). The Effect of Intra- and Interspecific Competition on Coexistence in Multispecies Communities. *The American Naturalist*, *188*(1), E1–E12.

Barrull, J., Mate, I., Ruiz-Olmo, J., Casanovas, J. G., Gosàlbez, J., & Salicrú, M. (2014). Factors and mechanisms that explain coexistence in a Mediterranean carnivore assemblage: An integrated study based on camera trapping and diet. *Mammalian Biology*, *79*(2), 123–131. https://doi.org/10.1016/j.mambio.2013.11.004

Bartoń, K. (2023). *MuMIn: Multi-Model Inference* (Version 1.47.5) [Computer software]. https://cran.r-project.org/web/packages/MuMIn/index.html

Beggs, R., Pierson, J., Tulloch, A. I. T., Blanchard, W., Westgate, M., & Lindenmayer, D. (2020). An empirical test of the mechanistic underpinnings of interference competition. *Oikos*, *129*(1), 93–105. https://doi.org/10.1111/oik.06583

Brooks, M. E., Kristensen, K., Benthem, K. J. van, Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378–400.

Brown, J. S. (1988). Patch Use as an Indicator of Habitat Preference, Predation Risk, and Competition. *Behavioral Ecology and Sociobiology*, *22*(1), 37–47.

Bureau of Meteorology. (2022). *Jervis Bay, NSW - March 2022—Daily Weather Observations*. http://www.bom.gov.au/climate/dwo/202303/html/IDCJDW2067.202303.shtml

Burgos, T., Salesa, J., Fedriani, J. M., Escribano-Ávila, G., Jiménez, J., Krofel, M., Cancio, I., Hernández-Hernández, J., Rodríguez-Siles, J., & Virgós, E. (2023). Top-down and bottom-up effects modulate species co-existence in a context of top predator restoration. *Scientific Reports*, *13*(1), Article 1. https://doi.org/10.1038/s41598-023-31105-w

Burnham, K. P., & Anderson, D. R. (Eds.). (2002). Formal Inference From More Than One Model: Multimodel Inference (MMI). In *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (pp. 149–205). Springer. https://doi.org/10.1007/978-0-387-22456-5_4

Burrows, N. D., Algar, D., Robinson, A. D., Sinagra, J., Ward, B., & Liddelow, G. (2003). Controlling introduced predators in the Gibson Desert of Western Australia. *Journal of Arid Environments*, *55*(4), 691–713. https://doi.org/10.1016/S0140-1963(02)00317-8

Casula, P., Luiselli, L., Milana, G., & Amori, G. (2017). Habitat structure and disturbance affect small mammal populations in Mediterranean forests. *Basic and Applied Ecology*, *19*, 76–83. https://doi.org/10.1016/j.baae.2016.11.003

Chard, M., Martin, J., French, K., & Major, R. E. (2017). Rainfall events drive foraging choices by an urban coloniser. *Urban Ecosystems*, *20*(6), 1285–1290. https://doi.org/10.1007/s11252-017-0680-3

Cordero, S., Gálvez, F., & Fontúrbel, F. E. (2024). Temporal and behavioural niche partitioning underlies coexistence within a native-exotic rodent assemblage exploiting a high-value limited resource. *Austral Ecology*, *49*(7), e13560. https://doi.org/10.1111/aec.13560

Corman, A.-M., Mendel, B., Voigt, C. C., & Garthe, S. (2016). Varying foraging patterns in response to competition? A multicolony approach in a generalist seabird. *Ecology and Evolution*, *6*(4), 974–986. https://doi.org/10.1002/ece3.1884

De Pascalis, F., Austin, R. E., Green, J. A., Arnould, J. P. Y., Imperio, S., Maugeri, M., Haakonsson, J., Cecere, J. G., & Rubolini, D. (2022). Influence of rainfall on foraging behavior of a tropical seabird. *Behavioral Ecology*, *33*(2), 343–351. https://doi.org/10.1093/beheco/arab134

Denny, C. K., Stenhouse, G. B., & Nielsen, S. E. (2018). Scales of selection and perception: Landscape heterogeneity of an important food resource influences habitat use by a large omnivore. *Wildlife Biology*, *2018*(1), wlb.00409. https://doi.org/10.2981/wlb.00409

Denny, K. N., Bilodeau, K. N., Dumont, C. A., & Olson, Z. H. (2021). Separating effects of spatial location and microhabitat density on perceived predation risk in small

The effect of competitor presence on the foraging decisions of small mammals mammals. *Acta Ethologica*, *24*(2), 79–85. https://doi.org/10.1007/s10211-021-00365-y

Dexter, N., Hudson, M., James, S., MacGregor, C., & Lindenmayer, D. B. (2013). Unintended Consequences of Invasive Predator Control in an Australian Forest: Overabundant Wallabies and Vegetation Change. *PLOS ONE*, *8*(8), e69087. https://doi.org/10.1371/journal.pone.0069087

Dickman, C. R. (2011). Competition, Animal. In *Competition, Animal* (pp. 117–122). University of California Press. https://doi.org/10.1525/9780520948433-031

Esri. (2022). *ArcGIS Pro 3.0.3* [Computer software]. Esri.

Friedemann, G., Leshem, Y., Kerem, L., Shacham, B., Bar-Massada, A., McClain, K. M., Bohrer, G., & Izhaki, I. (2016). Multidimensional differentiation in foraging resource use during breeding of two sympatric top predators. *Scientific Reports*, *6*(1), Article 1. https://doi.org/10.1038/srep35031

Godsoe, W., Murray, R., & Plank, M. J. (2015). The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography*, *38*(11), 1071–1079. https://doi.org/10.1111/ecog.01134

Hagy, H. M., Stafford, J. D., Smith, R. V., Yetter, A. P., Hine, C. S., Horath, M. M., & Whelan, C. J. (2017). Opportunity costs influence food selection and giving-up density of dabbling ducks. *Journal of Avian Biology*, *48*(6), 804–814. https://doi.org/10.1111/jav.01275

Halliday, W. D., & Morris, D. W. (2013). Safety from predators or competitors? Interference competition leads to apparent predation risk. *Journal of Mammalogy*, *94*(6), 1380–1392.

Heavener, S. J., Carthey, A. J. R., & Banks, P. B. (2014). Competitive naïveté between a highly successful invader and a functionally similar native species. *Oecologia*, *175*(1), 73–84. https://doi.org/10.1007/s00442-013-2874-6

Hickling, G. J., & Day, T. D. (2024). Brushtail possums (*Trichosurus vulpecula*) dominate dama wallabies (*Notamacropus eugenii*) and Bennett's wallabies (*Notamacropus rufogriseus*) at bait feeders: Implications for invasive species management. *Wildlife Research*, *51*(8). https://doi.org/10.1071/WR24016

Kanishka, A. M., Blanchard, W., Lavery, T. H., Robinson, N. M., Dexter, N., Dickman, C. R., MacGregor, C., & Lindenmayer, D. B. (2023). Environmental variables influence patterns of mammal co-occurrence following introduced predator control. *PLOS ONE*, *18*(11), e0292919. https://doi.org/10.1371/journal.pone.0292919

Karlsson, M. F., de Souza, E. O., Ayelo, P. M., Zannou, J. A., Mègnigbèto, G. S. B., & Bokonon-Ganta, A. H. (2018). Interspecific competition between egg parasitoids: Native *Fopius caudatus* and exotic *Fopius arisanus*, in *Ceratitis cosyra*. *Biological Control*, *117*, 172–181. https://doi.org/10.1016/j.biocontrol.2017.11.010

Kassinis, N. I., Zotos, S., Charalambidou, I., Roulin, A., & Vogiatzakis, I. N. (2024). Competitive interactions of two sympatric raptors affecting their spatial distribution in an island environment. *Journal of Ornithology*. https://doi.org/10.1007/s10336-023-02124-1

King, C. M., & Moors, P. J. (1979). On Co-Existence, Foraging Strategy and the Biogeography of Weasels and Stoats (*Mustela nivalis* and *M. erminea*) in Britain. *Oecologia*, *39*(2), 129–150. JSTOR.

Kopecký, M., Macek, M., & Wild, J. (2021). Topographic Wetness Index calculation guidelines based on measured soil moisture and plant species composition. *Science of The Total Environment*, *757*, 143785. https://doi.org/10.1016/j.scitotenv.2020.143785

Lees, D. M., Watchorn, D. J., Driscoll, D. A., Doherty, T. S., Lees, D. M., Watchorn, D. J., Driscoll, D. A., & Doherty, T. S. (2022). Microhabitat selection by small mammals in response to fire. *Australian Journal of Zoology*, *69*(3), 67–79. https://doi.org/10.1071/ZO21022

Lindenmayer, D. B., Blanchard, W., Evans, M. J., Beggs, R., Lavery, T., Florance, D., Crane, C., Smith, D., Siegrist, A., Lang, E., & Scheele, B. C. (2023). Context dependency in interference competition among birds in an endangered woodland ecosystem. *Diversity and Distributions*, *29*(4), 556–571. https://doi.org/10.1111/ddi.13680

Lindenmayer, D. B., MacGregor, C., Welsh, A., Donnelly, C., Crane, M., Michael, D., Montague-Drake, R., Cunningham, R. B., Brown, D., Fortescue, M., Dexter, N., Hudson, M., Gill, A. M., Lindenmayer, D. B., MacGregor, C., Welsh, A., Donnelly, C., Crane, M., Michael, D., … Gill, A. M. (2008). Contrasting mammal responses to vegetation type and fire. *Wildlife Research*, *35*(5), 395–408. https://doi.org/10.1071/WR07156

Lindenmayer, D. B., Wood, J., MacGregor, C., Foster, C., Scheele, B., Tulloch, A., Barton, P., Banks, S., Robinson, N., Dexter, N., O'Loughlin, L. S., & Legge, S. (2018). Conservation conundrums and the challenges of managing unexplained declines of multiple species. *Biological Conservation*, *221*, 279–292. https://doi.org/10.1016/j.biocon.2018.03.007

Linley, G. D., Pauligk, Y., Marneweck, C., Ritchie, E. G., Linley, G. D., Pauligk, Y., Marneweck, C., & Ritchie, E. G. (2020). Moon phase and nocturnal activity of native Australian mammals. *Australian Mammalogy*, *43*(2), 190–195. https://doi.org/10.1071/AM19070

Liu, Z.-X., Dayananda, B., Jeffree, R. A., Tian, C., Zhang, Y.-Y., Yu, B., Zheng, Y., Jing, Y., Si, P.-Y., & Li, J.-Q. (2020). Giant panda distribution and habitat preference: The influence of sympatric large mammals. *Global Ecology and Conservation*, *24*, e01221. https://doi.org/10.1016/j.gecco.2020.e01221

Lovari, S., Minder, I., Ferretti, F., Mucci, N., Randi, E., & Pellizzi, B. (2013). Common and snow leopards share prey, but not habitats: Competition avoidance by large predators? *Journal of Zoology*, *291*(2), 127–135. https://doi.org/10.1111/jzo.12053

Macgregor, C., Blanchard, W., Stein, J., & Lindenmayer, D. (2020). Factors influencing the occurrence of the Southern Long-nosed Bandicoot (*Perameles nasuta* Geoffroy) during a population irruption and decline. *Austral Ecology*, *45*. https://doi.org/10.1111/aec.12930

McCain, C. M., King, S. R. B., Szewczyk, T., & Beck, J. (2018). Small mammal species richness is directly linked to regional productivity, but decoupled from food resources, abundance, or habitat complexity. *Journal of Biogeography*, *45*(11), 2533–2545. https://doi.org/10.1111/jbi.13432

Mella, V. S. A., Possell, M., Troxell-Smith, S. M., & McArthur, C. (2018). Visit, consume and quit: Patch quality affects the three stages of foraging. *Journal of Animal Ecology*, *87*(6), 1615–1626. https://doi.org/10.1111/1365-2656.12882

Mella, V. S. A., Ward, A. J. W., Banks, P. B., & McArthur, C. (2015). Personality affects the foraging response of a mammalian herbivore to the dual costs of food and fear. *Oecologia*, *177*(1), 293–303. https://doi.org/10.1007/s00442-014-3110-8

Mérő, T. O., Bocz, R., Polyák, L., Horváth, G., & Lengyel, S. (2015). Local habitat management and landscape-scale restoration influence small-mammal communities in grasslands. *Animal Conservation*, *18*(5), 442–450. https://doi.org/10.1111/acv.12191

Mónus, F., & Barta, Z. (2016). Is Foraging Time Limited During Winter? – A Feeding Experiment with Tree Sparrows Under Different Predation Risk. *Ethology*, *122*(1), 20–29. https://doi.org/10.1111/eth.12439

Moseby, K. E., Neilly, H., Read, J. L., & Crisp, H. A. (2012). Interactions between a Top Order Predator and Exotic Mesopredators in the Australian Rangelands. *International Journal of Ecology*, *2012*, e250352. https://doi.org/10.1155/2012/250352

Pays, O., Blanchard, P., Valeix, M., Chamaillé-Jammes, S., Duncan, P., Périquet, S., Lombard, M., Ncube, G., Tarakini, T., Makuwe, E., & Fritz, H. (2012). Detecting predators and locating competitors while foraging: An experimental study of a medium-sized herbivore in an African savanna. *Oecologia*, *169*(2), 419–430. https://doi.org/10.1007/s00442-011-2218-3

Périquet, S., Mapendere, C., Revilla, E., Banda, J., Macdonald, D. W., Loveridge, A. J., & Fritz, H. (2016). A potential role for interference competition with lions in den selection and attendance by spotted hyaenas. *Mammalian Biology*, *81*(3), 227–234. https://doi.org/10.1016/j.mambio.2015.10.005

Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to Death? The Effects of Intimidation and Consumption in Predator–Prey Interactions. *Ecology*, *86*(2), 501–509. https://doi.org/10.1890/04-0719

Prugh, L. R., & Golden, C. D. (2014). Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology*, *83*(2), 504–514. https://doi.org/10.1111/1365-2656.12148

R Core Team. (2021). *R: A Language and Environment for Statistical Computing* [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Radovics, D., Szabolcs, M., Lengyel, S., & Mizsei, E. (2023). Hide or die when the winds bring wings: Predator avoidance by activity shift in a mountain snake. *Frontiers in Zoology*, *20*(1), Article 1. https://doi.org/10.1186/s12983-023-00497-w

Rayan, D. M., & Linkie, M. (2016). Managing conservation flagship species in competition: Tiger, leopard and dhole in Malaysia. *Biological Conservation*, *204*, 360–366. https://doi.org/10.1016/j.biocon.2016.11.009

Searle, K. R., Thompson Hobbs, N., & Shipley, L. A. (2005). Should I stay or should I go? Patch departure decisions by herbivores at multiple scales. *Oikos*, *111*(3), 417–424. https://doi.org/10.1111/j.0030-1299.2005.13918.x

Shuai, L.-Y., Song, Y.-L., Kotler, B. P., Embar, K., & Zeng, Z.-G. (2016). Foraging behaviour in East Asian desert rodents and its implications on coexistence. *Israel Journal of Ecology and Evolution*, *62*(3–4), 171–177. https://doi.org/10.1080/15659801.2015.1045279

Śmielak, M. K., Ballard, G., Fleming, P. J. S., Körtner, G., Vernes, K., & Reid, N. (2023). Brushtail possum terrestrial activity patterns are driven by climatic conditions, breeding and moonlight intensity. *Mammal Research*, *68*(4), 547–560. https://doi.org/10.1007/s13364-023-00691-5

Strauß, A., Solmsdorff, K. Y., Pech, R., & Jacob, J. (2008). Rats on the run: Removal of alien terrestrial predators affects bush rat behaviour. *Behavioral Ecology and Sociobiology*, *62*(10), 1551–1558. https://doi.org/10.1007/s00265-008-0584-6

Taws, N. (1998). *Fire and vegetation management in Jervis Bay Territory*. Taws Botanical Research.

Taylor, P., Swan, M., Sitters, H., Smith, A., & Di Stefano, J. (2023). Small mammals reduce activity during high moon illumination under risk of predation by introduced predators. *Scientific Reports*, *13*(1), 10532. https://doi.org/10.1038/s41598-023-37166-1

Tides4Fishing. (2023). *Lunar calendar 2023 of lunar phases and eclipses*. https://tides4fishing.com/lunar-calendar

Veit, R. R., & Harrison, N. M. (2017). Positive Interactions among Foraging Seabirds, Marine Mammals and Fishes and Implications for Their Conservation. *Frontiers in Ecology and Evolution*, *5*. https://www.frontiersin.org/articles/10.3389/fevo.2017.00121

Welsh, A. H., Cunningham, R. B., Donnelly, C. F., & Lindenmayer, D. B. (1996). Modelling the abundance of rare species: Statistical models for counts with extra zeros. *Ecological Modelling*, *88*(1), 297–308. https://doi.org/10.1016/0304-3800(95)00113-1

Wereszczuk, A., & Zalewski, A. (2015). Spatial Niche Segregation of Sympatric Stone Marten and Pine Marten – Avoidance of Competition or Selection of Optimal Habitat? *PLoS ONE*, *10*(10), e0139852. https://doi.org/10.1371/journal.pone.0139852

Williams, C. A., & Albertson, J. D. (2006). Dynamical effects of the statistical structure of annual rainfall on dryland vegetation. *Global Change Biology*, *12*(5), 777–792. https://doi.org/10.1111/j.1365-2486.2006.01111.x

Xu, T., & Hutchinson, M. (2011). *ANUCLIM VERSION 6.1 User's Guide* [Dataset]. The Australian National University, Fenner School of Environment and Society, Canberra.

Chapter 5 Quantifying the dietary overlap of two co-occurring mammal species using DNA metabarcoding to assess potential competition

5.1 Abstract

Interspecific competition is often assumed in ecosystems where co-occurring species have similar resource requirements. The potential for competition can be investigated by measuring the diet overlap of putative competitor species. The degree of potential competition between dietary generalist species sharing wide ranges of food resources has rarely been quantified. We examined dietary overlap between two naturally co-occurring dietary generalist species; common brushtail possums *Trichosurus vulpecula* and bush rats *Rattus fuscipes*. To gauge the potential for competition, we conducted a diet analysis using DNA extracted from faecal samples to identify the range of food items consumed by both species within a shared ecosystem and quantify their dietary overlap. We used DNA metabarcoding on faecal samples to extract plant, fungal, and invertebrate DNA, identifying diet items and quantifying dietary range and overlap. The species' diets were substantially similar, with an 83.9% overlap in dietary items. Bush rats had a large dietary range, consisting of many plant and fungal species, and some invertebrates, with almost no within-species variation. Possums had a more restricted dietary range, consisting primarily of plants. We suggest that the larger dietary range of the bush rat helps buffer it from the impacts of competition by providing greater access to food types. We conclude that, despite the high ostensible overlap in the foods consumed by dietary generalist species, fine-scale partitioning of food resources may be a key mechanism to alleviate competition and permit co-existence.

5.2 Introduction

Food resources are vital for animal growth, survival, and reproduction. However, the availability of these resources, especially when in short supply, can influence the behaviours and decision-making of foragers and their interactions with other individuals (Corman et al., 2016). Scarce food resources can result in species shifting when and where they forage, and what they forage on, diet switching and adapting their foraging behaviours (Chard et al., 2017; Favreau et al., 2018). Group-living animals such as grey kangaroos *Macropus giganteus* often forage in smaller groups during periods of low food availability and adjust their feeding behaviours, such as by increasing vigilance, to reduce risks of predation (Favreau et al., 2018). In other group-living species, such as some seabirds, high population sizes can induce individuals to travel further to forage to reduce the potential for intraspecific competition (Corman et al., 2016; Lamb et al., 2017). Food availability can also influence the choice of food types (Chard et al., 2017).

For example, Australian white ibis *Threskiornis molucca* prefer invertebrates when they are available after rain but increases their consumption of anthropogenic sources of food when invertebrates are scarce (Chard et al., 2017). Black-footed titi monkeys *Cellicebus nigrifrons* in south-eastern Brazil will similarly switch and broaden their diet range when their preferred diet of fleshy fruits is unavailable (Nagy-Reis & Setz, 2017).

Although food availability and quality often determine the foraging decisions of individuals within a population, this can also have powerful effects on individuals of different species if these taxa have overlapping niches and compete with each other for food (Bell et al., 2023; Kumpan et al., 2019; Santosa et al., 2012). For example, Santosa et al. (2012) found that white-bearded gibbons *Hylobates albibarbis* and leaf monkeys *Presbytis rubicunda* in West Kalimantan shifted their foraging patch use in response to the availability of food, avoiding each other when food was scarce and being most likely to share foraging patches when fruit availability was high. Furthermore, Bell et al. (2023) showed that foraging patterns in the presence of competition can have long-term influences on the activity and distribution of multiple interacting species within ecological communities, with subordinate foragers exhibiting spatial and temporal avoidance of dominant species.

The intensity and effects of interspecific dietary competition can change with fluctuating availability of shared food resources (Prevedello et al., 2013). Resources can become limited through the increased abundance of one or more competitor species (Dexter et al., 2013; Treloar et al., 2021). According to Treloar et al. (2021), as the population density of one species increases, the availability of shared resources for heterospecific individuals decreases, which can lead to more intense competition and declines of subordinate species. Understanding how species are sharing resources at different levels of resource availability can be vital for predicting when competition becomes mutually detrimental, especially when accounting for changing environmental conditions (Gebremedhin et al., 2016).

Trophic, or dietary, generalists are often viewed as being more resilient to environmental change than their specialist counterparts as they can switch to alternative food if components of their diet become scarce (Lloyd & Vetter, 2019; Treloar et al., 2021). For example, the boodie *Bettongia lesueur*, in Western Australia, is characterised by behavioural plasticity and a broad dietary niche, allowing the species to adapt readily to new environments when it is moved in conservation translocations (Bice & Moseby, 2008; Treloar et al., 2021). However, dietary generalist species are usually also considered to be weaker competitors when compared to specialists, as specialists tend to compete for a restricted set of resources, whereas generalists will switch their use of resources in response to resource limitation (Barnes & Murphy, 2023; de Carvalho et al., 2019; Püttker et al., 2019). This can result in generalist species having patchy or 'checkerboard' distributions within communities of specialists or thriving primarily in environments where specialists are absent (Nordberg & Schwarzkopf, 2019; Püttker et al., 2019). Where dietary generalist species do co-occur with specialists, they will often segregate spatially or temporally, or in their diet, to avoid aggressive competitive interactions (Kent et al., 2022). Conversely, generalist-generalist interactions have rarely been investigated (Barnes & Murphy, 2023), despite theoretical interest and expectations that high overlap along much of the food resource axis between generalist species should increase the likelihood of competition between them (Dickman, 2011).

Although competition between species can be confirmed only in carefully controlled removal or addition experiments in which scarce resources are identified (Dickman, 2011), a common first step in clarifying the potential for competitive interactions is to measure the extent of niche overlap between putative competitor species (Villsen et al., 2022). If food is suspected to be a scarce resource, the species' diets need to be described and compared (Nordberg & Schwarzkopf, 2019; Wang et al., 2023). However, for dietary generalist species, this can be a difficult task owing to the wide range of food types that may be consumed (Calver & Loneragan, 2024). High dietary breadth at the population level can arise if all animals consume a similarly wide range of foods or if individuals specialise in different food types (Van Valen, 1965). In the latter case, consumers may exhibit age, sex, habitat or even personality-related differences in their diets, with the population when viewed collectively having a generalist diet (Bolnick et al., 2003; C. R. Dickman & Newsome, 2015; Woo et al., 2008).

One tool that is becoming increasingly popular to assess both dietary niche breadth and niche overlap is DNA metabarcoding (Wang et al., 2023; Yoccoz, 2012). DNA metabarcoding studies on the diet of animals utilise the degraded DNA in faecal samples to identify the diversity of taxa likely to have been consumed, especially when compared to histological and morphological methods (Alemany et al., 2023; Villsen et al., 2022). The "dietary barcodes" for different species allow assessment of their dietary niches and comparison of dietary overlap (Villsen et al., 2022; Wang et al., 2023). Species with very similar diets can be interpreted as having a higher potential for competition (Klure et al., 2023; Villsen et al., 2022). For example, a study of the diets of sympatric woodrats *Neotoma bryanti* and *N. lepida* in the USA used DNA metabarcoding to determine that while there was overlap in the plant component of their diets, the uneven consumption of arthropods during the dry period reduced interspecies competition (Klure et al., 2023).

The study we report here focused on the diets of the bush rat *Rattus fuscipes*, a native Australian rodent (~100 g), and the common brushtail possum *Trichosurus vulpecula* (hereafter 'possum', ~2 kg), a partly arboreal marsupial, within Booderee National Park (BNP) in south-eastern Australia. Both species are considered to be generalist omnivores (Callander, 2018; Cruz et al., 2012) that consume similar ranges of plants, fungi, invertebrates, and other food types, although dietary overlap has not been assessed in any sites where the two species co-occur. Recent studies of these species within BNP have demonstrated that, for several years, possums have increased in abundance, while bush rats have decreased (Kanishka et al., 2023; Lindenmayer et al., 2018). The decline in bush rats may be a response to the increase in the number of possums, which are considerably larger and potentially competitively dominant (Kanishka et al., 2023). The two species are taxonomically distinct and differ in behaviour and habitat use, with bush rats being largely ground-dwelling and exhibiting a preference for dense, complex vegetation, and possums being partly arboreal (Callander, 2018; Cruz et al., 2012). However, possums also spend significant periods foraging on the ground and in the understorey (Cruz et al., 2012), increasing both the chance of encounter between species and the number and range of resources they share. We hypothesised that based on trophic niche partitioning theories (Villsen et al., 2022), as possum abundance increases, the number of possums and time spent on the ground will increase, leading to an increase in potential competition for shared food resources. We hypothesise this will have detrimental effects on the smaller and putatively subordinate bush rat (Dexter et al., 2013; Treloar et al., 2021).

Using DNA metabarcoding, we aimed to characterise the diets of bush rats and common brushtail possums at both a broad overall level and at a finer scale, characterising within-species variation by calculating their niche breadths and dietary ranges. We also aimed to determine the level of overlap in their diets at multiple scales. We anticipated that the degree of dietary overlap would provide an indication of the potential for competition between the two species, and potentially uncover a mechanism explaining their inverse numerical relationship in Booderee National Park. We predicted that: (1) the diets of common brushtail possums and bush rats would encompass a broad range of food types, (2) there would be a high overlap in the range of food types consumed by the two species, and (3) fine-scale differences in diet would occur within and between species with respect to sex, age, and vegetation type where animals were active.

5.3 Method

5.3.1 Ethics statement

This study was conducted in strict accordance with the recommendations in the *Australian Code for the Care and Use of Animals for Scientific Purposes*. The protocol was approved by the Animal Experimentation Ethics Committee at the Australian National University (Protocol Number: A2020/25).

5.3.2 Study area

We conducted our study at Booderee National Park (BNP), Jervis Bay Territory, Australia (Fig 5-1). Booderee National Park is co-owned and co-managed by the Wreck Bay Aboriginal Community and Parks Australia. It has a temperate climate (BOM, 2021). The Park has undergone an intensive program of poison baiting to reduce the numbers of the introduced red fox *Vulpes vulpes* since 2002 (Dexter et al., 2013; Lindenmayer et al., 2005, 2018). The reduction in predation pressure from the red fox has potentially allowed the possum population to increase (Lindenmayer et al., 2018). The remains of both possums and bush rats occur frequently in the diets of red foxes in coastal forest areas (Fleming et al., 2021). However, the removal of foxes by poison baiting has much stronger positive effects on possums than on bush rats (Banks, 1999; Dexter & Murray, 2009; Kovacs et al., 2012).

Figure 5-1. Satellite map of Booderee National Park, Jervis Bay Territory, Australia (Esri, 2022). All green, vegetated areas are within the boundary of BNP.

5.3.3 Faecal collection

We collected samples over two trapping periods: the first in October 2020 (40 samples), and the second between December 2021 and February 2022 (95 samples). These comprised 57 possum (from 52 individual possums) and 78 bush rat (from 76 individual bush rats) faecal samples. We collected samples fresh from cage traps and Elliott traps that had been set to capture the two species after the animals had been processed and released on the morning following capture (Lindenmayer et al., 2008; Macgregor et al., 2020). We stored the samples collected in the first period in ethanol in 5 ml tubes. We stored the samples collected in the second period with silica gel in 15 ml tubes at an approximate ratio of 1:4 faecal sample to silica gel. We stored all samples at -20°C prior to DNA extraction. We also recorded the sex and approximate life state (hereafter referred to as 'age', categories; adult, subadult, and juvenile) of all trapped animals, as well as the location and broad vegetation type (forest, woodland, rainforest, sedge, heath, shrub, and casuarina) where the samples were collected from (Appendix D.1) (Taws, 1998). We estimated age using visual information on body size and development of the external reproductive organs, distinguishing animals as either juveniles, subadults or adults.

5.3.4 DNA extraction

We extracted DNA from the faecal samples using the DNeasy PowerSoil Pro Kit (Qiagen, Hilden, Germany). To improve the amplification process, we cleaned the samples in several rounds, first with the DNeasy PowerClean Pro clean-up kit (Qiagen, Hilden, Germany), and second using Spri-Speed magnetic beads (Beckman Coulter, New South Wales, Australia). Extraction controls were used to check for any contamination.

We amplified each sample with primers to extract plant, fungal, or invertebrate DNA separately with polymerase chain reactions (PCRs). The primer we used for plant DNA was the chloroplast trnL intron (referred to as trnL) (Taberlet et al., 2007). The primer we used for fungal DNA was the ITS3/ITS4 primer which targets the 18S rRNA gene and Internal Transcribed Spacer region (referred to as ITS) (Nuske et al., 2018). The primer we used for invertebrate DNA was the mitochondrial cytochrome oxidase I sequence (referred to as COI) (Shutt et al., 2021). Negative PCR controls were included in all reactions.

We indexed the amplified DNA using the NEBNext® Multiplex Oligos dual index primers (New England Biolabs, Massachusetts, USA). We further cleaned the indexed amplified DNA with Sera-Mag™ SpeedBeads (Cytiva, Victoria Australia) and pooled the amplicons in equimolar volumes. We constructed a library using the V2 2 x 250 base pair kit (Illumina inc., California, USA). Finally, we sequenced the samples using the paired-end sequencing on an Illumina MiSeq sequencer (Illumina inc., California, USA).

5.3.5 Data analysis

We analysed all sequences using the dada2 ver. 1.16.0 (Callahan et al., 2016), Biostrings ver. 2.60.2 (Pagès et al., 2023) and Cutadapt ver. 4.7 (Martin, 2011) packages in R ver. 4.4.1 (R Core Team, 2021). Using the Biostrings and Cutadapt packages, we trimmed all sequences of the primer and adaptor sequences. We also used the dada2 package to filter sequences, check for error rates, and remove chimeric sequences.

We created three reference libraries, one for each taxon set. For the plant taxa, we used a plant ID list for BNP (collected by C. Foster) and collected the relevant sequences from NCBI Genbank (NCBI, 2023). We then checked these sequences using the AliView program (Larsson, 2014). For the invertebrate taxa, we collated sequence records from Canberra, Sydney, and Nowra, NSW (a town close to BNP) from the BOLD database (BOLD Systems, 2023). For the fungal taxa, we collected sequence records from Australia from the UNITE database (downloaded November 2022) (Nielsen et al., 2017). We created a subset of ectomycorrhizal fungi from the fungal records for subsequent analyses, to focus on fungi most likely to be actively consumed. We then assigned our sequences to taxa from the reference libraries using the 'assignTaxonomy' function in the dada2 package, which uses a Bayesian likelihood method to assign sequences to the most likely taxa, or the best fitting higher order taxa (i.e., order, family) (Callahan et al., 2016). For sequences that were not assigned during the Bayesian process and had been detected in the barcodes for five or more individuals of either species, we manually searched for these sequences in the NCBI nucleotide database (NCBI, 2023), using the BLASTn algorithm system (Altschul et al., 1990).

Of the resulting data, we dropped sequences with less than 10 reads for an individual. We then converted the reads to binomial data (i.e., 0 for <10 reads, identified as not present in the diet, and 1 for >10 reads, identified as present in the diet). Finally, we converted the sequences to their lowest assigned taxonomic level.

5.3.6 Statistical analysis

We used two methods to analyse and characterise the dietary niche range of bush rats and possums. Firstly, we analysed the frequency of items within bush rat and possum diets (i.e., the species' faecal samples) using chi-squared tests in R (R Core Team, 2021). This analysis informed us if there was an even or uneven spread in the consumption of the dietary items and allowed us to investigate diet items that were consumed more frequently (Pearson, 1900; Zarkami et al., 2020). We additionally used chi-squared analysis to investigate within-species variation in diets. The within-species variables we used were the sex and age of individuals and the broad vegetation type in which we trapped animals.

Secondly, we used the 'niche.width' function from the spaa package ver. 0.0.2 (Zhang, 2016) to calculate the niche breadth of each species using Levins' measure of niche breadth (Levins, 1968). Levins' measure calculates the uniformity of the distribution of resources used by individuals (Krebs, 2014; Levins, 1968). The higher the value of Levins' measure, the broader the dietary range of the species (Krebs, 2014; Levins, 1968). To compare the diet ranges based on Levins' measures between species, we compared the difference in Levins' measures to a permuted dataset, with 10,000 permutations, to calculate a predicted p-value of the difference in scores. We calculated Levins' measures for each species and for each within-species category.

We additionally used two methods to calculate the dietary overlap between the study species. Firstly, we used the “niche.overlap” function from the spaa package ver. 0.0.2 (Zhang, 2016) to calculate the Pianka index of similarity (Pianka, 1972; Wang et al., 2023). The Pianka index calculates a proportion of overlap between two categories based on the distribution of resources used by each category (Pianka, 1972; Wang et al., 2023).

Secondly, we performed a PERMANOVA using Jaccard’s measure of similarity using the vegan package ver. 2.6-4 (Oksanen et al., 2022). We first tested the homogeneity of group dispersions using the ‘betadisper’ function to determine if the data were dispersed normally (Oksanen et al., 2022). We calculated a dissimilarity matrix between the dietary content of the individuals by calculating a Jaccard similarity matrix, using the ‘vegdist’ function (Oksanen et al., 2022). Jaccard’s similarity index measures the proportion of the number of samples in common between datasets (Kefford et al., 2010). We then compared matrices between the species using the ‘adonis2’ function (Oksanen et al., 2022) to calculate a PERMANOVA, which assesses differences between groups (Anderson, 2017).

5.4 Results

5.4.1 Overall niche use

Between the two species, we identified 150 different dietary items to the lowest taxonomic level. We detected a total of 769 sequences within the faecal samples of bush rats (n = 78), which we identified as belonging to 130 different taxa. Of these, 54.9% (n = 422) comprised plant material, 34.5% (n = 265) ectomycorrhizal fungi, and 10.7% (n = 82) comprised invertebrates. Possums had a much smaller range of diet items within the collected faecal samples (n = 57), with 194 sequences detected from 39 different taxa. Of these, 70.1% (n = 136) comprised plant material, 23.7% (n = 46) were ectomycorrhizal fungi, and 6.2% (n = 12) were invertebrates.

Bush rats had a dietary niche breadth of 30.337, with most of their faecal samples consisting of plant material, then fungi, and only a relatively small number of invertebrates (Fig 5-2). There was a significant difference in the frequency that diet items were identified in the samples, indicating that bush rats mostly consumed particular plant materials (χ^2_{84} = 1239.9, $p < 0.001$). Possums, relative to bush rats, had a much smaller dietary breadth of 14.254. Possum faeces, similar to bush rats, consisted primarily of plant material, followed by fungi, and almost no invertebrates (Fig 5-2). There was a significant difference in the frequency with which diet items were identified in the samples, suggesting that some items were consumed more frequently than others (χ^2_{84} = 863.95, $p < 0.001$).

The Pianka index indicated that bush rats and possums shared 83.9% of their diet (Pianka = 0.839). The diets of bush rats and possums were found to be not statistically significantly different (F_{22} = 1.044, p = 0.233). The species (i.e., bush rat or possum) explained 19.3% of the differences we observed in the data.

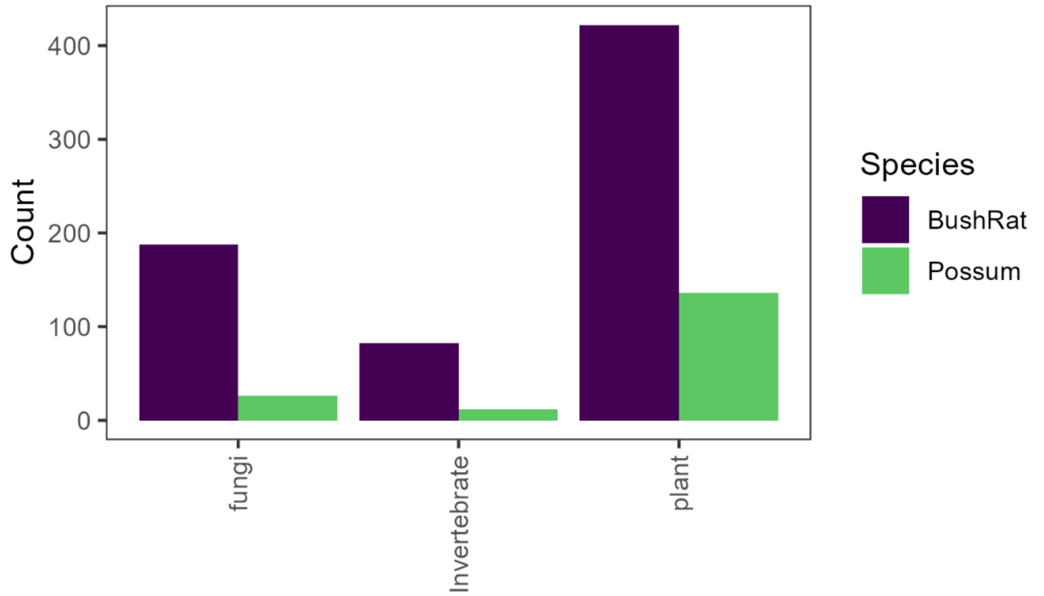


Figure 5-2. Numbers of diet items (i.e., counts) within each major taxon group that were found in faecal samples of bush rats and common brushtail possums.

5.4.2 Plant diet items

We identified 33 dietary items within plant taxa from the faecal samples, with bush rats consuming all 33, and possums consuming 19. The breadths of the species' diets were not significantly different, although bush rats had a larger dietary niche breadth (15.381), compared to possums (9.859). Both species displayed significant differences in the frequency of occurrence of different plant materials in their faecal samples (Bush rats: χ^2_{32} = 483.39, p < 0.001, Possums: χ^2_{32} = 319.21, p < 0.001). Both species consumed more plants from the order Poales (grasses and sedges) than other plant groups. For diet items identified to the species level, bush rats mostly consumed prickly couch grass *Zoysia macrantha* (Poaceae), and possums mostly consumed wombat berry *Eustrephus latifolius* (Asparagaceae) (Fig 5-3).

Within species, there was no difference in the dietary ranges of males and females for either bush rats or possums (Table 5-1). All groups showed that some plant materials were consumed at a higher frequency than others (Table 5-1). There was also no difference in the plant dietary ranges between age groups of either bush rats or possums (Table 5-1). Similarly, all groups consumed some plant materials more than others (Table 5-1). Bush rats showed similar diet ranges between individuals in different habitat types (Table 5-1). There was an even frequency of consumption in bush rats in scrubland and heathland habitats, but an uneven frequency of consumption in bush rats in forest, woodland, shrubland, rainforest and sedgeland habitats. Possums did show different diet ranges between individuals in different habitat types, with possums in forest habitats having a higher diet range (10.028), and possums in casuarina habitats having a restricted diet range (1) (Table 5-1). There was an uneven frequency of consumption for most possums across habitats, with evidence that mostly Poales plants were consumed; however, there was an even frequency of consumption for possums in casuarina habitats (Table 5-1).

Overall, the Pianka index indicated an overlap of 85.2% between the diets of bush rats and possums (0.852). However, PERMANOVA indicated the consumption of plant diet items by bush rats and possums to be significantly different ($F_{22} = 21.224$, $p = 0.016$). The species (i.e., bush rat or possum) accounts for 22.8% of the differences we observed in the data. Most of the overlap was found in the orders Fabales (an order of flowering plants) and Poales (Fig 5-3).

Table 5-1. The Levins' measure of niche breadth and chi-squared results for within-species patterns for plant diet items. Dashes (-) represent categories where no samples were collected.

	Bush Rats			**Possum**		
			Sex			
	Levins	X^2	P value	Levins	X^2	P value
Male	15.469	402.33	< 0.001	9.858	293.44	< 0.001
Female	13.210	190.27	< 0.001	9.283	150.75	< 0.001
NR	13.087	101.94	< 0.001	8.067	34.000	0.371
			Age			
Adult	16.011	369.28	< 0.001	9.858	293.44	< 0.001
Subadult	15.781	82.921	< 0.001	6.368	46.000	0.052
Juvenile	7.562	74.000	< 0.001	-	-	-
NR	11.965	91.423	< 0.001	-	-	-
			Habitat			
Casuarina	-	-	-	1.000	32.000	0.467
Forest	11.864	151.44	< 0.001	10.028	190.140	< 0.001
Heathland	10.314	41.789	0.115	-	-	-
Rainforest	13.158	75.400	< 0.001	4.765	53.333	0.010
Scrubland	12.000	42.000	0.111	-	74.857	< 0.001
Sedgeland	10.782	68.000	< 0.001	-	-	-
Shrubland	15.956	141.000	< 0.001	7.229	-	-
Woodland	12.261	133.62	< 0.001	5.556	49.400	0.025

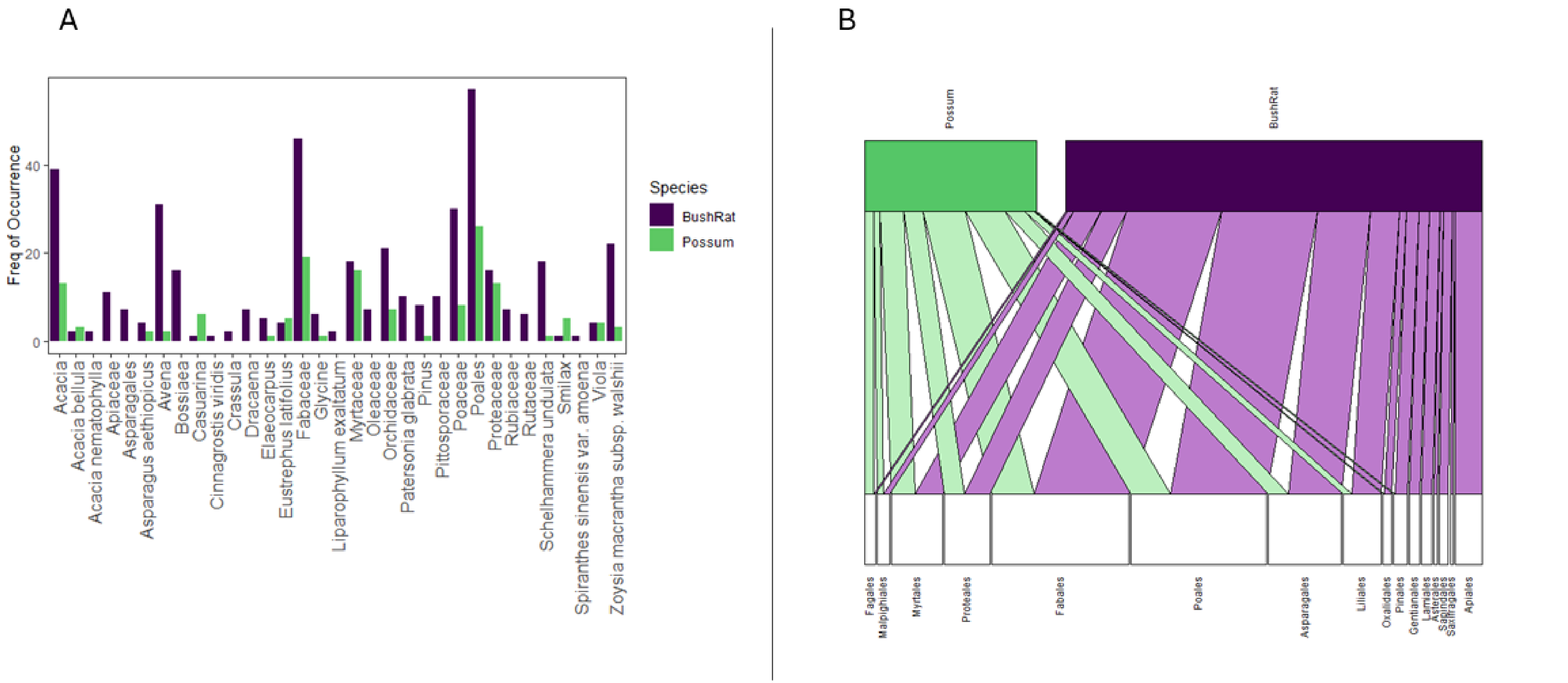


Figure 5-3. (A) Frequency of occurrence of the number of plant items determined, at the lowest identified taxonomic level. (B) A bipartite plot of the plant diet items found in the scats of bush rats and common brushtail possums at the ordinal level.

5.4.3 Invertebrate diet items

We identified 24 invertebrate taxa from faecal samples; bush rats consumed 23 of these, and possums consumed seven. There was no difference in the invertebrate dietary niche breadths of bush rats (11.023) and possums (5.538). Bush rats had an uneven frequency of occurrence of invertebrate diet items (χ^2_{23} = 96.537, p < 0.001), mostly consuming invertebrates in the order Neuroptera (net-winged insects). Possums also had an uneven frequency of occurrence of diet items (χ^2_{23} = 40, p = 0.015), mostly consuming invertebrates in the orders Neuroptera and Hymenoptera (including bees, wasps, etc.) (Fig 5-4). Of diet items identified to species level, bush rats mostly consumed western black quill mayflies *Rhithrogena hageni*.

Within species, for both bush rats and possums, males and females had relatively similar invertebrate dietary niche breadths (Table 5-2). Male and female bush rats consumed some items more frequently than others (Table 5-2), with both more frequently consuming Neuroptera compared with other invertebrates. Male and female possums, conversely, had a more even spread in their diet items (Table 5-2). Adult and subadult bush rats had a greater dietary niche breadth than juvenile bush rats (Table 5-2). In comparison, only adult possums consumed invertebrates. Subadult and juvenile bush rats had an even frequency of consumption. Adult bush rats and possums both consumed Neuroptera more frequently than other insect groups. The dietary niche breadth of individual bush rats and possums were relatively similar regardless of the habitat type in which they were found (Table 5-2). Additionally, with the exception of bush rats in shrubland habitats, there was an even frequency of consumption across the different habitat types (Table 5-2).

Overall, the Pianka overlap index showed an overlap of 73.8% in the invertebrate diets of bush rats and possums. However, the invertebrate diets of bush rats and possums were significantly different (F_{22} = 1.212, p = 0.042). The species (i.e., bush rat or possum) accounted for 40.7% of the differences we observed in the data. The greatest overlaps were for the Hymenoptera and Neuroptera orders (Fig 5-4).

Table 5-2. The Levins' measure of niche breadth and chi-squared results for within-species patterns for invertebrate diet items. INF represent categories with too few samples to calculate the niche breadth and chi-squared. Dashes (-) represent categories where no samples were collected.

	Bush Rats			**Possum**		
			Sex			
	Levins	X^2	P value	Levins	X^2	P value
Male	11.215	61.556	< 0.001	5.538	40.000	0.015
Female	6.785	53.286	< 0.001	6.250	28.400	0.201
NR	8.522	50.857	0.001	INF	NA	NA

Age						
Adult	11.365	64.483	< 0.001	5.538	40.000	P = 0.015
Subadult	10.286	16.000	0.855	INF	NA	NA
Juvenile	5.000	19.000	0.701	-	-	-
NR	6.564	50.474	0.001	-	-	-
Habitat						
Casuarina	-	-	-	INF	NaN	NA
Forest	7.200	28.000	0.216	1.000	23.000	0.461
Heathland	4.500	26.000	0.301	-	-	-
Rainforest	8.758	29.588	0.162	1.000	23.000	0.461
Scrubland	5.000	19.000	0.701	-	-	-
Sedgeland	3.000	21.000	0.581	-	-	-
Shrubland	8.018	41.857	0.009	2.000	22.000	0.520
Woodland	8.100	35.333	0.048	3.000	21.000	0.581

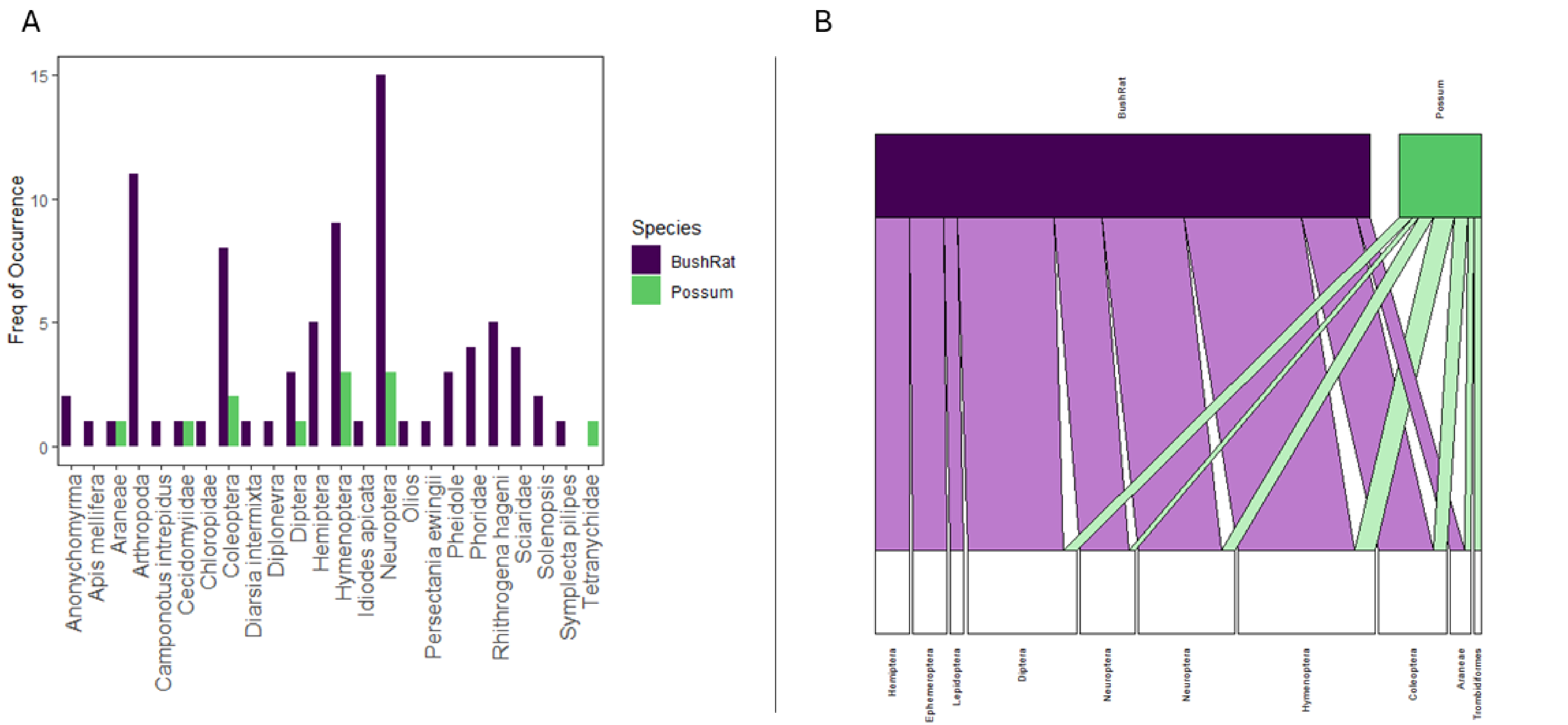


Figure 5-4. (A) Frequency of occurrence of the number of invertebrate diet items detected, at the lowest identified taxonomic level. (B) A bipartite plot of invertebrate diet items found in the scats of bush rats and common brushtail possums at the ordinal level.

5.4.4 Fungi diet items

We identified 93 different ectomycorrhizal fungi from faecal samples; bush rats consumed 82 of these and possums consumed 12. There was no substantial difference in the diet ranges of bush rats (9.984) and possums (3.045) (Fig 5-5). Both species showed differences in the frequency of occurrence of fungal items in the diet (bush rats: $\chi^2_{92} = 339.23$, $p < 0.001$, possums: $\chi^2_{92} = 213.08$, $p < 0.001$), with both mostly consuming fungal diet items from the order Hysterangiales (an order of truffles) (Fig 5-5).

Within species, for both bush rats and possums, males and females did not have substantially different diet ranges (Table 5-3). Males and females of both species consumed some fungal items more than others, based on a chi-squared analysis (Table 5-3), with all mostly consuming items from the genus Hysterangium. The diet ranges of different age categories for both species were also not substantially different (Table 5-3). All age categories, except subadult possums which consumed items evenly, mostly consumed items from the genus Hysterangium (Table 5-3). Habitat types similarly did not produce different diet ranges for either bush rats or possums (Table 5-3). Most individuals in different habitat types consumed some items more than others, with all mostly consuming taxa in the genus Hysterangium (Table 5-3). The exception was possums in either woodland or rainforest habitats, which had an even frequency of consumption (Table 5-3).

Overall, there was an 88.2% overlap in the fungal diets of bush rats and possums (Pianka index = 0.882). Additionally, the fungal composition of bush rat and possum diets was not significantly different ($F_{19} = 1.058$, $p = 0.276$). Of this, the species (i.e., bush rats or possums) accounted for 24.5% of the differences we observed in the data. Most of the overlap in the diet arose from consumption of fungi in the order Hysterangiales (Fig 5-5).

Table 5-3. The Levins' measure of niche breadth and chi-squared results for within-species patterns for fungal diet items. INF represents categories with too few samples to calculate the niche breadth and chi-squared. Dashes (-) represent categories with no samples to calculate the niche breadth and chi-squared. Dashes (-) represent categories where no samples were collected.

	Bush Rats			**Possum**		
			Sex			
	Levins	X^2	P value	Levins	X^2	P value
Male	9.832	279.010	< 0.001	2.739	193.670	< 0.001
Female	8.379	126.440	< 0.001	2.964	109.770	< 0.001
NR	9.188	75.757	< 0.001	3.571	34.200	0.160
			Age			
Adult	10.113	256.460	< 0.001	2.739	193.670	< 0.001

Subadult	7.364	75.667	< 0.001	3.000	25.000	0.574
Juvenile	6.533	46.000	0.013	-	-	-
NR	7.860	74.310	< 0.001	-	-	-
			Habitat			
Casuarina	-	-	-	INF	NA	NA
Forest	8.225	137.040	< 0.001	2.945	153.110	< 0.001
Heathland	2.778	45.400	0.015	-	-	-
Rainforest	6.451	90.185	< 0.001	2.000	26.000	0.519
Scrubland	5.556	40.400	0.047	-	-	-
Sedgeland	4.765	43.889	0.021	-	-	-
Shrubland	9.887	78.767	< 0.001	1.800	43.677	0.022
Woodland	7.563	99.973	< 0.001	3.000	25.000	0.574

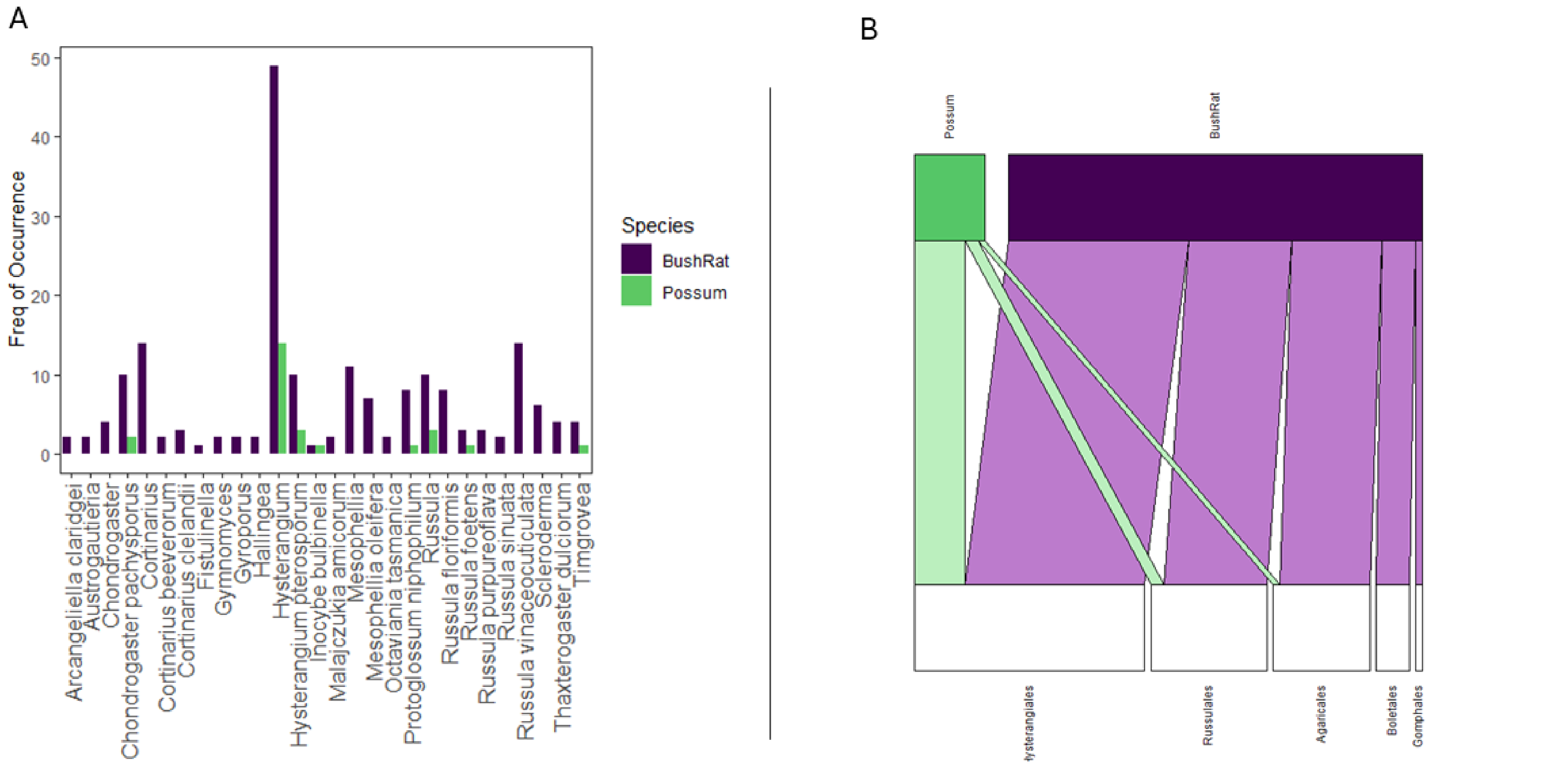


Figure 5-5. (A) Frequency of occurrence of the number of fungal diet items detected, at the lowest identified taxonomic level. (B) A bipartite plot of the overlap of fungal diet items found in the scats of bush rats and common brushtail possums at the ordinal level

5.5 Discussion

Understanding how bush rats and possums use and share resources is a vital step in assessing the likelihood of interspecific competition (Wang et al., 2023). Food is one of the main resources that species compete for, whether it is by one species exploiting a resource more efficiently than others, or by fighting for access (Bell et al., 2023; Kumpan et al., 2019; Santosa et al., 2012), with dietary overlap providing an indication of the potential for competition (Villsen et al., 2022).

Here, using DNA metabarcoding, we found that both species consumed a large range of food resources, indicative of dietary generalists, and providing support for our first prediction. We found additionally that most of the items consumed by possums were also consumed by bush rats, thus supporting our second prediction. However, differences in diet came down to bush rats having a much larger dietary range compared to possums, consuming many items that possums do not. Our findings provide some evidentiary support that is consistent with competition being a mechanism that could account for the inverse numerical relationship between the two study species that we have observed in BNP (Kanishka et al., 2023). We, however, found few fine-scale differences between age and sex components of the population, and some habitat-related differences in diet, disproving our third prediction. Below, we explore the diets of the two species in more detail and the likelihood and consequences of competition when it occurs between dietary generalists.

5.5.1 The diets of bush rats and common brushtail possums

Both bush rats and common brushtail possums are considered omnivorous generalists (Cruz et al., 2012; Vernes et al., 2015), an observation that we corroborated for these species in BNP. Possums and bush rats are widely distributed throughout Australia and commonly co-occur in south-eastern and south-western coastal regions (Callander, 2018; How & Hillcox, 2000). Possums have additionally become an invasive species in New Zealand, where they consume varied plant species that do not occur in their natural range (Glen et al., 2012). The wide range of food types in the diet of possums, including plant material, invertebrates, anthropogenic foods and, occasionally, eggs and nestling birds (Glen et al., 2012; Gloury & Handasyde, 2016; Herath et al., 2021; Scoleri et al., 2020), reflects the ability of possums to track diverse food resources on the ground and in trees (Cruz et al., 2012). It may also reflect the large differences in personality types and individual foraging preferences within local populations (Cruz et al., 2012; Herath et al., 2021). Bush rats consume many types of plants, invertebrates, and fungi (Vernes et al., 2015; Wanniarachchi et al., 2022). The species also shows dietary shifts in response to seasonal differences in the availability of different food types as well as to environmental changes, such as those induced by fire (Vernes et al., 2015; Wanniarachchi et al., 2022). Dietary switching has previously allowed the bush rat to maintain relatively stable populations by shifting from preferred to less-preferred foods when preferred foods become scarce (C. Dickman & Happold, 2022).

At BNP, most of the plants eaten by both species are found in the understorey, particularly grasses like prickly couch grass *Zoysia macrantha*, legumes, and other flowering plants. Given the time of sampling, in the late spring through summer, these plant taxa were likely to be producing seeds and fruits that may be more preferred than leaves owing to their higher energy and nutrient contents (Morrant & Petit, 2012), although we were unable to confirm which parts of the plants the species were consuming. Consumption of understorey plants was expected for bush rats, which are predominantly ground-dwelling, but less so for possums, which spend a significant proportion of time moving and foraging above ground in trees (Gloury & Handasyde, 2016; How & Hillcox, 2000). For example, increased ground-level foraging by possums could reflect the availability of higher quality food on the ground and lower understorey but could also be a result of lower predation risk due to the long-term reduction of red fox activity by poison baiting at BNP (Dexter et al., 2013).

A notable difference in the diets of possums and bush rats was that, while most of the possum diet was plant material, a substantial proportion of the bush rat diet comprised truffle-type fungi. Bush rats have previously been noted to be mycophagous, or consumers of fungi, so our results align with earlier studies (Vernes et al., 2015). Mountain brushtail possums *Trichosurus caninus*, a species closely related to common brushtail possums, have also been found to be mycophagous (Claridge & Lindenmayer, 1998). Invertebrates comprised the smallest proportion of both species' diets, with possums consuming a near-negligible amount. The invertebrates detected were mostly winged insects, particularly lacewings, mayflies, bees and wasps. Consumption of winged insects is surprising but may reflect the ingestion of larval rather than adult forms, as larvae would be easier for bush rats and possums to find in soil or under leaf litter.

5.5.2 Limitations

There are several limitations to DNA metabarcoding which became apparent in this study and limit the conclusions and in-depth investigation of both species' diets. First, many primers struggled to reach species-level identification, limiting our species-level comparisons of diet (Namin et al., 2022). Most of the sequences identified in our study were identified at the order or genus level, while only a few were identified at the species level. While these results do provide a good overview of the types of dietary items that both species are consuming regularly (e.g., understorey plants), we do not know the precise degree of dietary overlap between bush rats and possums, as they may consume different species within the same genus (Villsen et al., 2022). Additionally, unlike histological and morphological methods, DNA metabarcoding can only reveal the identity of the diet item but does not yield information about what parts of that item are being consumed (Alemany et al., 2023). As mentioned above, while we can assume that both species consumed large amounts of flowering plants, based on the season when sampling took place, we cannot confirm if they consumed petals, leaves, roots, or other plant parts (Alemany et al., 2023). There is also potential for misidentification of similar species; for example, *Acacia bellula* and *A. nematophylla* were both identified using the BLASTn tool, but neither have previously been found in or near Jervis Bay (Sritharan et al., 2021). This could be a result of a lack of reference data for many species, limiting the tools' ability to assign species effectively. Finally, we must account for the chance that some detections in both species may have resulted from incidental ingestion, due to the species being a natural part of the gut microbiome, or even from contamination during the collection and processing steps. This can be seen in the large number of non-ectomycorrhizal fungi that were identified in the faecal samples.

5.5.3 Generalist-generalist competition

With substantial overlap in their diets, there is potential for competition to occur between bush rats and common brushtail possums (Wang et al., 2023) which, if confirmed, would be an example of generalist-generalist competition (Barnes & Murphy, 2023). According to Barnes and Murphy (2023), dietary generalist pairs are more likely to compete indirectly than directly, with the most generalist species – the moths *Malacosoma californicum* and *Hyphantria cunea* – in their study being temporally segregated. In Japan, the effect of competition from invasive raccoons *Procyon lotor* on native raccoon dogs *Nyctereutes procyonoides* was reduced because, while both species are generalist omnivores, they displayed different diet preferences in habitats where they co-occurred compared to where they foraged alone (Osaki et al., 2019). Osaki et al. (2019) noted that coexistence was helped by raccoon control programs that have kept raccoons at low density and that the situation may be different if raccoons increased and occupied all habitats where raccoon dogs were present. At BNP, possum activity has increased over many years due to the active management of red foxes in BNP (Kanishka et al., 2023). Although we cannot rule out the possibility that bush rats and possums encounter each other directly, this seems unlikely due to the rapid flight response of both species to auditory, visual or sometimes olfactory disturbance (Fardell et al., 2021, 2022;

Warneke, 1971). Instead, indirect interactions mediated by spatial and/or temporal avoidance are more likely, with the bush rat responding to the presence of the larger possum by diversifying the range of foods that it consumes.

Dietary generalist species often exhibit opportunistic feeding behaviours (de Carvalho et al., 2019; Osaki et al., 2019), consuming food types that may be only temporarily available or switching to less preferred foods if favoured foods are not available or are too costly to acquire. Following a severe fire, for example, Dickman and Happold (2022) found that bush rats increased their consumption of ferns and other less preferred foods that are available immediately post-fire until preferred foods – dicotyledonous plants and fungi – had recovered. Opportunistic feeding can also be a product of avoiding competition (de Carvalho et al., 2019), as noted above in the case of raccoon dogs (Osaki et al., 2019). At BNP, we suggest that dietary opportunism provides a buffer for the bush rat to reduce the potential effects of competition from possums by providing exclusive access to a particularly diverse range of food types, and possibly also through diet switching. As diet switching can be confidently detected only by tracking changes in a forager's diet over time (or space) in relation to the food resources that are available, we suspect but cannot confirm the operation of diet switching in the bush rat at BNP.

Although there are very few areas within the broad geographical range of the bush rat where common brushtail possums do not also occur, we suggest it is unlikely that the dietary generalism of bush rats has evolved to reduce competition for food with possums. Bush rats have relatively small home ranges (<1 ha), limited dispersal ability and exhibit considerable flexibility in the range of microhabitats they inhabit (Ball et al., 2005; Fordyce et al., 2016; Reif et al., 2016). Dietary generalism in these circumstances may be selectively advantageous, with rats being able to shift between food resources that likely vary over time and with disturbances in their restricted home range areas (Fordyce et al., 2016; Peakall et al., 2006). Dietary generalist species often show considerable flexibility in habitat use and behaviours (Reif et al., 2016), as do many members of the genus Rattus (Aplin & Ford, 2014). In fragmented habitats in Madagascar, a generalist folivore, the golden-crowned sifaka *Propithecus tattersalli*, similarly demonstrates plasticity in its diet which allows it to exploit remnant habitat patches and cope with limited dispersal opportunities (Quéméré et al., 2013). Dietary generalists are often likely to be more resilient to environmental disturbances such as fire or habitat fragmentation than dietary specialists (C. Dickman & Happold, 2022; Quéméré et al., 2013). We, therefore, suggest that the ability to exploit varied food items also confers some resilience when the disturbance is in the form of a larger and dominant competitor.

5.5.4 Managing food competition

Bush rats are not threatened over their geographical range, but they experience localised population declines due to habitat loss and fragmentation, predation, and, in BNP, potential competition with common brushtail possums. In protected areas where managers are charged with retaining populations of all native species, how might dietary generalists such as the bush rat best be conserved? As the diverse diets of such species appear to provide a buffer against environmental disturbances and allow fine-scale partitioning of food resources with dominant competitors (Adams et al., 2014; de Carvalho et al., 2019; Osaki et al., 2019), management should seek to retain the full spectrum of food resources. At BNP, management to reduce the adverse effects on bush rats of competition with common brushtail possums may be as simple as ensuring that plant diversity is retained or promoted (Băncilă et al., 2023; Casula et al., 2017; Vernes et al., 2015). Promotion of plant diversity should ensure that co-dependent invertebrates and fungi are also supported, thus increasing available dietary items for bush rats and other dietary generalist species (Băncilă et al., 2023). Identifying the key food resources used and shared by at least the more common consumer species would be a fruitful research direction for managers of BNP and other protected areas.

5.6 Conclusion

Both bush rats and common brushtail possums are dietary generalists that show substantial overlap in their broad diets. This similarity in diets suggests that, in periods of restricted food availability, competition between bush rats and possums could have detrimental effects. However, both species are capable of utilising parts of the food resource base at finer scales of individual food types, and possibly also of switching diets to maximise the benefits of consuming such foods relative to the costs. In the case of the bush rat, a broad-ranging diet likely provides a buffer against the negative impacts of competition from the larger brushtail possum, reducing their risk of encounters with possums by constraining their dietary range and foraging in safer habitats. Our results demonstrate that, even when there is high similarity in the foods consumed by dietary generalist species, fine-scale partitioning of food types within and between competitor populations, or possibly diet switching, of food resources may be important in alleviating competition and permitting co-existence.

5.7 References

Adams, A. L., Recio, M. R., Robertson, B. C., Dickinson, K. J. M., & van Heezik, Y. (2014). Understanding home range behaviour and resource selection of invasive common brushtail possums (*Trichosurus vulpecula*) in urban environments. *Biological Invasions*, *16*(9), 1791–1804. https://doi.org/10.1007/s10530-013-0627-4

Alemany, I., Pérez-Cembranos, A., Castro, J. A., Picornell, A., Pérez-Mellado, V., & Ramon, C. (2023). Diet of the Insular Lizard, *Podarcis lilfordi* (Günther, 1874): Complementary Morphological and Molecular Approaches. *Animals*, *13*(3), Article 3. https://doi.org/10.3390/ani13030507

Altschul, S. F., Gish, W., Miller, W., Myers, E. W., & Lipman, D. J. (1990). Basic local alignment search tool. *Journal of Molecular Biology*, *215*(3), 403–410. https://doi.org/10.1016/S0022-2836(05)80360-2

Anderson, M. J. (2017). Permutational Multivariate Analysis of Variance (PERMANOVA). In *Wiley StatsRef: Statistics Reference Online* (pp. 1–15). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118445112.stat07841

Aplin, K., & Ford, F. (2014). Murine rodents: Late but highly successful invaders. In H. H. T. Prins & I. J. Gordon (Eds.), *Invasion Biology and Ecological Theory: Insights from a Continent in Transformation* (pp. 196–240). Cambridge University Press. https://doi.org/10.1017/CBO9781139565424.012

Ball, S. J., Ramsey, D., Nugent, G., Warburton, B., Efford, M., Ball, S. J., Ramsey, D., Nugent, G., Warburton, B., & Efford, M. (2005). A method for estimating wildlife detection probabilities in relation to home-range use: Insights from a field study on the common brushtail possum (*Trichosurus vulpecula*). *Wildlife Research*, *32*(3), 217–227. https://doi.org/10.1071/WR03125

Băncilă, R. I., Cogălniceanu, D., Manu, M., Plăiaşu, R., Stănescu, F., Memedemin, D., Skolka, M., Tofan, L., & Lăcătuşu, A. (2023). A Multi-Community Approach in Biodiversity Assessment of a Peat Bog in the Southern Carpathians (Romania) and Implications for Conservation. *Environmental Entomology*, *52*(2), 217–229. https://doi.org/10.1093/ee/nvad004

Banks, P. B. (1999). Predation by introduced foxes on native bush rats in Australia: Do foxes take the doomed surplus? *Journal of Applied Ecology*, *36*(6), 1063–1071. https://doi.org/10.1046/j.1365-2664.1999.00463.x

Barnes, E. E., & Murphy, S. M. (2023). Bottom-up and top-down pressures mediate competition between two generalist insects. *Ecology*, *104*(3), e3957. https://doi.org/10.1002/ecy.3957

Bell, E., Fisher, J. T., Darimont, C., Hart, H., & Bone, C. (2023). Influence of heterospecifics on mesocarnivore behaviour at shared scavenging opportunities in the Canadian Rocky Mountains. *Scientific Reports*, *13*(1), Article 1. https://doi.org/10.1038/s41598-023-34911-4

Bice, J., & Moseby, K. (2008). Diets of the re-introduced greater bilby (*Macrotis lagotis*) and burrowing bettong (*Bettongia lesueur*) in the Arid Recovery Reserve, Northern South Australia. *Australian Mammalogy*, *30*(1), 1–12. https://doi.org/10.1071/am08001

BOLD Systems. (2023). *Bold Systems v4*. https://www.boldsystems.org/

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, *161*(1), 1–28. https://doi.org/10.1086/343878

BOM. (2021). *Climate statistics for Australian locations*. http://www.bom.gov.au/climate/averages/tables/cw_068151.shtml

Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A., & Holmes, S. P. (2016). DADA2: High-resolution sample inference from Illumina amplicon data. *Nature Methods*, *13*(7), Article 7. https://doi.org/10.1038/nmeth.3869

Callander, M. (2018). *Translocation and reintroduction of native bush rats (Rattus fuscipes) into Sydney Harbour National Park: Restoring ecosystem function*. https://researchdirect.westernsydney.edu.au/islandora/object/uws%3A47378/

Calver, M., & Loneragan, N. (2024). *Quantifying Diets of Wildlife and Fish: Practical and Applied Methods*. CSIRO publishing. https://www.nhbs.com/quantifying-diets-of-wildlife-and-fish-book

Casula, P., Luiselli, L., Milana, G., & Amori, G. (2017). Habitat structure and disturbance affect small mammal populations in Mediterranean forests. *Basic and Applied Ecology*, *19*, 76–83. https://doi.org/10.1016/j.baae.2016.11.003

Chard, M., Martin, J., French, K., & Major, R. E. (2017). Rainfall events drive foraging choices by an urban coloniser. *Urban Ecosystems*, *20*(6), 1285–1290. https://doi.org/10.1007/s11252-017-0680-3

Claridge, A. W., & Lindenmayer, D. B. (1998). Consumption of hypogeous fungi by the mountain brushtail possum (*Trichosurus caninus*) in eastern Australia. *Mycological Research*, *102*(3), 269–272. https://doi.org/10.1017/S0953756297004978

Corman, A.-M., Mendel, B., Voigt, C. C., & Garthe, S. (2016). Varying foraging patterns in response to competition? A multicolony approach in a generalist seabird. *Ecology and Evolution*, *6*(4), 974–986. https://doi.org/10.1002/ece3.1884

Cruz, J., Sutherland, D. R., Martin, G. R., & Leung, L. K.-P. (2012). Are smaller subspecies of common brushtail possums more omnivorous than larger ones? *Austral Ecology*, *37*(8), 893–902. https://doi.org/10.1111/j.1442-9993.2011.02346.x

de Carvalho, D. R., de Castro, D. M. P., Callisto, M., Chaves, A. J. de M., Moreira, M. Z., & Pompeu, P. S. (2019). Stable isotopes and stomach content analyses indicate omnivorous habits and opportunistic feeding behavior of an invasive fish. *Aquatic Ecology*, *53*(3), 365–381. https://doi.org/10.1007/s10452-019-09695-3

Dexter, N., Hudson, M., James, S., MacGregor, C., & Lindenmayer, D. B. (2013). Unintended Consequences of Invasive Predator Control in an Australian Forest: Overabundant Wallabies and Vegetation Change. *PLOS ONE*, *8*(8), e69087. https://doi.org/10.1371/journal.pone.0069087

Dexter, N., & Murray, A. (2009). The impact of fox control on the relative abundance of forest mammals in East Gippsland, Victoria. *Wildlife Research*, *36*(3), 252–261. https://doi.org/10.1071/WR08135

Dickman, C., & Happold, D. (2022). Demographic and dietary responses of small mammals to high severity fire. *Australian Zoologist*, *42*. https://doi.org/10.7882/AZ.2022.018

Dickman, C. R. (2011). Competition, Animal. In *Competition, Animal* (pp. 117–122). University of California Press. https://doi.org/10.1525/9780520948433-031

Dickman, C. R., & Newsome, T. M. (2015). Individual hunting behaviour and prey specialisation in the house cat *Felis catus*: Implications for conservation and management. *Applied Animal Behaviour Science*, *173*, 76–87. https://doi.org/10.1016/j.applanim.2014.09.021

Esri. (2022). *ArcGIS Pro 3.0.3* [Computer software]. Esri.

Fardell, L. L., Nano, C. E. M., Pavey, C. R., & Dickman, C. R. (2021). Small Prey Animal Habitat Use in Landscapes of Fear: Effects of Predator Presence and Human Activity Along an Urban Disturbance Gradient. *Frontiers in Ecology and Evolution*, *9*. https://www.frontiersin.org/articles/10.3389/fevo.2021.750094

Fardell, L. L., Nano, C. E. M., Pavey, C. R., & Dickman, C. R. (2022). Small Prey Animal Foraging Behaviors in Landscapes of Fear: Effects of Predator Presence and Human Activity Along an Urban Disturbance Gradient. *Frontiers in Ecology and Evolution*, *10*. https://www.frontiersin.org/articles/10.3389/fevo.2022.805891

Favreau, F.-R., Goldizen, A. W., Fritz, H., & Pays, O. (2018). Food supply fluctuations constrain group sizes of kangaroos and in turn shape their vigilance and feeding strategies. *Animal Behaviour*, *135*, 165–176. https://doi.org/10.1016/j.anbehav.2017.11.020

Fleming, P. A., Crawford, H. M., Stobo-Wilson, A. M., Dawson, S. J., Dickman, C. R., Dundas, S. J., Gentle, M. N., Newsome, T. M., O’Connor, J., Palmer, R., Riley, J., Ritchie, E. G., Speed, J., Saunders, G., Stuart, J.-M. D., Thompson, E., Turpin, J. M.,

& Woinarski, J. C. Z. (2021). Diet of the introduced red fox *Vulpes vulpes* in Australia: Analysis of temporal and spatial patterns. *Mammal Review*, *51*(4), 508–527. https://doi.org/10.1111/mam.12251

Fordyce, A., Hradsky, B. A., Ritchie, E. G., & Di Stefano, J. (2016). Fire affects microhabitat selection, movement patterns, and body condition of an Australian rodent (*Rattus fuscipes*). *Journal of Mammalogy*, *97*(1), 102–111.

Gebremedhin, B., Flagstad, Ø., Bekele, A., Chala, D., Bakkestuen, V., Boessenkool, S., Popp, M., Gussarova, G., Schrøder-Nielsen, A., Nemomissa, S., Brochmann, C., Stenseth, N. C., & Epp, L. S. (2016). DNA Metabarcoding Reveals Diet Overlap between the Endangered Walia Ibex and Domestic Goats—Implications for Conservation. *PLOS ONE*, *11*(7), e0159133. https://doi.org/10.1371/journal.pone.0159133

Glen, A. S., Byrom, A. E., Pech, R. P., Cruz, J., Schwab, A., Sweetapple, P. J., Yockney, I., Nugent, G., Coleman, M., & Whitford, J. (2012). Ecology of brushtail possums in a New Zealand dryland ecosystem. *New Zealand Journal of Ecology; Christchurch*, *36*(1), 29–37.

Gloury, A. M., & Handasyde, K. A. (2016). Comparative dietary ecology of two congeneric marsupial folivores. *Austral Ecology*, *41*(4), 355–366. https://doi.org/10.1111/aec.12320

Herath, A. P. H. M., Wat, K. K. Y., Banks, P. B., & McArthur, C. (2021). Animal personality drives individual dietary specialisation across multiple dimensions in a mammalian herbivore. *Functional Ecology*, *35*(10), 2253–2265. https://doi.org/10.1111/1365-2435.13893

How, R. A., & Hillcox, S. J. (2000). Brushtail possum, *Trichosurus vulpecula*, populations in south-western Australia: Demography, diet and conservation status. *Wildlife Research*, *27*(1), 81–89. Scopus. https://doi.org/10.1071/WR98064

Kanishka, A. M., Blanchard, W., Lavery, T. H., Robinson, N. M., Dexter, N., Dickman, C. R., MacGregor, C., & Lindenmayer, D. B. (2023). Environmental variables influence patterns of mammal co-occurrence following introduced predator control. *PLOS ONE*, *18*(11), e0292919. https://doi.org/10.1371/journal.pone.0292919

Kefford, B. J., Schäfer, R. B., Liess, M., Goonan, P., Metzeling, L., & Nugegoda, D. (2010). A similarity-index–based method to estimate chemical concentration limits protective for ecological communities. *Environmental Toxicology and Chemistry*, *29*(9), 2123–2131. https://doi.org/10.1002/etc.256

Kent, C. M., Huh, K. M., Hunter, S. C., Judson, K., Powell, L. L., & Sherry, T. W. (2022). High resource overlap and small dietary differences are widespread in food-limited warbler (Parulidae) communities. *Ibis*, *164*(1), 44–59. https://doi.org/10.1111/ibi.13006

Klure, D. M., Cragun, B. J., & Dearing, M. D. (2023). Sympatric rodents in a desert shrubland differ in arthropod consumption. *Journal of Arid Environments*, *214*, 104999. https://doi.org/10.1016/j.jaridenv.2023.104999

Kovacs, E. K., Crowther, M. S., Webb, J. K., & Dickman, C. R. (2012). Population and behavioural responses of native prey to alien predation. *Oecologia*, *168*(4), 947–957. https://doi.org/10.1007/s00442-011-2168-9

Krebs, C. J. (2014). *Ecological Methodology* (3rd ed.). Benjamin/Cummings.

Kumpan, L. T., Rothman, J. M., Chapman, C. A., & Teichroeb, J. A. (2019). Playing it safe? Solitary vervet monkeys (*Chlorocebus pygerythrus*) choose high-quality foods more than those in competition. *American Journal of Primatology*, *81*(7), e23002. https://doi.org/10.1002/ajp.23002

Lamb, J. S., Satgé, Y. G., & Jodice, P. G. R. (2017). Influence of density-dependent competition on foraging and migratory behavior of a subtropical colonial seabird. *Ecology and Evolution*, *7*(16), 6469–6481. https://doi.org/10.1002/ece3.3216

Larsson, A. (2014). AliView: A fast and lightweight alignment viewer and editor for large datasets. *Bioinformatics*, *30*(22), 3276–3278. https://doi.org/10.1093/bioinformatics/btu531

Levins, R. (1968). *Evolution in Changing Environments: Some Theoretical Explorations. (MPB-2)*. Princeton University Press. https://doi.org/10.2307/j.ctvx5wbbh

Lindenmayer, D. B., Cunningham, R. B., & Peakall, R. (2005). The Recovery of Populations of Bush Rat *Rattus fuscipes* in Forest Fragments Following Major Population Reduction. *Journal of Applied Ecology*, *42*(4), 649–658.

Lindenmayer, D. B., MacGregor, C., Welsh, A., Donnelly, C., Crane, M., Michael, D., Montague-Drake, R., Cunningham, R. B., Brown, D., Fortescue, M., Dexter, N., Hudson, M., Gill, A. M., Lindenmayer, D. B., MacGregor, C., Welsh, A., Donnelly, C., Crane, M., Michael, D., … Gill, A. M. (2008). Contrasting mammal responses to vegetation type and fire. *Wildlife Research*, *35*(5), 395–408. https://doi.org/10.1071/WR07156

Lindenmayer, D. B., Wood, J., MacGregor, C., Foster, C., Scheele, B., Tulloch, A., Barton, P., Banks, S., Robinson, N., Dexter, N., O'Loughlin, L. S., & Legge, S. (2018). Conservation conundrums and the challenges of managing unexplained declines of multiple species. *Biological Conservation*, *221*, 279–292. https://doi.org/10.1016/j.biocon.2018.03.007

Lloyd, K. J., & Vetter, S. (2019). Generalist trophic ecology in a changing habitat: The case of the four-striped mouse in a woody-encroached savannah. *African Journal of Ecology*, *57*(3), 371–381. https://doi.org/10.1111/aje.12613

Macgregor, C., Blanchard, W., Stein, J., & Lindenmayer, D. (2020). Factors influencing the occurrence of the Southern Long-nosed Bandicoot (*Perameles nasuta* Geoffroy) during a population irruption and decline. *Austral Ecology*, *45*. https://doi.org/10.1111/aec.12930

Martin, M. (2011). Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet.Journal*, *17*(1), Article 1. https://doi.org/10.14806/ej.17.1.200

Morrant, D. S., & Petit, S. (2012). Strategies of a small nectarivorous marsupial, the western pygmy-possum, in response to seasonal variation in food availability. *Journal of Mammalogy*, *93*(6), 1525–1535. https://doi.org/10.1644/12-MAMM-A-031.1

Nagy-Reis, M. B., & Setz, E. Z. F. (2017). Foraging strategies of black-fronted titi monkeys (*Callicebus nigrifrons*) in relation to food availability in a seasonal tropical forest. *Primates*, *58*(1), 149–158. https://doi.org/10.1007/s10329-016-0556-9

Namin, S. M., Son, M., & Jung, C. (2022). Current methodologies in construction of plant-pollinator network with emphasize on the application of DNA metabarcoding approach. *Journal of Ecology and Environment*, *46*. https://doi.org/10.5141/jee.22.003

NCBI. (2023). *National Center for Biotechnology Information*. https://www.ncbi.nlm.nih.gov/

Nielsen, A., Reitan, T., Rinvoll, A. W., & Brysting, A. K. (2017). Effects of competition and climate on a crop pollinator community. *Agriculture, Ecosystems & Environment*, *246*, 253–260. https://doi.org/10.1016/j.agee.2017.06.006

Nordberg, E. J., & Schwarzkopf, L. (2019). Reduced competition may allow generalist species to benefit from habitat homogenization. *Journal of Applied Ecology*, *56*(2), 305–318. https://doi.org/10.1111/1365-2664.13299

Nuske, S. J., Anslan, S., Tedersoo, L., Bonner, M. T. L., Congdon, B. C., & Abell, S. E. (2018). The endangered northern bettong, *Bettongia tropica*, performs a unique and potentially irreplaceable dispersal function for ectomycorrhizal truffle fungi. *Molecular Ecology*, *27*(23), 4960–4971. https://doi.org/10.1111/mec.14916

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M. D., Durand, S., … Weedon, J. (2022). *vegan: Community Ecology Package* (Version 2.6-4) [Computer software]. https://cran.r-project.org/web/packages/vegan/index.html

Osaki, A., Sashika, M., Abe, G., Shinjo, K., Fujimoto, A., Nakai, M., Shimozuru, M., & Tsubota, T. (2019). Comparison of feeding habits and habitat use between invasive raccoons and native raccoon dogs in Hokkaido, Japan. *BMC Ecology*, *19*(1), 35. https://doi.org/10.1186/s12898-019-0249-5

Pagès, H., Aboyoun, P., Gentleman, R., DebRoy, S., Carey, V., Delhomme, N., Ernst, F., Khan, H., Lakshman, A., O'Neill, K., Obenchain, V., Ramos, M., Vill, A., Wokaty, J., & Wright, E. (2023). *Biostrings: Efficient manipulation of biological strings* (Version 2.70.1) [Computer software]. Bioconductor version: Release (3.18). https://doi.org/10.18129/B9.bioc.Biostrings

Peakall, R., Ebert, D., Cunningham, R., & Lindenmayer, D. (2006). Mark–recapture by genetic tagging reveals restricted movements by bush rats (*Rattus fuscipes*) in a fragmented landscape. *Journal of Zoology*, *268*(2), 207–216. https://doi.org/10.1111/j.1469-7998.2005.00011.x

Pearson, K. (1900). X. On the criterion that a given system of deviations from the probable in the case of a correlated system of variables is such that it can be reasonably supposed to have arisen from random sampling. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science*, *50*(302), 157–175. https://doi.org/10.1080/14786440009463897

Pianka, E. R. (1972). R and K Selection or b and d Selection? *The American Naturalist*, *106*(951), 581–588. JSTOR.

Prevedello, J. A., Dickman, C. R., Vieira, M. V., & Vieira, E. M. (2013). Population responses of small mammals to food supply and predators: A global meta-analysis. *Journal of Animal Ecology*, *82*(5), 927–936. https://doi.org/10.1111/1365-2656.12072

Püttker, T., Barros, C. S., Pinotti, B. T., Bueno, A. A., & Pardini, R. (2019). Co-occurrence patterns of rodents at multiple spatial scales: Competitive release of generalists following habitat loss? *Journal of Mammalogy*, *100*(4), 1229–1242. https://doi.org/10.1093/jmammal/gyz083

Quéméré, E., Hibert, F., Miquel, C., Lhuillier, E., Rasolondraibe, E., Champeau, J., Rabarivola, C., Nusbaumer, L., Chatelain, C., Gautier, L., Ranirison, P., Crouau-Roy, B., Taberlet, P., & Chikhi, L. (2013). A DNA Metabarcoding Study of a Primate Dietary Diversity and Plasticity across Its Entire Fragmented Range. *PLOS ONE*, *8*(3), e58971. https://doi.org/10.1371/journal.pone.0058971

R Core Team. (2021). *R: A Language and Environment for Statistical Computing* [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Reif, J., Hořák, D., Krištín, A., Kopsová, L., & Devictor, V. (2016). Linking habitat specialization with species' traits in European birds. *Oikos*, *125*(3), 405–413. https://doi.org/10.1111/oik.02276

Santosa, Y., Taqiuddin, Mustari, A. H., & Rahman, D. A. (2012). Cohabitation Study of the Leaf Monkey and Bornean White-Bearded Gibbons in Gunung Palung National Park, West Kalimantan. *HAYATI Journal of Biosciences*, *19*(3), 115–123. https://doi.org/10.4308/hjb.19.3.115

Scoleri, V. P., Johnson, C. N., Vertigan, P., & Jones, M. E. (2020). Conservation trade-offs: Island introduction of a threatened predator suppresses invasive mesopredators but eliminates a seabird colony. *Biological Conservation*, *248*, 108635. https://doi.org/10.1016/j.biocon.2020.108635

Shutt, J. D., Trivedi, U. H., & Nicholls, J. A. (2021). Faecal metabarcoding reveals pervasive long-distance impacts of garden bird feeding. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1951), 20210480. https://doi.org/10.1098/rspb.2021.0480

Sritharan, M. S., Scheele, B. C., Blanchard, W., & Lindenmayer, D. B. (2021). Spatial associations between plants and vegetation community characteristics provide insights into the processes influencing plant rarity. *PLOS ONE*, *16*(12), e0260215. https://doi.org/10.1371/journal.pone.0260215

Taberlet, P., Coissac, E., Pompanon, F., Gielly, L., Miquel, C., Valentini, A., Vermat, T., Corthier, G., Brochmann, C., & Willerslev, E. (2007). Power and limitations of the chloroplast trnL (UAA) intron for plant DNA barcoding. *Nucleic Acids Research*, *35*(3), e14. https://doi.org/10.1093/nar/gkl938

Taws, N. (1998). *Fire and vegetation management in Jervis Bay Territory*. Taws Botanical Research.

Treloar, S., Lohr, C., Hopkins, A. J. M., & Davis, R. A. (2021). Rapid population expansion of Boodie (Burrowing Bettong, *Bettongia lesueur*) creates potential for resource competition with Mala (Rufous Hare-wallaby, *Lagorchestes hirsutus*). *Ecological Management & Restoration*, *22*(S1), 54–57. https://doi.org/10.1111/emr.12471

Van Valen, L. (1965). Morphological Variation and Width of Ecological Niche. *The American Naturalist*, *99*(908), 377–390.

Vernes, K., Cooper, T., & Green, S. (2015). Seasonal fungal diets of small mammals in an Australian temperate forest ecosystem. *Fungal Ecology*, *18*, 107–114. https://doi.org/10.1016/j.funeco.2015.09.015

Villsen, K., Corse, E., Archambaud-Suard, G., Héran, K., Meglécz, E., Ereskovsky, A. V., Chappaz, R., & Dubut, V. (2022). Diet Metabarcoding Reveals Extensive Dietary Overlap between Two Benthic Stream Fishes (*Zingel asper* and *Cottus gobio*) and Provides Insights into Their Coexistence. *Diversity*, *14*(5), Article 5. https://doi.org/10.3390/d14050412

Wang, D., Hu, X., Li, M., Liu, J., Tang, M., Liu, W., Zhan, J., Xu, Y., & Zhang, W. (2023). Diet composition and interspecific niche of Taohongling Sika deer (*Cervus nippon kopschi*) and its sympatric Reeve’s muntjac (*Muntiacus reevesi*) and Chinese hare (*Lepus sinensis*) in winter (Animalia, Mammalia). *ZooKeys*, *1149*, 17–36. https://doi.org/10.3897/zookeys.1149.96936

Wanniarachchi, S., Swan, M., Nevil, P., & York, A. (2022). Using eDNA metabarcoding to understand the effect of fire on the diet of small mammals in a woodland ecosystem. *Ecology and Evolution*, *12*(11), e9457. https://doi.org/10.1002/ece3.9457

Warneke, R. M. (1971). A field study of the Australian bush rat, *Rattus fuscipes* (Waterhouse) (Rodentia, Muridae). *Wildlife Contributions. Fisheries & Wildlife Department, Victoria*, *14*, 1–115.

Woo, K. J., Elliott, K. H., Davidson, M., Gaston, A. J., & Davoren, G. K. (2008). Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *Journal of Animal Ecology*, *77*(6), 1082–1091. https://doi.org/10.1111/j.1365-2656.2008.01429.x

Yoccoz, N. G. (2012). The future of environmental DNA in ecology. *Molecular Ecology*, *21*(8), 2031–2038. https://doi.org/10.1111/j.1365-294X.2012.05505.x

Zarkami, R., Hesami, H., & Sadeghi Pasvisheh, R. (2020). Assessment, monitoring and modelling of the abundance of Dunaliella salina Teod in the Meighan wetland, Iran using decision tree model. *Environmental Monitoring and Assessment*, *192*(3), 172. https://doi.org/10.1007/s10661-020-8148-y

Zhang, J. (2016). *spaa: SPecies Association Analysis* (Version 0.2.2) [R package version 0.2.2; R package version 0.2.2]. R package version 0.2.2. https://cran.r-project.org/web/packages/spaa/index.html

Chapter 6 Overall Discussion

This thesis aimed to investigate potential competition between two co-occurring native mammal species – the bush rat *Rattus fuscipes* and the common brushtail possum *Trichosurus vulpecula* – after a disturbance had led to elevated population growth in Booderee National Park (BNP), which has been linked to the removal of red foxes *Vulpes vulpes* (Dexter et al., 2013; Lindenmayer et al., 2018). Simultaneously, bush rats have been in decline, with no clear cause (Lindenmayer et al., 2018). I investigated this decline by assessing the relationship between common brushtail possums and bush rats to determine whether possums contributed to the decline of bush rats in BNP. I predicted that the relationship would most likely be characterised by competitive interactions.

My research has revealed that there is a negative association between bush rats and common brushtail possums, suggesting that possums have contributed, and continue to contribute, to the decline of bush rats in BNP. The process appears to be a competitive one. In arriving at this conclusion, I addressed three aims.

Firstly, I aimed to quantify changes in co-occurrence of the two species over time (Chapter 3). Using a Bayesian regression model, I found a long-term negative association between bush rats and possums, confirming that as possum numbers grew, bush rat abundance declined.

My second aim was to document evidence of competitive interactions through a manipulative experimental design (Chapter 4). I provided supplementary food sources across sites where possums and rats co-occurred, but restricted possum access at half of these sites. While I did not document direct competitive interactions, I did find that possum activity was associated with bush rat foraging (i.e., eating supplementary food) for shorter periods. I concluded that possums have a negative influence on the foraging frequency and giving-up patterns of bush rats at food sources.

Finally, I aimed to determine if there was a significant overlap in food resource use by the two species, specifically by investigating the diets of bush rats and possums (Chapter 5). I found that bush rats and possums had wide dietary ranges, with both showing some preference for plant material. I also found that the diets of the two species were significantly similar, suggesting a high potential for competition. However, bush rats also showed a greater range in diet than possums, consuming a larger variety of invertebrates and fungi, which should allow them to switch diets or focus on alternative food types if their preferred plant material was being consumed by possums. I concluded that, while there was significant potential for competition, this is buffered by bush rats' greater dietary range. This buffering effect could be expected to reduce the chance of significant population declines in bush rats, but perhaps not stop population declines altogether.

6.1 Nature of the negative association

Based on the results of my three data-based chapters (Chapters 3-5), I suggest that the negative association between bush rats and common brushtail possums arises from temporal avoidance, which in turn results in restricted foraging activity by bush rats. Avoidance is a behavioural response to potential aggressive interactions and can be a response to both predators and dominant competitors (Astete et al., 2017; Barrull et al., 2014). In many mammal species, such avoidance is primarily demonstrated by the segregation of, or total avoidance of, shared space (Rayan & Linkie, 2016; Traba et al., 2016). However, my results demonstrate that the association between possums and bush rats did not result in competitive exclusion, and therefore, I cannot characterise this avoidance as spatial (Castillo-Alvino & Marvá, 2020; Dallas et al., 2019). Temporal avoidance, as I have referred to it in this thesis, can be described as a fine-scale pattern of a species' use of the same habitat as that of a co-occurring species, but at times that do not coincide (Bell et al., 2023; Friedemann et al., 2016). While this can promote co-existence through the segregation of resource use and reduction in the likelihood of aggressive interactions, temporal avoidance can lead to restricted foraging through reduced time spent foraging or increased time spent in energetically costly behaviours such as vigilance or flight (Bell et al., 2023; Shuai et al., 2016).

One of the major limitations of this thesis is that, despite using multiple methods to test for and quantify competition, I could not find evidence to provide unambiguous confirmation that competition occurred. To do this would have required continuous removal of possums from replicate study areas, with simultaneous control areas where possums remained, with population monitoring over a period of time sufficient for bush rats to show a numerical response (Dickman, 2011; Hart et al., 2018). Such a large-scale experiment would be logistically challenging, expensive and – depending on the fate of removed possums – ethically debatable. However, I suggest that competition remains the most likely inference that can be drawn. In addition, the mechanism is most likely to be interference competition rather than exploitative competition. Possums have previously been documented as being aggressive (Youngentob et al., 2012), and their large size compared to bush rats would likely gain them a considerable advantage in pair-wise encounters. By contrast, it is unlikely that the negative association we observed between the two species arises from exploitative competition (Ferguson et al., 2013). This is based in part on the dietary range results (Chapter 5), which show that bush rats consume a greater range of dietary items than possums, potentially using diet switching to buffer against competitive interactions (de Carvalho et al., 2019; Osaki et al., 2019). There were no instances detected of bush rats foraging alongside possums, as might be expected if the interaction between the species was mediated by exploitation; instead, partitioning of activity in the same habitat is suggestive of avoidance of potentially aggressive interactions by bush rats on a fine temporal scale.

6.2 Other factors influencing the decline

This thesis provides evidence of other factors that are likely contributing to the decline of bush rats in BNP, and possibly other areas in Australia. Two major factors found to be associated with bush rat declines were fire and high rainfall. Bush rats, both in this study and in previous research, are strongly impacted by wildfires and often take multiple years to recover their abundance (Arthur et al., 2012; Lindenmayer et al., 2008). Similarly, the results of my third chapter, which took place at the tail end of a major flooding event in New South Wales, Australia (Fryirs et al., 2023), demonstrated that high rainfall events restrict foraging behaviour, especially foraging frequency and length. Previous research has likewise shown that many species are negatively impacted by high rainfall events and will forage less as a response (Chard et al., 2017; Śmielak et al., 2023).

6.3 Competition and conservation

The major change in the ecosystem that I considered in this thesis was the removal of the invasive red fox from BNP, which was a conservation intervention designed to reduce red fox predation on small native mammals (Dexter et al., 2013; Lindenmayer et al., 2018). As my literature review demonstrates (Chapter 2), competition is often not considered in conservation interventions, although it can lead to unexpected consequences (Heinen et al., 2020; Lindenmayer et al., 2018). Considering that often many interactions are indirect and hard to predict, it is not surprising that potential negative consequences such as a decline in bush rat numbers were overlooked during the conception of the fox baiting program. However, my study agrees with the growing consensus that it is important to observe, study and conceptualise ecosystems to inform modelling techniques, such as predictive modelling, trophic webs, and random forest, to predict the impacts of unexpected interactions (Bode et al., 2015; Llewelyn et al., 2023). Additionally, it is important to monitor these impacts after the implementation of a conservation intervention to learn and improve our understanding of the species interactions that characterise natural systems (Bode et al., 2015; Llewelyn et al., 2023; Lurgi et al., 2018).

6.4 Future directions and limitations

The major limitation of this study was the inability to fully quantify the nature of the negative association between bush rats and possums. This is because of the complexity of competition, which often involves indirect interactions that can be difficult to expose (Hart et al., 2018) and the practical difficulty of implementing field experiments that can critically quantify competition. There are, nonetheless, several further lines of investigation that can increase our understanding of this relationship. First, it would be valuable to measure resource availability, especially in terms of plant availability, to determine if there are limitations in shared, preferred dietary items (Kral-O'Brien et al., 2023). Second, it would be insightful to measure the movement patterns and proximity of the two species to determine spatial overlaps (Tosa et al., 2015). Research suggests that competition increases with increased population densities, resulting in closer proximity of individuals (Bird et al., 2019), as well as an increased probability of interspecific encounters (Dickman & Woodside, 1983). It would also be interesting to investigate other interactions, such as the predation of rats by possums (Alemany et al., 2023; Scoleri et al., 2020). Although no evidence of such predation was found in the present study, it may be a rare event that is likely to be detected only with a much larger sampling effort. Finally, with further analyses, it would be beneficial to fit dynamic time-series models, such as the models used by Gause, to further explore the concepts of muti-species interactions (Gause, 1934; Jørgensen et al., 2007).

Other factors could be investigated to untangle the drivers of the decline of bush rats in BNP. One is to examine predation of bush rats by other species, such as powerful owls *Ninox strenua* (Lindenmayer et al., 2018), however, this has not been commonly observed. This could be done using the same DNA metabarcoding techniques used in the project to investigate the diet and prey choice of powerful owls and other predators (Lu et al., 2021). It would also be useful to explore the impact of macropods, which have been shown to be strong competitors with other herbivores and which also have a significant impact on the vegetation in BNP (Dexter et al., 2012; White & Fleming, 2021). This could be investigated by comparing the abundance of bush rats within and outside of macropod exclosures, which have been set up in BNP to investigate the effects of macropods on vegetation (Chard et al., 2022).

As this thesis has demonstrated, there is evidence that possums have a negative influence on bush rat populations. The challenge now is how to efficiently manage this association to prevent further negative outcomes such as the potential local loss of bush rats from BNP. There are two key management options that may be feasible: (1) managing possum populations, and (2) managing vegetation availability. Managing possum populations includes reducing population numbers or spatially restricting possums, both of which may reduce the impact of the species on small vertebrates within the ecosystem (Beggs et al., 2020; Bellingham et al., 2016; Lurgi et al., 2018). However, these actions can be ineffective or result in unforeseen negative outcomes if not carried out carefully (Beggs et al., 2020; Bellingham et al., 2016). In addition, population control actions, such as culling native species, are often unethical (Beggs et al., 2019). The alternative method is to manage vegetation availability and structure in the ecosystem. Increased vegetation structure may allow small mammals, like bush rats, to find refuge from dominant competitors, thereby protecting them from negative interactions (Casula et al., 2017). Managing vegetation structure and diversity may also have the added benefit of increasing available food resources, once again limiting opportunities from negative interactions (Băncilă et al., 2023). However, such a management action could also have negative consequences, as increased vegetation may also result in higher fuel loads, resulting in high-severity fires in an already fire-prone ecosystem (Rachmawati et al., 2018).

Managing vegetation is unlikely to be a simple task, or even to be feasible at scale, even if unexpected consequences of increasing vegetation diversity and structure can be ruled out (Casula et al., 2017; Rachmawati et al., 2018). A further possibility is to use “artificial vegetation”, or “vegetation replacement structures”. For example, the establishment of simple wire mesh structures has been advocated recently to provide shelter for small vertebrates from larger predators where above-ground vegetation has been removed locally by fire (Watchorn et al., 2024). Such structures are simple, cheap and easy to construct and, if implemented at BNP, could provide loci within the landscapes where bush rats would have security of access from possums. Of course, any management action that is taken should take a holistic ecosystem approach, considering the impacts on key species and interactions at all levels, from vegetation to the top predators (Casula et al., 2017; Prevedello et al., 2013).

6.5 References

Alemany, I., Pérez-Cembranos, A., Castro, J. A., Picornell, A., Pérez-Mellado, V., & Ramon, C. (2023). Diet of the Insular Lizard, *Podarcis lilfordi* (Günther, 1874): Complementary Morphological and Molecular Approaches. *Animals*, *13*(3), Article 3. https://doi.org/10.3390/ani13030507

Arthur, A. D., Catling, P. C., & Reid, A. (2012). Relative influence of habitat structure, species interactions and rainfall on the post-fire population dynamics of ground-dwelling vertebrates. *Austral Ecology*, *37*(8), 958–970. https://doi.org/10.1111/j.1442-9993.2011.02355.x

Astete, S., Marinho-Filho, J., Kajin, M., Penido, G., Zimbres, B., Sollmann, R., Jácomo, A. T. A., Tôrres, N. M., & Silveira, L. (2017). Forced neighbours: Coexistence between jaguars and pumas in a harsh environment. *Journal of Arid Environments*, *146*, 27–34. https://doi.org/10.1016/j.jaridenv.2017.07.005

Băncilă, R. I., Cogălniceanu, D., Manu, M., Plăiaşu, R., Stănescu, F., Memedemin, D., Skolka, M., Tofan, L., & Lăcătuşu, A. (2023). A Multi-Community Approach in Biodiversity Assessment of a Peat Bog in the Southern Carpathians (Romania) and Implications for Conservation. *Environmental Entomology*, *52*(2), 217–229. https://doi.org/10.1093/ee/nvad004

Barrull, J., Mate, I., Ruiz-Olmo, J., Casanovas, J. G., Gosàlbez, J., & Salicrú, M. (2014). Factors and mechanisms that explain coexistence in a Mediterranean carnivore assemblage: An integrated study based on camera trapping and diet. *Mammalian Biology*, *79*(2), 123–131. https://doi.org/10.1016/j.mambio.2013.11.004

Beggs, R., Pierson, J., Tulloch, A. I. T., Blanchard, W., Westgate, M. J., & Lindenmayer, D. (2019). An experimental test of a compensatory nest predation model following lethal control of an overabundant native species. *Biological Conservation*, *231*, 122–132. https://doi.org/10.1016/j.biocon.2019.01.003

Beggs, R., Pierson, J., Tulloch, A. I. T., Blanchard, W., Westgate, M., & Lindenmayer, D. (2020). An empirical test of the mechanistic underpinnings of interference competition. *Oikos*, *129*(1), 93–105. https://doi.org/10.1111/oik.06583

Bell, E., Fisher, J. T., Darimont, C., Hart, H., & Bone, C. (2023). Influence of heterospecifics on mesocarnivore behaviour at shared scavenging opportunities in the Canadian Rocky Mountains. *Scientific Reports*, *13*(1), Article 1. https://doi.org/10.1038/s41598-023-34911-4

Bellingham, P. J., Kardol, P., Bonner, K. I., Buxton, R. P., Morse, C. W., & Wardle, D. A. (2016). Browsing by an invasive herbivore promotes development of plant and soil communities during primary succession. *Journal of Ecology*, *104*(6), 1505–1517. https://doi.org/10.1111/1365-2745.12624

Bird, G., Kaczvinsky, C., Wilson, A. E., & Hardy, N. B. (2019). When do herbivorous insects compete? A phylogenetic meta-analysis. *Ecology Letters*, *22*(5), 875–883. https://doi.org/10.1111/ele.13245

Bode, M., Baker, C. M., & Plein, M. (2015). Eradicating down the food chain: Optimal multispecies eradication schedules for a commonly encountered invaded island ecosystem. *Journal of Applied Ecology*, *52*(3), 571–579. https://doi.org/10.1111/1365-2664.12429

Castillo-Alvino, H., & Marvá, M. (2020). The competition model with Holling type II competitive response to interfering time. *Journal of Biological Dynamics*, *14*(1), 222–244. https://doi.org/10.1080/17513758.2020.1742392

Casula, P., Luiselli, L., Milana, G., & Amori, G. (2017). Habitat structure and disturbance affect small mammal populations in Mediterranean forests. *Basic and Applied Ecology*, *19*, 76–83. https://doi.org/10.1016/j.baae.2016.11.003

Chard, M., Foster, C. N., Lindenmayer, D. B., Cary, G. J., MacGregor, C. I., & Blanchard, W. (2022). Post-fire pickings: Large herbivores alter understory vegetation communities in a coastal eucalypt forest. *Ecology and Evolution*, *12*(4), e8828. https://doi.org/10.1002/ece3.8828

Chard, M., Martin, J., French, K., & Major, R. E. (2017). Rainfall events drive foraging choices by an urban coloniser. *Urban Ecosystems*, *20*(6), 1285–1290. https://doi.org/10.1007/s11252-017-0680-3

Dallas, T., Melbourne, B. A., & Hastings, A. (2019). When can competition and dispersal lead to checkerboard distributions? *Journal of Animal Ecology*, *88*(2), 269–276. Scopus. https://doi.org/10.1111/1365-2656.12913 de Carvalho, D. R., de Castro, D. M. P., Callisto, M., Chaves, A. J. de M., Moreira, M. Z., & Pompeu, P. S. (2019). Stable isotopes and stomach content analyses indicate omnivorous habits and opportunistic feeding behavior of an invasive fish. *Aquatic Ecology*, *53*(3), 365–381. https://doi.org/10.1007/s10452-019-09695-3

Dexter, N., Hudson, M., James, S., MacGregor, C., & Lindenmayer, D. B. (2013). Unintended Consequences of Invasive Predator Control in an Australian Forest: Overabundant Wallabies and Vegetation Change. *PLOS ONE*, *8*(8), e69087. https://doi.org/10.1371/journal.pone.0069087

Dexter, N., Ramsey, D. S. L., MacGregor, C., & Lindenmayer, D. (2012). Predicting Ecosystem Wide Impacts of Wallaby Management Using a Fuzzy Cognitive Map. *Ecosystems*, *15*(8), 1363–1379. JSTOR.

Dickman, C. R. (2011). Competition, Animal. In *Competition, Animal* (pp. 117–122). University of California Press. https://doi.org/10.1525/9780520948433-031

Dickman, C. R., & Woodside, D. P. (1983). A test of a competition model with reference to three species of small mammals in south-eastern Australia. *Oecologia*, *60*(1), 127–134. https://doi.org/10.1007/BF00379332

Ferguson, N., White, C. R., & Marshall, D. J. (2013). Competition in benthic marine invertebrates: The unrecognized role of exploitative competition for oxygen. *Ecology*, *94*(1), 126–135.

Friedemann, G., Leshem, Y., Kerem, L., Shacham, B., Bar-Massada, A., McClain, K. M., Bohrer, G., & Izhaki, I. (2016). Multidimensional differentiation in foraging resource use during breeding of two sympatric top predators. *Scientific Reports*, *6*(1), Article 1. https://doi.org/10.1038/srep35031

Fryirs, K., Zhang, N., Ralph, T. J., & Arash, A. M. (2023). Natural flood management: Lessons and opportunities from the catastrophic 2021–2022 floods in eastern Australia. *Earth Surface Processes and Landforms*, *48*(9), 1649–1664. https://doi.org/10.1002/esp.5647

Gause, G. F. (1934). EXPERIMENTAL ANALYSIS OF VITO VOLTERRA'S MATHEMATICAL THEORY OF THE STRUGGLE FOR EXISTENCE. Science (New York, N.Y.), 79(2036), 16–17. https://doi.org/10.1126/science.79.2036.16-a

Hart, S. P., Freckleton, R. P., & Levine, J. M. (2018). How to quantify competitive ability. *Journal of Ecology*, *106*(5), 1902–1909. https://doi.org/10.1111/1365-2745.12954

Heinen, J. H., Rahbek, C., & Borregaard, M. K. (2020). Conservation of species interactions to achieve self-sustaining ecosystems. *Ecography*, *43*(11), 1603–1611. https://doi.org/10.1111/ecog.04980

Jørgensen, S. E., Bastianoni, S., Müller, F., Patten, B. C., Fath, B. D., Marques, J. C., Nielsen, S. N., Tiezzi, E., & Ulanowicz, R. E. (2007). 6—Ecosystems have complex dynamics (growth and development). In S. E. Jørgensen, S. Bastianoni, F. Müller, B. C. Patten, B. D. Fath, J. C. Marques, S. N. Nielsen, E. Tiezzi, & R. E. Ulanowicz (Eds.), *A New Ecology* (pp. 103–142). Elsevier Science B.V. https://doi.org/10.1016/B978-044453160-5/50006-4

Kral-O'Brien, K. C., Roberton, B., Duquette, C. A., Hovick, T. J., & Harmon, J. P. (2023). A mechanistic framework for studying indirect effects of large vertebrate herbivores on pollinators. *Arthropod-Plant Interactions*, *17*(3), 263–274. https://doi.org/10.1007/s11829-023-09964-x

Lindenmayer, D. B., MacGregor, C., Welsh, A., Donnelly, C., Crane, M., Michael, D., Montague-Drake, R., Cunningham, R. B., Brown, D., Fortescue, M., Dexter, N., Hudson, M., Gill, A. M., Lindenmayer, D. B., MacGregor, C., Welsh, A., Donnelly, C., Crane, M., Michael, D., … Gill, A. M. (2008). Contrasting mammal responses to vegetation type and fire. *Wildlife Research*, *35*(5), 395–408. https://doi.org/10.1071/WR07156

Lindenmayer, D. B., Wood, J., MacGregor, C., Foster, C., Scheele, B., Tulloch, A., Barton, P., Banks, S., Robinson, N., Dexter, N., O'Loughlin, L. S., & Legge, S. (2018). Conservation conundrums and the challenges of managing unexplained declines of multiple species. *Biological Conservation*, *221*, 279–292. https://doi.org/10.1016/j.biocon.2018.03.007

Llewelyn, J., Strona, G., Dickman, C. R., Greenville, A. C., Wardle, G. M., Lee, M. S. Y., Doherty, S., Shabani, F., Saltré, F., & Bradshaw, C. J. A. (2023). Predicting predator–prey interactions in terrestrial endotherms using random forest. *Ecography*, *2023*(9), e06619. https://doi.org/10.1111/ecog.06619

Lu, Q., Xiao, L., Cheng, C., Lu, Z., Zhao, J., & Yao, M. (2021). Snow Leopard Dietary Preferences and Livestock Predation Revealed by Fecal DNA Metabarcoding: No Evidence for Apparent Competition Between Wild and Domestic Prey. *Frontiers in Ecology and Evolution*, *9*. https://www.frontiersin.org/articles/10.3389/fevo.2021.783546

Lurgi, M., Ritchie, E. G., & Fordham, D. A. (2018). Eradicating abundant invasive prey could cause unexpected and varied biodiversity outcomes: The importance of multispecies interactions. *Journal of Applied Ecology*, *55*(5), 2396–2407. https://doi.org/10.1111/1365-2664.13188

Osaki, A., Sashika, M., Abe, G., Shinjo, K., Fujimoto, A., Nakai, M., Shimozuru, M., & Tsubota, T. (2019). Comparison of feeding habits and habitat use between invasive raccoons and native raccoon dogs in Hokkaido, Japan. *BMC Ecology*, *19*(1), 35. https://doi.org/10.1186/s12898-019-0249-5

Prevedello, J. A., Dickman, C. R., Vieira, M. V., & Vieira, E. M. (2013). Population responses of small mammals to food supply and predators: A global meta-analysis. *Journal of Animal Ecology*, *82*(5), 927–936. https://doi.org/10.1111/1365-2656.12072

Rachmawati, R., Ozlen, M., Hearne, J., & Reinke, K. (2018). Fuel treatment planning: Fragmenting high fuel load areas while maintaining availability and connectivity of faunal habitat. *Applied Mathematical Modelling*, *54*, 298–310. https://doi.org/10.1016/j.apm.2017.09.045

Rayan, D. M., & Linkie, M. (2016). Managing conservation flagship species in competition: Tiger, leopard and dhole in Malaysia. *Biological Conservation*, *204*, 360–366. https://doi.org/10.1016/j.biocon.2016.11.009

Scoleri, V. P., Johnson, C. N., Vertigan, P., & Jones, M. E. (2020). Conservation trade-offs: Island introduction of a threatened predator suppresses invasive mesopredators but eliminates a seabird colony. *Biological Conservation*, *248*, 108635. https://doi.org/10.1016/j.biocon.2020.108635

Shuai, L.-Y., Song, Y.-L., Kotler, B. P., Embar, K., & Zeng, Z.-G. (2016). Foraging behaviour in East Asian desert rodents and its implications on coexistence. *Israel Journal of Ecology and Evolution*, *62*(3–4), 171–177. https://doi.org/10.1080/15659801.2015.1045279

Śmielak, M. K., Ballard, G., Fleming, P. J. S., Körtner, G., Vernes, K., & Reid, N. (2023). Brushtail possum terrestrial activity patterns are driven by climatic conditions, breeding and moonlight intensity. *Mammal Research*, *68*(4), 547–560. https://doi.org/10.1007/s13364-023-00691-5

Tosa, M. I., Schauber, E. M., & Nielsen, C. K. (2015). Familiarity breeds contempt: Combining proximity loggers and GPS reveals female white-tailed deer (*Odocoileus virginianus*) avoiding close contact with neighbors. *Journal of Wildlife Diseases*, *51*(1), 79–88. Scopus. https://doi.org/10.7589/2013-06-139

Traba, J., Casals, P., Broto, F., Camprodon, J., Giralt, D., Guixé, D., Mechergui, R., Rios, A., Sales, S., Taull, M., Ammari, Y., Solano, D., & Bota, G. (2016). Coexistence and habitat partitioning at micro- and macro-scales of rodent species in a North African desert (Bou-Hedma National Park, Tunisia). *Journal of Arid Environments*, *131*, 46–58. https://doi.org/10.1016/j.jaridenv.2016.04.002

Watchorn, D. J., Dickman, C. R., Greenville, A., Wilson, B. A., Garkaklis, M. J., Driscoll, D. A., Hodgens, P., Hoadley, D., Groffen, H., & Doherty, T. S. (2024). Artificial refuges provide post-fire habitat for small vertebrates. *Biological Conservation*, *291*, 110501. https://doi.org/10.1016/j.biocon.2024.110501

White, J. L., & Fleming, P. A. (2021). Potential for dietary competition between the threatened black-flanked rock-wallaby and sympatric western grey kangaroo. *Australian Mammalogy*, *44*(2), 243–255. https://doi.org/10.1071/AM20049

Youngentob, K. N., Yoon, H.-J., Coggan, N., & Lindenmayer, D. B. (2012). Edge effects influence competition dynamics: A case study of four sympatric arboreal marsupials. *Biological Conservation*, *155*, 68–76. https://doi.org/10.1016/j.biocon.2012.05.015

Chapter 7 Conclusions

The results of this thesis have demonstrated clear evidence of a negative association between bush rats and common brushtail possums (Chapters 3-5). This association is most likely characterised by bush rats temporally avoiding possums, leading to restricted foraging activity that, over time, reduces individual fitness and population numbers of bush rats. The two species may not be competing directly for food resources, despite a large overlap in dietary range, as the bush rats have a broader dietary range and being omnivores, are able to eat foods that possums avoid, or switch food resources. I followed a meticulous process to try to understand the causes of declines of bush rats. I undertook a systematic review of the system and conceptualised possible causes of decline, I examined patterns of activity and abundance between the two species, and I explored and experimentally investigated the nature of possible competitive interactions. However, despite using multiple methods, I was unable to definitively determine if the nature of this increasing population of common brushtail possums has significantly contributed to the decline of bush rats in Booderee National Park, and that competition is the most likely cause. There are many future avenues for this research, including the investigation of other factors that are contributing to this decline, such as the increasing frequency of extreme weather events, and investigating methods of managing this association, such as reducing possum populations, restricting possum access to local areas by fencing, and managing Booderee National Park's plant diversity.

My research revealed that conservation efforts, like controlling invasive predators, can trigger cascading, unexpected and sometimes negative effects on the structure and composition of ecological communities. When predator populations are reduced, it can disrupt the abundance and population growth patterns of particular species, leading to instability in existing ecological interactions. Moreover, many of these interactions are either indirect or challenging to track and address. To remedy these unforeseen outcomes, meticulous and holistic ecosystem management is essential, including the conceptual mapping of interactions such as food webs.

Appendix A

Appendix for Chapter 2

Appendix A.1. The questionnaire we developed to collect qualitative and quantitative data from the articles, including explanations of the categorical results. *Question 1* describes the intervention strategy used. *Questions 4* and *6* were used to address the first prediction. *Questions 5* and *7* were used to address the second prediction. *Questions 8, 9, 10,* and *12* were used to address the third prediction.

1) What type of intervention strategy was implemented?
   a) Reintroduction (includes captive breeding programs)
   b) Eradication
   c) Protected area
   d) Protected species
   e) Artificial habitat (AH) (includes zoo captive studies)
2) How long (in years) between the implementation of the intervention and the time the study took place?
   a) -1 (During)
   b) No. of years past (starting at 0 years, i.e., directly post)
3) What part of the ecosystem was the focus of the study?
   a) Habitat
   b) Species
   c) Community
   d) Human
4) Were competitive interactions investigated as a factor in the study or a conclusion?
   a) Investigated
   b) Conclusion
5) What were the outcomes of competition?
   a) Displacement
   b) Coexistence
   c) Decline
   d) Density-dependent
   e) None
6) Based on the first scale, how likely did researchers report that patterns were interpreted as being competition?
   a) (1) competition was a less likely interpretation (i.e., mentioned in a single paragraph of the discussion, or purposely controlled for so it was less likely to account for observed patterns)
   b) (2) competition was a likely interpretation of patterns, but there were other interpretations considered to be just as likely
   c) (3) competition was considered as the most likely interpretation of observed patters (i.e., pre-investigation, recorded as investigated, or post-investigated, recorded as a conclusion)
7) Based on the second scale, what were the interpreted outcomes of conservation on the post-intervention ecosystem?
   a) (-2) competition has an influential negative effect on the system (important factor for the intervention)
   b) (-1) competition has a mild negative effect on specific species in the system
   c) (0) competition has no notable impact on the system
   d) (1) competition has a mild positive effect on specific species in the system
   e) (2) competition has an influential positive effect on the system (important factor for the intervention)
8) What was the mechanism of competition?

   a) Interference
   b) Exploitative
   c) Apparent
   d) Both (i.e., interference and exploitative)

9) How many species were involved in the interaction?
   a) Intraspecific
   b) Interspecific
   c) Intra- and Inter-
10) How many species were involved?
11) What resource were they competing for?
   a) Food
   b) Space
   c) Both
   d) Other
   e) na
12) What was the trophic guild of species involved?
   a) Multiple
   b) Carnivore
   c) Omnivore
   d) Herbivore
13) What was the feeding class of the species?
   a) Predator
   b) Pollinator
   c) Grazer
   d) Bottom feeder
   e) Multiple
14) What is the taxonomic class of the species?
15) What was the time length of the study?
16) Was the experiment conducted within a laboratory or in the field?
17) What was the approximate size of the area (or reserve) the study took place in?
18) How many study sites were there?
19) How many samples were recorded?
20) What country did this study take place in?
21) What type of habitat did the study take place in?

Appendix A.2. A table including the raw data collected based on the questionnaire for each article reviewed. Each column is labelled QX, with X referring to the question number presented in *Appendix A.1.*

Paper	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8	Q9	Q10	Q11	Q12	Q13	Q14	Q15	Q16	Q17	Q18	Q19	Q20	Q21
Aburto-Oropeza *et al.*, 2015	protected area	9	Habitat	conclusion	coexistence	1	1	na	inter	community	food	multiple	multiple	multiple	1 month	field	na	147	441	Mexico	reef
Akter *et al.*, 2020	protected area	33	Habitat	conclusion	displacement	3	-2	na	inter	3	food	herbivore	pollinator	Insecta	4 months	field	na	12	144	Bangladesh	wetland
Almeida *et al.*, 2013	protected area	na	community	conclusion	decline	2	-1	interference	intra- and inter-	1	space	carnviore	predator	Malacostraca	2 months	field	1420 km^2	26	260	UK	freshwater
Andersen ,1992	artificial	na	Species	conclusion	coexistence	1	0	na	intra- and inter-	1	food	herbivore	grazer	Mammalia	4 months	field	23.5 ha	3	225	Denmark	grassland
Anderson *et al.*, 2000	introduction	0	Species	investigated	coexistence	2	0	interference	intra	1	space	omnivore	na	Aves	3 months	laboratory	na	2	8	USA	marine
Asnagi *et al.*, 2015	protected area	na	Habitat	conclusion	displacement	1	0	interference	inter	community	space	multiple	multiple	multiple	18 months	field	na	5	25	Italy	marine
Astete *et al.*, 2017	protected area	na	Habitat	investigated	coexistence	3	1	interference	inter	2	food	carnviore	predator	Mammalia	2 years	field	1291.40 km^2	1	58	Brazil	semi-arid
Atwood and Gese, 2008	introduction	0	Species	investigated	coexistence	3	-1	interference	inter	2	food	carnviore	predator	Mammalia	3 years	field	680 km^2	1	93	USA	heterogenous
Azzellino *et al.*, 2017	protected area	na	Habitat	conclusion	coexistence	3	0	na	inter	5	food	carnviore	predator	Mammalia	25 years	field	29000 km^2	1	4656	Italy	marine
Baladrón *et al.*, 2021	artificial	0	community	conclusion	displacement	2	-1	interference	intra	2	space	omnivore	predator	Actinopterygii	18 days	laboratory	na	4	20	Portugal	marine
Balestrieri *et al.*, 2010	protected area	na	Species	conclusion	displacement	2	-1	interference	inter	2	food	carnviore	predator	Mammalia	19 years	field	10 km^2	2	119	Italy	forest

Balme *et al.*, 2009	protected area	0	community	investigated	coexistence	3	0	na	inter	community	food	carnviore	predator	Mammalia	3 years	field	660 km^2	1	42	South Africa	grassland
Barrett *et al.*, 2009	protected area	10	Habitat	conclusion	none	2	0	na	intra- and inter-	community	food	multiple	multiple	multiple	10 years	field	na	24	480	Australia	reef
Barría *et al.*, 2018	protected area	2	Habitat	conclusion	coexistence	1	0	na	inter	4	food	carnviore	predator	Chondrichthyes	3 months	field	2051 km^2	2	198	Spain	marine
Barrull *et al.*, 2014	protected species	na	Species	investigated	coexistence	3	0	interference	inter	3	food	carnviore	predator	Mammalia	1 year	field	22100 ha	75	842	Spain	forest
Beggs *et al.*, 2019	eradication	0	community	investigated	displacement	3	0	interference	inter	community	food	herbivore	multiple	Aves	3 years	field	49 ha	8	128	Australia	woodland
Belton *et al.*, 2018	protected area	na	Habitat	investigated	coexistence	2	0	na	intra	1	food	carnviore	predator	Mammalia	2 years	field	5000 km^2	4	na	South Africa	woodland
Berger *et al.*, 1999	artificial	5	Species	conclusion	coexistence	1	-1	na	intra	1	both	herbivore	grazer	Mammalia	1 year	field	0.42 km^2	1	12	Germany	grassland
Berman *et al.*, 2013	protected area	25	Habitat	conclusion	displacement	1	-1	exploitative	inter	community	space	omnivore	filter feeder	Porifera	1 year	field	1500 ha	3	15	Wales	reef
Bhattacharjee *et al.*, 2018	protected area	na	Habitat	conclusion	decline	2	-2	interference	inter	community	food	multiple	multiple	Mammalia	na	field	4000 km^2	7	3487	India	arid
Blanco and Waltert, 2013	protected area	na	Species	conclusion	decline	1	1	na	intra- and inter-	4	food	herbivore	grazer	Mammalia	2 months	field	128.7 km^2	1	32	Uganda	forest
Bliege Bird *et al.*, 2018	restoration	na	Habitat	conclusion	decline	1	2	interference	inter	community	food	carnviore	predator	Mammalia	3 years	field	76 ha	76	228	Australia	semi-arid
Boitani, 1992	protected species	na	Species	conclusion	decline	2	-2	na	inter	1	food	carnviore	predator	Mammalia	na	field	400 km^2	2	11	Italy	alpine
Bourgeois *et al.*, 2015	artificial	0	Species	conclusion	decline	2	1	na	intra- and inter-	2	space	carnviore	predator	Aves	12 years	field	1894 ha	2	95	France	coastal

Bridgman *et al.*, 2013	eradication	na	Species	investigated	decline	3	-1	interference	inter	2	food	omnivore	predator	Mammalia	3 years	laboratory	na	1	16	New Zealand	forest
Bronstein and Loya, 2014	protected area	17	Habitat	conclusion	displacement	2	-1	na	intra- and inter-	community	both	herbivore	grazer	Echinodermata	3 years	field	1 m^2	6	360	Zanzibar	reef
Brunk *et al.*, 2021	protected species	3	Species	conclusion	displacement	1	1	interference	intra	1	food	carnviore	predator	Aves	9 years	field	4300 acres	2	172	USA	forest
Burnham-Curtis *et al.*, 1995	introduction	na	Species	conclusion	displacement	1	1	na	intra	1	space	carnviore	predator	Actinopterygii	4 days	field	na	5	na	USA	freshwater
Cabrera Walsh and Maestro, 2014	biological control	0	Species	investigated	decline	3	-1	exploitative	inter	2	food	herbivore	grazer	Insecta	13 weeks	laboratory	na	40	170	Argentina	freshwater
Camphuysen *et al.*, 2012	protected area	na	Habitat	conclusion	coexistence	1	0	exploitative	intra- and inter-	community	food	carnviore	predator	Aves	32 years	field	9972 km^2	2	44832	Scotland	marine
Cartes *et al.*, 2021	protected area	na	community	conclusion	coexistence	1	1	na	inter	community	food	carnviore	predator	Decapoda	3 years	field	na	3	531	Spain	marine
Casoli *et al.*, 2020	restoration	5	Habitat	conclusion	decline	1	0	na	inter	community	both	omnivore	bottom feeder	Gymnolaemata	3 years	field	unclear	4	1057	Italy	marine
Chaverra *et al.*, 2019	protected area	33	Habitat	investigated	displacement	2	2	na	inter	community	space	herbivore	grazer	multiple	104 days	field	225cm^2	3	36	Chile	reef
Ciucci *et al.*, 2020	protected area	82	Habitat	conclusion	coexistence	1	0	na	intra	1	food	carnviore	predator	Mammalia	6 years	field	1294km^2	4	9546	Italy	forest
Colombini *et al.*, 2013	protected area	na	Habitat	investigated	decline	2	-1	na	inter	2	food	herbivore	grazer	Malacostraca	3 years	field	30m^2	20	24602	Italy	beach
Corbalán *et al.*, 2006	protected area	na	Habitat	conclusion	displacement	1	1	na	intra- and inter-	4	both	herbivore	grazer	Mammalia	4 years	field	12800 ha	192	11836	Argentina	heterogenous
Curveira-Santos *et al.*, 2017	protected area	117	Habitat	investigated	coexistence	3	0	interference	inter	6	food	carnviore	predator	Mammalia	4 months	field	180km^2	54	1645	Portugal	forest

dela Cruz *et al.*, 2015	introduction	0	Species	control	decline	1	0	na	inter	2	space	carnviore	predator	Anthozoa	2 years	both	na	12	720	Phillippines	reef
Díaz-Puente *et al.*, 2020	Protected species	0	Species	investigated	decline	3	-1	na	intra	1	food	herbivore	grazer	Bivalvia	16 months	both	na	2	50	Spain	reef
Díez *et al.*, 2014	restoration	0	Habitat	conclusion	displacement	3	-1	na	inter	community	space	multiple	multiple	multiple	28 years	field	na	11	2249	Spain	reef
Doherty, 1982	introduction	0	Species	investigated	displacement	3	-1	both	intra- and inter-	2	space	omnivore	na	Actinopterygii	1 year	field	na	35	56	Australia	reef
Doray *et al.*, 2018	protected area	na	Habitat	conclusion	decline	2	-1	na	inter	community	food	multiple	multiple	multiple	6 years	field	na	1	27	France	marine
du Bus de Warnaffe and Lebrun, 2004	protected area	150	Habitat	conclusion	displacement	2	-1	na	inter	community	na	carnviore	predator	Insecta	8 months	field	15 ha	22	127	Belgium	forest
Edgar and Barrett, 1999	protected area	2	Habitat	conclusion	decline	1	-1	exploitative	inter	community	food	multiple	multiple	multiple	6 years	field	250 m	23	552	Australia	reef
Edinger and Risk, 2000	Policy	0	Species	investigated	coexistence	3	0	na	inter	community	na	carnviore	predator	Anthozoa	2 years	field	na	37	444	Indonesia	reef
Elliott *et al.*, 2021	protected area	na	Habitat	investigated	displacement	3	-1	exploitative	inter	community	food	herbivore	pollinator	Insecta	10 weeks	field	200 m^2	3	2772	Australia	heathland
Eltz *et al.*, 2003	protected area	na	Habitat	conclusion	coexistence	1	0	exploitative	inter	community	food	herbivore	pollinator	Insecta	20 months	field	103094 ha	3	275	Borneo	forest
Fang *et al.*, 2021	introduction	0	Species	conclusion	decline	1	-1	na	intra- and inter-	1	food	omnivore	na	Actinopterygii	2 years	both	na	8	1864	China	freshwater
Ferry *et al.*, 2020	Artificial	na	community	investigated	coexistence	3	0	both	inter	community	food	herbivore	grazer	Mammalia	4 months	field	7000 km^2	4	121	Zimbabwe	semi-arid
Finlayson *et al.*, 2008	introduction	0	Species	investigated	decline	3	-1	na	inter	4	food	multiple	multiple	Mammalia	1 year	field	64000 ha	1	2564	Australia	semi-arid

Fisher et al., 2014	introduction	36	Species	investigated	displacement	3	-2	apparent	inter	3	other	omnivore	na	Mammalia	6 months	field	300 km length	1	na	Canada	coastal
Forcada *et al.*, 2008	protected area	20	Habitat	conclusion	decline	1	1	na	inter	community	both	multiple	multiple	multiple	14 months	field	1400 ha	21	126	Spain	marine
Ford *et al.*, 2018	protected area	8	Habitat	conclusion	displacement	2	-1	na	inter	community	space	carnviore	predator	multiple	6 months	field	na	3	9	Fiji	reef
Fox *et al.*, 1991	protected area	na	Species	conclusion	decline	3	-1	na	inter	community	food	herbivore	grazer	Mammalia	10 years	field	60000 km^2	1	519	India	grassland
Garcia *et al.*, 2015	protected area	9	Habitat	conclusion	displacement	1	0	na	intra- and inter-	2	both	multiple	multiple	Actinopterygii	2 years	field	956 ha	1	68	Martinique	reef
Ginn *et al.*, 2018	restoration	na	Habitat	investigated	decline	3	-2	exploitative	inter	community	food	omnivore	bottom feeder	Bivalvia	7 years	both	722 km^2	747	1584	Canada	freshwater
Goodman and Reid, 2017	Artificial	0	Species	conclusion	none	1	0	na	intra	1	space	carnviore	predator	Cephalaspidomorphi	2 days	field	na	5	164	USA	freshwater
Guillemain *et al.*, 2002	protected area	14	Habitat	conclusion	displacement	3	-2	interference	intra- and inter-	6	both	omnivore	na	Aves	4 years	field	2185	2	602	France	freshwater
Häfliger *et al.*, 2005	biological control	0	Habitat	conclusion	decline	2	-1	interference	inter	2	other	herbivore	grazer	Insecta	4 years	field	na	15	1500	Europe	heterogenous
Hammer *et al.*, 2018	introduction	na	Species	investigated	coexistence	3	0	na	inter	4	food	omnivore	prey	Actinopterygii	39 years	field	191200 ha	1	6661	Sweden	freshwater
Hanmer *et al.*, 2018	Artificial	na	Species	investigated	displacement	3	-2	exploitative	inter	community	food	multiple	multiple	multiple	881 days	field	72 km^2	20	89651	UK	urban
Hendon and Rakocinski, 2016	introduction	0	Species	conclusion	decline	2	-1	na	inter	1	food	carnviore	predator	Actinopterygii	6 months	field	na	12	190	USA	marine
Herr *et al.*, 2009	protected area	na	Habitat	investigated	decline	3	-2	both	inter	1	food	carnviore	predator	Mammalia	7 years	field	na	1	na	Germany	marine

Herremans and Herremans-	protected area	na	Habitat	conclusion	none	1	0	na	inter	3	food	carnviore	scavenger	Aves	5 years	field	15070 km^2	53	1762	Botswana	woodland
Huyser *et al.*, 2000	eradication	0	community	conclusion	decline	2	-1	na	inter	community	food	multiple	multiple	Aves	30 years	field	335 km^2	2	na	Marion Island	coastal
Jaffuel *et al.*, 2016	biological control	0	Habitat	investigated	decline	3	-1	interference	intra- and inter-	community	food	na	parasite	Chromadora	9 years	field	na	96	3840	Switzerland	agriculture
Jennings *et al.*, 2010	protected area	na	Habitat	conclusion	displacement	1	1	interference	inter	1	food	carnviore	predator	Mammalia	2 years	field	60338 ha	11	1148	Malaysia	forest
Kaiser *et al.*, 2018	Policy	na	community	conclusion	decline	2	-1	na	inter	community	food	carnviore	predator	Decapoda	na	field	na	na	na	Barents Sea	marine
Kamler *et al.*, 2015	protected area	na	Species	investigated	coexistence	3	2	interference	inter	3	both	carnviore	predator	Mammalia	6 months	field	110 km^2	4	na	South Africa	heterogenous
Karlsson *et al.*, 2018	biological control	na	Habitat	investigated	coexistence	3	-1	both	inter	3	other	herbivore	parasite	Insecta	na	laboratory	na	6	79	Benin	agriculture
Khadka and James, 2016	protected area	31	Habitat	conclusion	displacement	1	0	interference	inter	community	food	herbivore	grazer	Mammalia	2 years	field	7629 km^2	1	418	Nepal	heterogenous
Kritensen *et al.*, 2020	restoration	1	community	conclusion	decline	1	-1	na	intra- and inter-	community	na	carnviore	predator	Actinopterygii	6 years	field	900 ha	2	42	Denmark	freshwater
Lamichhane *et al.*, 2020	protected area	40	Species	conclusion	coexistence	1	0	interference	inter	community	food	herbivore	grazer	Mammalia	1 month	field	270 km^2	30	90	Nepal	heterogenous
Lau *et al.*, 2011	protected area	11	Species	conclusion	decline	1	-1	na	intra	1	food	omnivore	predator	Echinodermata	1 year	field	na	3	329	China	reef
LeTourneux *et al.*, 2021	eradication	20	community	conclusion	decline	1	-1	apparent	intra	1	food	herbivore	grazer	Aves	14 years	field	na	1	3113	Canada	freshwater
Li *et al.*, 2020	protected area	na	Habitat	conclusion	coexistence	1	0	na	inter	community	food	multiple	multiple	Mammalia	32 years	field	660000 ha	3	16	Kenya	savannah

Lieury *et al.*, 2015	protected species	0	Species	conclusion	decline	1	-1	interference	intra	1	food	carnviore	scavenger	Aves	16 years	field	na	54	171	France	heterogenous
Lioy *et al.*, 2016	Artificial	0	Species	investigated	decline	3	-2	exploitative	inter	2	food	herbivore	grazer	Mammalia	na	field	na	6	274	Italy	woodland
Liu *et al.*, 2020	protected area	na	Species	investigated	displacement	3	-2	interference	inter	community	food	herbivore	grazer	Mammalia	14 months	field	322.97 km^2	27	2512	China	forest
Lloyd and Powlesland, 1994	introduction	na	Species	conclusion	decline	3	-1	na	inter	community	food	herbivore	grazer	Aves	na	field	5052 ha	4	65	New Zealand	forest
Loucif *et al.*, 2021	protected area	26	Habitat	investigated	displacement	3	-2	interference	intra- and inter-	3	space	omnivore	na	Aves	2 years	field	2400 ha	1	50	Algeria	freshwater
M'soka *et al.*, 2016	protected area	38	Habitat	investigated	displacement	3	1	interference	inter	2	food	carnviore	predator	Mammalia	3 years	field	3600 km^2	5	233	Zambia	grassland
Mace and Mills, 2017	biological control	0	Species	control	density-dependence	1	0	na	intra	1	na	herbivore	grazer	Insecta	2 years	field	na	4	248	USA	agriculture
Marticorena *et al.*, 2021	protected area	na	Habitat	conclusion	displacement	1	-1	na	inter	community	both	multiple	multiple	multiple	3 years	field	na	13	26	Atlantic Ocean	marine
McClanahan *et al.*, 1994	protected area	15	Habitat	investigated	displacement	3	-2	interference	inter	community	food	herbivore	grazer	Actinopterygii	2 years	field	26 km^2	6	120	Kenya	reef
McClanahan, 2000	protected area	na	community	investigated	decline	3	-1	na	inter	3	food	carnviore	predator	Actinopterygii	10 years	field	na	9	54	Kenya	reef
McCook and Chapman, 1997	protected area	0	Habitat	investigated	density-dependence	3	0	na	intra- and inter-	community	space	multiple	multiple	multiple	5 years	field	1410 m	17	85	Canada	coastal
Mohanty *et al.*, 2009	Artificial	na	Habitat	investigated	coexistence	2	1	na	inter	community	both	herbivore	grazer	multiple	4 years	field	3.5 ha	4	na	India	agriculture
Molina-Hernández *et al.*, 2018	protected area	2	community	conclusion	coexistence	1	0	na	inter	community	both	multiple	multiple	Actinopterygii	2 years	field	12 km^2	41	na	Mexico	reef

Momanyi *et al.*, 2006	biological control	0	Species	conclusion	displacement	3	-2	interference	inter	2	other	omnivore	parasite	Insecta	1 year	field	na	16	96	Kenya	agriculture
Moore *et al.*, 2020	Artificial	0	community	conclusion	displacement	1	0	na	inter	community	space	multiple	multiple	multiple	16 months	field	na	3	12	USA	reef
Nash *et al.*, 2008	Artificial	0	Habitat	conclusion	none	1	0	na	inter	2	food	multiple	multiple	Insecta	6 months	both	na	2	20	Australia	agriculture
Nie *et al.*, 2019	Protected species	30	Species	investigated	decline	3	-2	interference	inter	2	food	herbivore	grazer	Mammalia	9 years	field	na	1	830	China	forest
Nordlund and Gullström, 2013	protected area	na	Habitat	conclusion	none	1	0	na	intra	1	na	multiple	multiple	multiple	4 months	field	na	3	15	Mozambique	marine
Oldenburg *et al.*, 2007	introduction	na	Species	conclusion	decline	2	-2	na	inter	6	food	multiple	multiple	Actinopterygii	na	field	na	1	na	USA	freshwater
Oro *et al.*, 2009	protected species	0	Species	conclusion	displacement	3	-2	interference	inter	community	na	multiple	multiple	Aves	27 years	field	1100 ha	1	13	Spain	coastal
Osman and Whitlatch, 2004	introduction	0	Species	conclusion	decline	2	-1	na	inter	community	space	multiple	multiple	multiple	2 years	field	na	2	80	USA	estuary
Périquet *et al.*, 2016	protected area	na	Species	conclusion	displacement	1	-1	interference	inter	2	space	carnviore	predator	Mammalia	3 years	field	14600 km^2	4	8	Zimbabwe	savannah
Perkins-Visser *et al.*, 1996	introduction	0	Species	conclusion	displacement	1	-1	interference	intra	1	food	carnviore	predator	Malacostraca	5 weeks	field	na	2	16	USA	marine
Pichegru *et al.*, 2012	protected area	0	Species	conclusion	displacement	2	-2	na	inter	1	food	carnviore	predator	Aves	3 years	field	20 km-radius	2	668	Caribbean	coastal
Ranglack and du Toit, 2015	Artificial	50	Habitat	conclusion	coexistence	1	0	na	intra	1	food	herbivore	grazer	Mammalia	3 years	field	148.23 km^2	1	198	USA	heterogenous
Rayan and Linkie, 2016	protected area	3	Species	investigated	displacement	3	-2	interference	inter	3	both	carnviore	predator	Mammalia	19 months	field	800 km^2	2	33727	Malaysia	forest

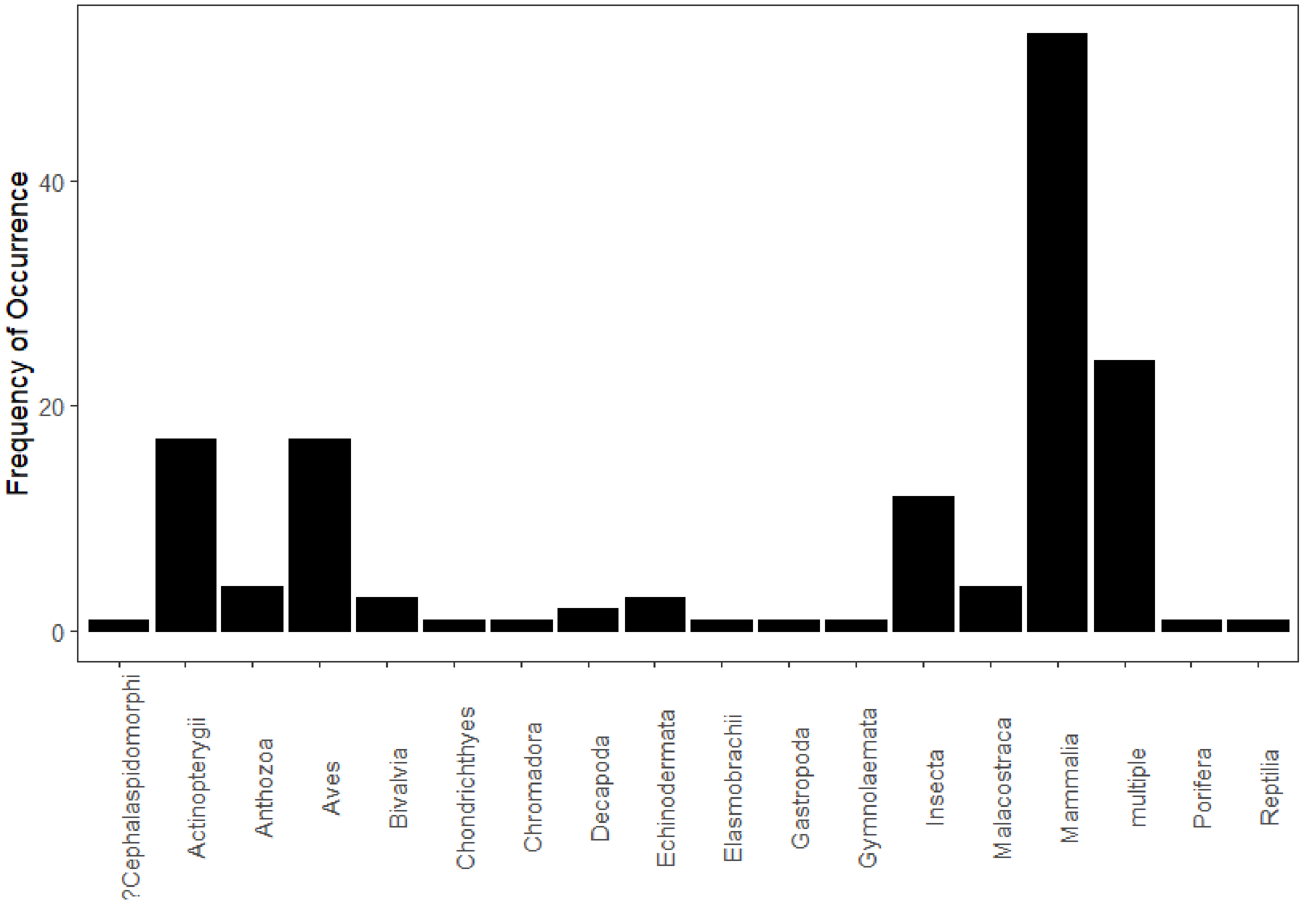
Retzer *et al.*, 2006	protected area	7	Species	conclusion	displacement	3	-2	interference	inter	community	food	herbivore	grazer	Mammalia	na	field	21700 km^2	1	210	Mongolia	semi-arid
Richard-Hansen *et al.*, 2000	introduction	0	Species	investigated	coexistence	2	0	interference	intra	1	space	omnivore	na	Mammalia	18 months	field	150 km^2	1	16	French Guiana	forest
Rico-Sánchez *et al.*, 2020	protected area	na	community	conclusion	decline	2	-2	na	inter	community	food	multiple	multiple	multiple	6 months	field	3800 km^2	15	60	Mexico	freshwater
Riera *et al.*, 2016	protected species	na	Species	conclusion	decline	2	-1	exploitative	inter	2	space	omnivore	na	Gastropoda	3 months	field	na	100	9240	Canary Islands	coastal
Robinson *et al.*, 2007	eradication	0	community	conclusion	coexistence	1	0	na	intra	1	space	omnivore	bottom feeder	Bivalvia	2 years	field	na	3	15	South Africa	coastal
Rodríguez *et al.*, 2019	protected area	0	Habitat	conclusion	coexistence	1	0	na	intra	1	food	herbivore	grazer	Mammalia	8 years	field	73 km^2	10	100	Argentina	heterogenous
Rowley, 2018	introduction	0	Species	control	decline	1	0	na	intra	1	space	omnivore	na	Anthozoa	1 year	field	600 km^2	2	192	Indonesia	reef
Ruiz *et al.*, 2021	Policy	na	Species	conclusion	coexistence	1	0	na	inter	community	food	multiple	multiple	multiple	3 years	field	na	163	482	Spain	marine
Sammarco *et al.*, 1985	introduction	0	Species	investigated	decline	3	-2	interference	inter	3	space	omnivore	filter feeder	Anthozoa	8 months	field	na	1	26	Australia	reef
Santos *et al.*, 2009	introduction	0	Species	conclusion	displacement	1	0	interference	intra	1	space	carnviore	predator	Reptilia	5 years	field	11.2 ha	4	365	Spain	forest
Santosa *et al.*, 2012	protected area	62	Habitat	investigated	coexistence	3	0	interference	inter	2	food	herbivore	grazer	Mammalia	7 months	field	1.500 ha	6	249	Borneo	forest
Sayer, 1977	protected area	na	Habitat	conclusion	decline	2	-1	na	inter	community	food	multiple	multiple	Mammalia	2 years	field	2200000 ha	3	na	Mali	savannah
Schmidt *et al.*, 2010	Protected species	18	Species	investigated	decline	2	-2	interference	inter	2	food	herbivore	grazer	Mammalia	na	field	na	1	150	USA	salt marsh

Schutte *et al.*, 2013	protected area	na	Species	investigated	coexistence	1	-1	interference	inter	1	food	carnviore	predator	Mammalia	3 years	field	250 km^2	4	2084	Kenya	semi-arid
Scoleri *et al.*, 2020	introduction	1	Species	investigated	decline	2	1	both	inter	3	food	multiple	multiple	Mammalia	4 years	field	9672 ha	3	20	Australia	forest
Shakya *et al.*, 2009	Artificial	0	Habitat	investigated	coexistence	2	0	apparent	inter	2	food	omnivore	predator	Insecta	na	laboratory	na	21	150	na	captive
Simon *et al.*, 2011	Artificial	5	Habitat	conclusion	displacement	2	-1	na	inter	community	food	multiple	multiple	Actinopterygii	4 months	field	na	4	320	Brazil	reef
Southwell *et al.*, 2017	protected area	na	Habitat	conclusion	decline	1	-1	na	inter	community	food	carnviore	predator	Aves	15 years	field	900 km^2	247	300	Antarctica	marine
Speed *et al.*, 2018	protected area	12	community	conclusion	coexistence	2	1	na	intra- and inter-	community	food	carnviore	predator	Elasmobrachii	2 years	field	593 km^2	3	na	Australia	reef
Spitzer *et al.*, 2021	Policy	na	Habitat	investigated	displacement	3	2	exploitative	inter	4	food	herbivore	grazer	Mammalia	3 years	field	na	2	378	Sweden	forest
Steinmetz *et al.*, 2013	protected area	na	Habitat	investigated	displacement	3	-1	both	inter	3	food	carnviore	predator	Mammalia	9 months	field	351 km^2	39	128	Thailand	forest
Suazo *et al.*, 2009	restoration	0	Species	conclusion	coexistence	1	0	na	inter	3	space	omnivore	na	multiple	10 months	field	6475 ha	1	360	USA	scrubland
Suski *et al.*, 2018	restoration	0	community	conclusion	decline	2	-1	both	inter	community	food	multiple	multiple	multiple	8 weeks	laboratory	na	3	48	Colombia	freshwater
Tarjuelo *et al.*, 2021	Policy	na	Habitat	conclusion	coexistence	2	1	na	intra- and inter-	community	space	multiple	multiple	Aves	5 years	field	na	15	120	Spain	agriculture
Taylor *et al.*, 2017	introduction	0	Species	conclusion	coexistence	1	0	na	intra	1	food	carnviore	predator	Actinopterygii	12 days	field	800 km^2	1	8	Australia	estuary
Teck *et al.*, 2017	protected area	6	Habitat	conclusion	decline	2	-1	exploitative	inter	2	both	herbivore	grazer	Echinodermata	3 years	field	na	30	143	USA	marine

Thorsen *et al.*, 2000	eradication	0	community	conclusion	decline	1	-1	na	inter	2	food	omnivore	multiple	multiple	na	field	210 ha	1	na	Seychelles	heterogenous
Tian *et al.*, 2019	protected area	52	Habitat	investigated	coexistence	3	0	interference	inter	community	both	multiple	multiple	multiple	11 months	field	32297 hm^2	33	33	China	forest
Toledo-Guedes *et al.*, 2014	protected area	na	Habitat	conclusion	decline	1	0	na	inter	community	food	multiple	multiple	multiple	2 years	field	na	6	432	Canary Islands	marine
Traba *et al.*, 2016	protected area	33	Habitat	conclusion	displacement	2	-1	interference	inter	6	both	multiple	multiple	Mammalia	1 month	field	245 ha	10	2000	Tunisa	desert
Tuboi and Hussain, 2019	protected area	na	Habitat	conclusion	decline	1	-1	na	intra	2	food	herbivore	grazer	Mammalia	2 years	field	40 km^2	1	18	India	grassland
van Beeck Calkoen *et al.*, 2020	protected area	na	Habitat	conclusion	decline	1	-1	na	inter	community	food	multiple	multiple	Mammalia	1 year	field	na	209	418	Europe	multiple
van Keeken *et al.*, 2007	protected area	na	Species	investigated	displacement	3	-2	na	intra- and inter-	community	both	carnviore	predator	Actinopterygii	101 years	field	na	1	na	North Sea	marine
Van Nieuwenhove *et al.*, 2016	biological control	0	Habitat	investigated	coexistence	3	-1	both	inter	2	other	omnivore	parasite	Insecta	na	field	na	2	396	Argentina	captive
Wallach *et al.*, 2009	protected species	na	Species	conclusion	decline	1	-1	na	inter	3	food	multiple	multiple	multiple	na	field	na	9	1476	Australia	multiple
Wallgren *et al.*, 2009	protected area	23	Habitat	conclusion	displacement	2	-1	exploitative	inter	community	food	multiple	multiple	Mammalia	1 year	field	40000 km^2	13	8409	Botswana	savannah
Walsh *et al.*, 2004	protected species	0	Species	conclusion	density-dependence	1	-1	na	intra	2	space	carnviore	predator	Actinopterygii	13 years	field	na	1	na	Canada	marine
Walton *et al.*, 2007	restoration	9	Habitat	investigated	displacement	2	-1	na	inter	3	food	carnviore	predator	Malacostraca	3 years	field	147.5 ha	4	810	Phillippines	mangrove
Wang *et al.*, 2018	protected area	na	Species	investigated	displacement	3	-2	interference	inter	1	food	carnviore	predator	Mammalia	120 days	field	4858 km^2	356	85454	China	heterogenous

Wang *et al.*, 2017	protected area	na	Species	conclusion	displacement	2	-1	interference	inter	1	food	carnviore	predator	Mammalia	1 year	field	5000 km^2	356	114854	China	heterogenous
Wangdi *et al.*, 2019	protected area	14	Species	conclusion	displacement	1	-2	interference	inter	1	food	herbivore	grazer	Mammalia	5 months	field	740.60 km^2	5	1520	Bhutan	heterogenous
Wolfenden *et al.*, 2015	protected species	32	Species	investigated	decline	3	-2	interference	inter	2	space	multiple	multiple	Aves	3 months	field	na	3	82	Mauritius	forest
Zhang *et al.*, 2021	Artificial	39	Species	investigated	coexistence	3	-2	interference	intra	1	other	herbivore	grazer	Mammalia	2 years	laboratory	na	2	18	China	captive
Zielinski *et al.*, 2017	protected area	na	Habitat	investigated	decline	3	-2	interference	inter	2	both	carnviore	predator	Mammalia	12 years	field	na	1	33519	USA	na
Zuccarino-Crowe *et al.*, 2016	protected area	0	Species	conclusion	decline	1	-1	na	intra	3	food	multiple	multiple	Actinopterygii	28 years	field	925 km^2	61	854	USA	freshwater

Appendix A.3. A bar graph detailing the number of taxa at the level of class that were recorded in the articles. The y-axis shows the number of times that a class was the featured species in the articles.



Appendix A.4. The reference list of articles analysed as part of the systematic review.

Aburto-Oropeza, O., Ezcurra, E., Moxley, J., Sánchez-Rodríguez, A., Mascareñas-Osorio, I., Sánchez-Ortiz, C., Erisman, B., & Ricketts, T. (2015). A framework to assess the health of rocky reefs linking geomorphology, community assemblage, and fish biomass. *Ecological Indicators*, *52*, 353–361. https://doi.org/10.1016/j.ecolind.2014.12.006

Akter, A., Biella, P., Batáry, P., & Klečka, J. (2020). Changing pollinator communities along a disturbance gradient in the Sundarbans mangrove forest: A case study on Acanthus ilicifolius and Avicennia officinalis. *Global Ecology and Conservation*, *24*, e01282. https://doi.org/10.1016/j.gecco.2020.e01282

Almeida, D., Argent, R., Ellis, A., England, J., & Copp, G. H. (2013). Environmental biology of an invasive population of signal crayfish in the River Stort catchment (southeastern England). *Limnologica*, *43*(3), 177–184. https://doi.org/10.1016/j.limno.2012.09.002

Andersen, K. F. (1992). Size, design and interspecific interactions as restrictors of natural behaviour in multi-species exhibits. 1. Activity and intraspecific interactions of plains zebra (equus burchelli). *Applied Animal Behaviour Science*, *34*(1), 157–174. https://doi.org/10.1016/S0168-1591(05)80064-4

Anderson, D. W., Newman, S. H., Kelly, P. R., Herzog, S. K., & Lewis, K. P. (2000). An experimental soft-release of oil-spill rehabilitated American coots (Fulica americana): I. Lingering effects on survival, condition and behavior. *Environmental Pollution*, *107*(3), 285–294. https://doi.org/10.1016/S0269-7491(99)00180-3

Asnaghi, V., Thrush, S. F., Hewitt, J. E., Mangialajo, L., Cattaneo-Vietti, R., & Chiantore, M. (2015). Colonisation processes and the role of coralline algae in rocky shore community dynamics. *Journal of Sea Research*, *95*, 132–138. https://doi.org/10.1016/j.seares.2014.07.012

Astete, S., Marinho-Filho, J., Kajin, M., Penido, G., Zimbres, B., Sollmann, R., Jácomo, A. T. A., Tôrres, N. M., & Silveira, L. (2017). Forced neighbours: Coexistence between jaguars and pumas in a harsh environment. *Journal of Arid Environments*, *146*, 27–34. https://doi.org/10.1016/j.jaridenv.2017.07.005

Atwood, T. C., & Gese, E. M. (2008). Coyotes and recolonizing wolves: Social rank mediates risk-conditional behaviour at ungulate carcasses. *Animal Behaviour*, *75*(3), 753–762. https://doi.org/10.1016/j.anbehav.2007.08.024

Azzellino, A., Airoldi, S., Lanfredi, C., Podestà, M., & Zanardelli, M. (2017). Cetacean response to environmental and anthropogenic drivers of change: Results of a 25-year distribution study in the northwestern Mediterranean Sea. *Geo and Bio-Diversity in the South West Atlantic Deep Sea: The Iatá-Piúna Expedition with the Manned Submersible Shinkai 6500*, *146*, 104–117. https://doi.org/10.1016/j.dsr2.2017.02.004

Baladrón, A., Costa, M. J., Bejarano, M. D., Pinheiro, A., & Boavida, I. (2021). Can vegetation provide shelter to cyprinid species under hydropeaking? *Science of The Total Environment*, *769*, 145339. https://doi.org/10.1016/j.scitotenv.2021.145339

Balestrieri, A., Remonti, L., Ruiz-González, A., Gómez-Moliner, B. J., Vergara, M., & Prigioni, C. (2010). Range expansion of the pine marten (Martes martes) in an agricultural landscape matrix (NW Italy). *Mammalian Biology*, *75*(5), 412–419. https://doi.org/10.1016/j.mambio.2009.05.003

Balme, G. A., Slotow, R., & Hunter, L. T. B. (2009). Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (Panthera pardus) population. *Biological Conservation*, *142*(11), 2681–2690. https://doi.org/10.1016/j.biocon.2009.06.020

Barrett, N. S., Buxton, C. D., & Edgar, G. J. (2009). Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection. *Journal of Experimental Marine Biology and Ecology*, *370*(1), 104–119. https://doi.org/10.1016/j.jembe.2008.12.005

Barría, C., Navarro, J., & Coll, M. (2018). Feeding habits of four sympatric sharks in two deep-water fishery areas of the western Mediterranean Sea. *Deep Sea Research Part I: Oceanographic Research Papers*, *142*, 34–43. https://doi.org/10.1016/j.dsr.2018.09.010

Barrull, J., Mate, I., Ruiz-Olmo, J., Casanovas, J. G., Gosàlbez, J., & Salicrú, M. (2014). Factors and mechanisms that explain coexistence in a Mediterranean carnivore assemblage: An integrated study based on camera trapping and diet. *Mammalian Biology*, *79*(2), 123–131. https://doi.org/10.1016/j.mambio.2013.11.004

Beggs, R., Pierson, J., Tulloch, A. I. T., Blanchard, W., Westgate, M. J., & Lindenmayer, D. (2019). An experimental test of a compensatory nest predation model following lethal control of an overabundant native species. *Biological Conservation*, *231*, 122–132. https://doi.org/10.1016/j.biocon.2019.01.003

Belton, L. E., Cameron, E. Z., & Dalerum, F. (2018). Social networks of spotted hyaenas in areas of contrasting human activity and infrastructure. *Animal Behaviour*, *135*, 13–23. https://doi.org/10.1016/j.anbehav.2017.10.027

Berger, A., Scheibe, K.-M., Eichhorn, K., Scheibe, A., & Streich, J. (1999). Diurnal and ultradian rhythms of behaviour in a mare group of Przewalski horse (Equus ferus przewalskii), measured through one year under semi-reserve conditions. *Applied Animal Behaviour Science*, *64*(1), 1–17. https://doi.org/10.1016/S0168-1591(99)00026-X

Berman, J., Burton, M., Gibbs, R., Lock, K., Newman, P., Jones, J., & Bell, J. (2013). Testing the suitability of a morphological monitoring approach for identifying temporal variability in a temperate sponge assemblage. *Journal for Nature Conservation*, *21*(3), 173–182. https://doi.org/10.1016/j.jnc.2012.12.003

Bhattacharjee, S., Kidwai, Z., Bhattarai, S., Bajpai, H., Reddy, G. V., & Yessoufou, K. (2018). A case for reconsidering the conservation status of former Closed Areas in arid landscapes of western India. *Journal for Nature Conservation*, *45*, 30–40. https://doi.org/10.1016/j.jnc.2018.07.006

Blanco, V., & Waltert, M. (2013). Does the tropical agricultural matrix bear potential for primate conservation? A baseline study from Western Uganda. *Journal for Nature Conservation*, *21*(6), 383–393. https://doi.org/10.1016/j.jnc.2013.04.001

Bliege Bird, R., Bird, D. W., Fernandez, L. E., Taylor, N., Taylor, W., & Nimmo, D. (2018). Aboriginal burning promotes fine-scale pyrodiversity and native predators in Australia's Western Desert. *Biological Conservation*, *219*, 110–118. https://doi.org/10.1016/j.biocon.2018.01.008

Boitani, L. (1992). Wolf research and conservation in Italy. *The Study and Management of Small Populations*, *61*(2), 125–132. https://doi.org/10.1016/0006-3207(92)91102-X

Bourgeois, K., Dromzée, S., & Vidal, E. (2015). Are artificial burrows efficient conservation tools for seabirds? A case study of two sympatric shearwaters on neighbouring islands and guidelines for improvement. *Biological Conservation*, *191*, 282–290. https://doi.org/10.1016/j.biocon.2015.07.002

Bridgman, L. J., Innes, J., Gillies, C., Fitzgerald, N. B., Miller, S., & King, C. M. (2013). Do ship rats display predatory behaviour towards house mice? *Animal Behaviour*, *86*(2), 257–268. https://doi.org/10.1016/j.anbehav.2013.05.013

Bronstein, O., & Loya, Y. (2014). Echinoid community structure and rates of herbivory and bioerosion on exposed and sheltered reefs. *Journal of Experimental Marine Biology and Ecology*, *456*, 8–17. https://doi.org/10.1016/j.jembe.2014.03.003

Brunk, K. M., West, E. H., Peery, M. Z., & Pidgeon, A. M. (2021). Reducing anthropogenic subsidies can curb density of overabundant predators in protected areas. *Biological Conservation*, *256*, 109081. https://doi.org/10.1016/j.biocon.2021.109081

Burnham-Curtis, M. K., Krueger, C. C., Schreiner, D. R., Johnson, J. E., Stewart, T. J., Horrall, R. M., MacCallum, W. R., Kenyon, R., & Lange, R. E. (1995). Genetic Strategies for Lake Trout Rehabilitation: A Synthesis. *International Conference on Restoration of Lake Trout in the Laurentian Great Lakes*, *21*, 477–486. https://doi.org/10.1016/S0380-1330(95)71119-4

Cabrera Walsh, G., & Maestro, M. (2014). Evaluation of intraguild interactions between two species of insect herbivores on Pistia stratiotes. *Biological Control*, *76*, 74–78. https://doi.org/10.1016/j.biocontrol.2014.05.005

Camphuysen, K. (C. J.), Shamoun-Baranes, J., Bouten, W., & Garthe, S. (2012). Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. *Seabirds and Marine Protected Areas Planning*, *156*, 22–29. https://doi.org/10.1016/j.biocon.2011.12.024

Cartes, J. E., Rodríguez-Ribas, R., Papiol, V., Valeiras, X., Punzón, A., Blanco, M., & Serrano, A. (2021). Biological condition and population structure of benthopelagic shrimps in the Galicia Bank (NE Atlantic): Intra- and interspecific patterns. *Deep Sea Research Part I: Oceanographic Research Papers*, *168*, 103434. https://doi.org/10.1016/j.dsr.2020.103434

Casoli, E., Mancini, G., Ventura, D., Pace, D. S., Belluscio, A., & Ardizzone, G. D. (2020). Reteporella spp. Success in the re-colonization of bare coralligenous reefs impacted by Costa Concordia shipwreck: The pioneer species you did not expect. *Marine Pollution Bulletin*, *161*, 111808. https://doi.org/10.1016/j.marpolbul.2020.111808

Chaverra, A., Wieters, E., Foggo, A., & Knights, A. M. (2019). Removal of intertidal grazers by human harvesting leads to alteration of species interactions, community structure and resilience to climate change. *Marine Environmental Research*, *146*, 57–65. https://doi.org/10.1016/j.marenvres.2019.03.003

Ciucci, P., Mancinelli, S., Boitani, L., Gallo, O., & Grottoli, L. (2020). Anthropogenic food subsidies hinder the ecological role of wolves: Insights for conservation of apex predators in human-modified landscapes. *Global Ecology and Conservation*, *21*, e00841. https://doi.org/10.1016/j.gecco.2019.e00841

Colombini, I., Fallaci, M., Gagnarli, E., Rossano, C., Scapini, F., & Chelazzi, L. (2013). The behavioural ecology of two sympatric talitrid species, Talitrus saltator (Montagu) and Orchestia gammarellus (Pallas) on a Tyrrhenian sandy beach dune system. *Estuarine, Coastal and Shelf Science*, *117*, 37–47. https://doi.org/10.1016/j.ecss.2012.09.016

Corbalán, V., Tabeni, S., & Ojeda, R. A. (2006). Assessment of habitat quality for four small mammal species of the Monte Desert, Argentina. *Mammalian Biology*, *71*(4), 227–237. https://doi.org/10.1016/j.mambio.2006.02.002

Curveira-Santos, G., Marques, T. A., Björklund, M., & Santos-Reis, M. (2017). Mediterranean mesocarnivores in spatially structured managed landscapes: Community organisation in time and space. *Agriculture, Ecosystems & Environment*, *237*, 280–289. https://doi.org/10.1016/j.agee.2016.12.037

dela Cruz, D. W., Rinkevich, B., Gomez, E. D., & Yap, H. T. (2015). Assessing an abridged nursery phase for slow growing corals used in coral restoration. *Ecological Engineering*, *84*, 408–415. https://doi.org/10.1016/j.ecoleng.2015.09.042

Díaz-Puente, B., Guiñez, R., Pita, A., Miñambres, M., & Presa, P. (2020). Genotype by environment interaction for shell length in Mytilus galloprovincialis. *Journal of Experimental Marine Biology and Ecology*, *522*, 151252. https://doi.org/10.1016/j.jembe.2019.151252

Díez, I., Santolaria, A., Muguerza, N., & Gorostiaga, J. M. (2014). Capacity for recovery of rocky subtidal assemblages following pollution abatement in a scenario of global change. *Marine Pollution Bulletin*, *86*(1), 197–209. https://doi.org/10.1016/j.marpolbul.2014.07.018

Doherty, P. J. (1982). Some effects of density on the juveniles of two species of tropical, territorial damselfish. *Journal of Experimental Marine Biology and Ecology*, *65*(3), 249–261. https://doi.org/10.1016/0022-0981(82)90057-0

Doray, M., Petitgas, P., Huret, M., Duhamel, E., Romagnan, J. B., Authier, M., Dupuy, C., & Spitz, J. (2018). Monitoring small pelagic fish in the Bay of Biscay ecosystem, using indicators from an integrated survey. *Multidisciplinary Integrated Surveys*, *166*, 168–188. https://doi.org/10.1016/j.pocean.2017.12.004

Dover, J. W. (1997). Conservation headlands: Effects on butterfly distribution and behaviour. *Agriculture, Ecosystems & Environment*, *63*(1), 31–49. https://doi.org/10.1016/S0167-8809(96)01120-6

du Bus de Warnaffe, G., & Lebrun, P. (2004). Effects of forest management on carabid beetles in Belgium: Implications for biodiversity conservation. *Biological Conservation*, *118*(2), 219–234. https://doi.org/10.1016/j.biocon.2003.08.015

Edgar, G. J., & Barrett, N. S. (1999). Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *Journal of Experimental Marine Biology and Ecology*, *242*(1), 107–144. https://doi.org/10.1016/S0022-0981(99)00098-2

Edinger, E. N., & Risk, M. J. (2000). Reef classification by coral morphology predicts coral reef conservation value. *Biological Conservation*, *92*(1), 1–13. https://doi.org/10.1016/S0006-3207(99)00067-1

Elliott, B., Wilson, R., Shapcott, A., Keller, A., Newis, R., Cannizzaro, C., Burwell, C., Smith, T., Leonhardt, S. D., Kämper, W., & Wallace, H. M. (2021). Pollen diets and niche overlap of honey bees and native bees in protected areas. *Basic and Applied Ecology*, *50*, 169–180. https://doi.org/10.1016/j.baae.2020.12.002

Eltz, T., Brühl, C. A., Imiyabir, Z., & Linsenmair, K. E. (2003). Nesting and nest trees of stingless bees (Apidae: Meliponini) in lowland dipterocarp forests in Sabah, Malaysia, with implications for forest management. *Forest Ecology and Management*, *172*(2), 301–313. https://doi.org/10.1016/S0378-1127(01)00792-7

Fang, D., Luo, Y.-T., Xu, D., Yang, X., & Wang, X. (2021). Relationship between genetic risk and stock enhancement of the silver carp (Hypophthalmichthys molitrix) in the Yangtze River. *Fisheries Research*, *235*, 105829. https://doi.org/10.1016/j.fishres.2020.105829

Ferry, N., Cordonnier, M., Hulot, F. D., Dakwa, F., Sebele, L., Dray, S., Fritz, H., & Valeix, M. (2020). Heterogeneity of water physico-chemical characteristics in artificially pumped waterholes: Do African herbivores drink at the same locations and does it lead to interference competition? *Journal of Arid Environments*, *173*, 104014. https://doi.org/10.1016/j.jaridenv.2019.104014

Finlayson, G. R., Vieira, E. M., Priddel, D., Wheeler, R., Bentley, J., & Dickman, C. R. (2008). Multi-scale patterns of habitat use by re-introduced mammals: A case study using medium-sized marsupials. *Biological Conservation*, *141*(1), 320–331. https://doi.org/10.1016/j.biocon.2007.10.008

Fisher, J. T., Pasztor, C., Wilson, A., Volpe, J. P., & Anholt, B. R. (2014). Recolonizing sea otters spatially segregate from pinnipeds on the Canadian Pacific coastline: The implications of segregation for species conservation. *Biological Conservation*, *177*, 148–155. https://doi.org/10.1016/j.biocon.2014.06.025

Forcada, A., Bayle-Sempere, J. T., Valle, C., & Sánchez-Jerez, P. (2008). Habitat continuity effects on gradients of fish biomass across marine protected area boundaries. *Marine Environmental Research*, *66*(5), 536–547. https://doi.org/10.1016/j.marenvres.2008.08.003

Ford, A. K., Eich, A., McAndrews, R. S., Mangubhai, S., Nugues, M. M., Bejarano, S., Moore, B. R., Rico, C., Wild, C., & Ferse, S. C. A. (2018). Evaluation of coral reef management effectiveness using conventional versus resilience-based metrics. *Ecological Indicators*, *85*, 308–317. https://doi.org/10.1016/j.ecolind.2017.10.002

Fox, J. L., Nurbu, C., & Chundawat, R. S. (1991). The mountain ungulates of Ladakh, India. *Biological Conservation*, *58*(2), 167–190. https://doi.org/10.1016/0006-3207(91)90118-S

Garcia, J., Mourier, J., & Lenfant, P. (2015). Spatial behavior of two coral reef fishes within a Caribbean marine protected area. *Marine Environmental Research*, *109*, 41–51. https://doi.org/10.1016/j.marenvres.2015.06.004

Ginn, B. K., Bolton, R., Coulombe, D., Fleischaker, T., & Yerex, G. (2018). Quantifying a shift in benthic dominance from zebra (Dreissena polymorpha) to quagga (Dreissena rostriformis bugensis) mussels in a large, inland lake. *Journal of Great Lakes Research*, *44*(2), 271–282. https://doi.org/10.1016/j.jglr.2017.12.003

Goodman, D. H., & Reid, S. B. (2017). Climbing above the competition: Innovative approaches and recommendations for improving Pacific Lamprey passage at fishways. *Ecological Engineering*, *107*, 224–232. https://doi.org/10.1016/j.ecoleng.2017.07.041

Guillemain, M., Fritz, H., & Duncan, P. (2002). The importance of protected areas as nocturnal feeding grounds for dabbling ducks wintering in western France. *Biological Conservation*, *103*(2), 183–198. https://doi.org/10.1016/S0006-3207(01)00120-3

Häfliger, P., Schwarzlaender, M., & Blossey, B. (2005). Biology of Platycephala planifrons (Diptera: Chloropidae) and its potential effectiveness as biological control agent for invasive Phragmites australis in North America. *Working at the Interface of Art and Science: How Best to Select an Agent for Classical Biological Control?*, *34*(3), 302–311. https://doi.org/10.1016/j.biocontrol.2005.05.016

Hammar, J., Axenrot, T., Degerman, E., Asp, A., Bergstrand, E., Enderlein, O., Filipsson, O., & Kylberg, E. (2018). Smelt (Osmerus eperlanus): Glacial relict, planktivore, predator, competitor, and key prey for the endangered Arctic char in Lake Vättern, southern Sweden. *Journal of Great Lakes Research*, *44*(1), 126–139. https://doi.org/10.1016/j.jglr.2017.11.008

Hanmer, H. J., Thomas, R. L., & Fellowes, M. D. E. (2018). Introduced Grey Squirrels subvert supplementary feeding of suburban wild birds. *Landscape and Urban Planning*, *177*, 10–18. https://doi.org/10.1016/j.landurbplan.2018.04.004

Hendon, J. R., & Rakocinski, C. F. (2016). Habitat-specific growth, survival and diet of late juvenile hatchery-reared spotted seatrout (Cynoscion nebulosus). *Journal of Experimental Marine Biology and Ecology*, *484*, 1–10. https://doi.org/10.1016/j.jembe.2016.07.012

Herr, H., Fock, H. O., & Siebert, U. (2009). Spatio-temporal associations between harbour porpoise Phocoena phocoena and specific fisheries in the German Bight. *Biological Conservation*, *142*(12), 2962–2972. https://doi.org/10.1016/j.biocon.2009.07.025

Herremans, M., & Herremans-Tonnoeyr, D. (2000). Land use and the conservation status of raptors in Botswana. *Biological Conservation*, *94*(1), 31–41. https://doi.org/10.1016/S0006-3207(99)00166-4

Huyser, O., Ryan, P. G., & Cooper, J. (2000). Changes in population size, habitat use and breedingbiology of lesser sheathbills (Chionis minor) at Marion Island: Impacts of cats, mice and climate change? *Biological Conservation*, *92*(3), 299–310. https://doi.org/10.1016/S0006-3207(99)00096-8

Jaffuel, G., Mäder, P., Blanco-Perez, R., Chiriboga, X., Fliessbach, A., Turlings, T. C. J., & Campos-Herrera, R. (2016). Prevalence and activity of entomopathogenic nematodes and their antagonists in soils that are subject to

different agricultural practices. *Agriculture, Ecosystems & Environment*, *230*, 329–340. https://doi.org/10.1016/j.agee.2016.06.009
Jennings, A. P., Zubaid, A., & Veron, G. (2010). Ranging behaviour, activity, habitat use, and morphology of the Malay civet (Viverra tangalunga) on Peninsular Malaysia and comparison with studies on Borneo and Sulawesi. *Mammalian Biology*, *75*(5), 437–446. https://doi.org/10.1016/j.mambio.2009.10.002
Kaiser, B. A., Kourantidou, M., & Fernandez, L. (2018). A case for the commons: The Snow Crab in the Barents. *Journal of Environmental Management*, *210*, 338–348. https://doi.org/10.1016/j.jenvman.2018.01.007
Kamler, J. F., Stenkewitz, U., Sliwa, A., Wilson, B., Lamberski, N., Herrick, J. R., & Macdonald, D. W. (2015). Ecological relationships of black-footed cats (Felis nigripes) and sympatric canids in South Africa. *Mammalian Biology*, *80*(2), 122–127. https://doi.org/10.1016/j.mambio.2014.11.004
Karlsson, M. F., de Souza, E. O., Ayelo, P. M., Zannou, J. A., Mègnigbèto, G. S. B., & Bokonon-Ganta, A. H. (2018). Interspecific competition between egg parasitoids: Native Fopius caudatus and exotic Fopius arisanus, in Ceratitis cosyra. *Biological Control*, *117*, 172–181. https://doi.org/10.1016/j.biocontrol.2017.11.010
Khadka, K. K., & James, D. A. (2016). Habitat selection by endangered Himalayan musk deer (Moschus chrysogaster) and impacts of livestock grazing in Nepal Himalaya: Implications for conservation. *Journal for Nature Conservation*, *31*, 38–42. https://doi.org/10.1016/j.jnc.2016.03.002
Kristensen, E., Sand-Jensen, K., Kristensen, J. S. B., Pedersen, M. E., Baastrup-Spohr, L., & Kragh, T. (2020). Early fish colonization and community development in a shallow re-established lake. *Ecological Engineering*, *155*, 105956. https://doi.org/10.1016/j.ecoleng.2020.105956
Lamichhane, S., Khanal, G., Karki, J. B., Aryal, C., & Acharya, S. (2020). Natural and anthropogenic correlates of habitat use by wild ungulates in Shuklaphanta National Park, Nepal. *Global Ecology and Conservation*, *24*, e01338. https://doi.org/10.1016/j.gecco.2020.e01338
Lau, D. C. C., Dumont, C. P., Lui, G. C. S., & Qiu, J.-W. (2011). Effectiveness of a small marine reserve in southern China in protecting the harvested sea urchin Anthocidaris crassispina: A mark-and-recapture study. *Biological Conservation*, *144*(11), 2674–2683. https://doi.org/10.1016/j.biocon.2011.07.027
LeTourneux, F., Grandmont, T., Dulude-de Broin, F., Martin, M.-C., Lefebvre, J., Kato, A., Bêty, J., Gauthier, G., & Legagneux, P. (2021). COVID19-induced reduction in human disturbance enhances fattening of an overabundant goose species. *Biological Conservation*, *255*, 108968. https://doi.org/10.1016/j.biocon.2021.108968
Li, W., Buitenwerf, R., Munk, M., Amoke, I., Bøcher, P. K., & Svenning, J.-C. (2020). Accelerating savanna degradation threatens the Maasai Mara socio-ecological system. *Global Environmental Change*, *60*, 102030. https://doi.org/10.1016/j.gloenvcha.2019.102030
Lieury, N., Gallardo, M., Ponchon, C., Besnard, A., & Millon, A. (2015). Relative contribution of local demography and immigration in the recovery of a geographically-isolated population of the endangered Egyptian vulture. *Biological Conservation*, *191*, 349–356. https://doi.org/10.1016/j.biocon.2015.07.008
Lioy, S., Mori, E., Wauters, L. A., & Bertolino, S. (2016). Weight operated see-saw feeding hoppers are not selective for red squirrels when greys are present. *Mammalian Biology*, *81*(4), 365–371. https://doi.org/10.1016/j.mambio.2016.03.008
Liu, Z.-X., Dayananda, B., Jeffree, R. A., Tian, C., Zhang, Y.-Y., Yu, B., Zheng, Y., Jing, Y., Si, P.-Y., & Li, J.-Q. (2020). Giant panda distribution and habitat preference: The influence of sympatric large mammals. *Global Ecology and Conservation*, *24*, e01221. https://doi.org/10.1016/j.gecco.2020.e01221
Lloyd, B. D., & Powlesland, R. G. (1994). The decline of kakapo Strigops habroptilus and attempts at conservation by translocation. *Biological Conservation*, *69*(1), 75–85. https://doi.org/10.1016/0006-3207(94)90330-1
Loucif, K., Maazi, M. C., Houhamdi, M., & Chenchouni, H. (2021). Nest site selection and breeding ecology of the Ferruginous Duck (Aythya nyroca) in Algeria. *Global Ecology and Conservation*, *26*, e01524. https://doi.org/10.1016/j.gecco.2021.e01524
Mace, K. C., & Mills, N. J. (2017). Connecting natural enemy metrics to biological control activity for aphids in California walnuts. *Biological Control*, *106*, 16–26. https://doi.org/10.1016/j.biocontrol.2016.11.009
Marticorena, J., Matabos, M., Ramirez-Llodra, E., Cathalot, C., Laes-Huon, A., Leroux, R., Hourdez, S., Donval, J.-P., & Sarrazin, J. (2021). Recovery of hydrothermal vent communities in response to an induced disturbance at the

Lucky Strike vent field (Mid-Atlantic Ridge). *Marine Environmental Research*, *168*, 105316. https://doi.org/10.1016/j.marenvres.2021.105316
McClanahan, T. R. (2000). Recovery of a coral reef keystone predator, Balistapus undulatus, in East African marine parks. *Biological Conservation*, *94*(2), 191–198. https://doi.org/10.1016/S0006-3207(99)00176-7
McClanahan, T. R., Nugues, M., & Mwachireya, S. (1994). Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: The role of reef management. *Journal of Experimental Marine Biology and Ecology*, *184*(2), 237–254. https://doi.org/10.1016/0022-0981(94)90007-8
McCook, L. J., & Chapman, A. R. O. (1997). Patterns and variations in natural succession following massive ice-scour of a rocky intertidal seashore. *Journal of Experimental Marine Biology and Ecology*, *214*(1), 121–147. https://doi.org/10.1016/S0022-0981(96)02751-7
Mohanty, R. K., Jena, S. K., Thakur, A. K., & Patil, D. U. (2009). Impact of high-density stocking and selective harvesting on yield and water productivity of deepwater rice–fish systems. *Agricultural Water Management*, *96*(12), 1844–1850. https://doi.org/10.1016/j.agwat.2009.08.006
Molina-Hernández, A. L., Garza-Pérez, J. R., & Aranda-Fragoso, A. (2018). Identifying management challenges and implementation shortcomings of a new fishing refuge: Akumal reef, Mexico. *Ocean & Coastal Management*, *161*, 127–140. https://doi.org/10.1016/j.ocecoaman.2018.04.030
Momanyi, C., Löhr, B., & Gitonga, L. (2006). Biological impact of the exotic parasitoid, Diadegma semiclausum (Hellen), of diamondback moth, Plutella xylostella L., in Kenya. *Biological Control*, *38*(2), 254–263. https://doi.org/10.1016/j.biocontrol.2006.03.003
Moore, C. S., Gittman, R. K., Puckett, B. J., Wellman, E. H., & Blakeslee, A. M. H. (2020). If you build it, they will come: Restoration positively influences free-living and parasite diversity in a restored tidal marsh. *Food Webs*, *25*, e00167. https://doi.org/10.1016/j.fooweb.2020.e00167
M'soka, J., Creel, S., Becker, M. S., & Droge, E. (2016). Spotted hyaena survival and density in a lion depleted ecosystem: The effects of prey availability, humans and competition between large carnivores in African savannahs. *Biological Conservation*, *201*, 348–355. https://doi.org/10.1016/j.biocon.2016.07.011
Nash, M. A., Thomson, L. J., Horne, P. A., & Hoffmann, A. A. (2008). Notonomus gravis (Chaudoir) (Coleoptera: Carabidae) predation of Deroceras reticulatum Müller (Gastropoda: Agriolimacidae), an example of fortuitous biological control. *Biological Control*, *47*(3), 328–334. https://doi.org/10.1016/j.biocontrol.2008.08.013
Nie, Y., Zhou, W., Gao, K., Swaisgood, R. R., & Wei, F. (2019). Seasonal competition between sympatric species for a key resource: Implications for conservation management. *Biological Conservation*, *234*, 1–6. https://doi.org/10.1016/j.biocon.2019.03.013
Nordlund, L. M., & Gullström, M. (2013). Biodiversity loss in seagrass meadows due to local invertebrate fisheries and harbour activities. *Estuarine, Coastal and Shelf Science*, *135*, 231–240. https://doi.org/10.1016/j.ecss.2013.10.019
Oldenburg, K., Stapanian, M. A., Ryan, P. A., & Holm, E. (2007). Potential Strategies for Recovery of Lake Whitefish and Lake Herring Stocks in Eastern Lake Erie. *Restoration of Native Species*, *33*, 46–58. https://doi.org/10.3394/0380-1330(2007)33[46:PSFROL]2.0.CO;2
Oro, D., Pérez-Rodríguez, A., Martínez-Vilalta, A., Bertolero, A., Vidal, F., & Genovart, M. (2009). Interference competition in a threatened seabird community: A paradox for a successful conservation. *Biological Conservation*, *142*(8), 1830–1835. https://doi.org/10.1016/j.biocon.2009.03.023
Osman, R. W., & Whitlatch, R. B. (2004). The control of the development of a marine benthic community by predation on recruits. *Journal of Experimental Marine Biology and Ecology*, *311*(1), 117–145. https://doi.org/10.1016/j.jembe.2004.05.001
Périquet, S., Mapendere, C., Revilla, E., Banda, J., Macdonald, D. W., Loveridge, A. J., & Fritz, H. (2016). A potential role for interference competition with lions in den selection and attendance by spotted hyaenas. *Mammalian Biology*, *81*(3), 227–234. https://doi.org/10.1016/j.mambio.2015.10.005
Perkins-Visser, E., Wolcott, T. G., & Wolcott, D. L. (1996). Nursery role of seagrass beds: Enhanced growth of juvenile blue crabs (Callinectes sapidus Rathbun). *Journal of Experimental Marine Biology and Ecology*, *198*(2), 155–173. https://doi.org/10.1016/0022-0981(96)00014-7

Pichegru, L., Ryan, P. G., van Eeden, R., Reid, T., Grémillet, D., & Wanless, R. (2012). Industrial fishing, no-take zones and endangered penguins. *Seabirds and Marine Protected Areas Planning*, *156*, 117–125. https://doi.org/10.1016/j.biocon.2011.12.013
Ranglack, D. H., & du Toit, J. T. (2015). Wild bison as ecological indicators of the effectiveness of management practices to increase forage quality on open rangeland. *Ecological Indicators*, *56*, 145–151. https://doi.org/10.1016/j.ecolind.2015.04.009
Rayan, D. M., & Linkie, M. (2016). Managing conservation flagship species in competition: Tiger, leopard and dhole in Malaysia. *Biological Conservation*, *204*, 360–366. https://doi.org/10.1016/j.biocon.2016.11.009
Retzer, V., Nadrowski, K., & Miehe, G. (2006). Variation of precipitation and its effect on phytomass production and consumption by livestock and large wild herbivores along an altitudinal gradient during a drought, South Gobi, Mongolia. *Journal of Arid Environments*, *66*(1), 135–150. https://doi.org/10.1016/j.jaridenv.2005.10.009
Richard-Hansen, C., Vié, J.-C., & de Thoisy, B. (2000). Translocation of red howler monkeys (Alouatta seniculus) in French Guiana. *Biological Conservation*, *93*(2), 247–253. https://doi.org/10.1016/S0006-3207(99)00136-6
Rico-Sánchez, A. E., Sundermann, A., López-López, E., Torres-Olvera, M. J., Mueller, S. A., & Haubrock, P. J. (2020). Biological diversity in protected areas: Not yet known but already threatened. *Global Ecology and Conservation*, *22*, e01006. https://doi.org/10.1016/j.gecco.2020.e01006
Riera, R., Pérez, Ó., Álvarez, O., Simón, D., Díaz, D., Monterroso, Ó., & Núñez, J. (2016). Clear regression of harvested intertidal mollusks. A 20-year (1994–2014) comparative study. *Marine Environmental Research*, *113*, 56–61. https://doi.org/10.1016/j.marenvres.2015.11.003
Robinson, T. B., Branch, G. M., Griffiths, C. L., & Govender, A. (2007). Effects of experimental harvesting on recruitment of an alien mussel Mytilus galloprovincialis. *Journal of Experimental Marine Biology and Ecology*, *345*(1), 1–11. https://doi.org/10.1016/j.jembe.2006.12.019
Rodríguez, V., Marino, A., Borrelli, L., Gavuzzo, A. B., & Pazos, G. (2019). Effect of population density on diet composition and dietary niche breadth of guanaco (Lama guanicoe, Müller 1776) in northeastern Patagonian steppes. *Journal of Arid Environments*, *170*, 104000. https://doi.org/10.1016/j.jaridenv.2019.104000
Rowley, S. J. (2018). Acclimatory capacity of the Gorgonian Isis hippuris Linnaeus, 1758 to environmental change in SE Sulawesi, Indonesia. *Journal of Experimental Marine Biology and Ecology*, *500*, 73–88. https://doi.org/10.1016/j.jembe.2017.12.012
Ruiz, J., Louzao, M., Oyarzabal, I., Arregi, L., Mugerza, E., & Uriarte, A. (2021). The Spanish purse-seine fishery targeting small pelagic species in the Bay of Biscay: Landings, discards and interactions with protected species. *Fisheries Research*, *239*, 105951. https://doi.org/10.1016/j.fishres.2021.105951
Sammarco, P. W., Coll, J. C., & La Barre, S. (1985). Competitive strategies of soft corals (Coelenterata: Octocorallia). II. Variable defensive responses and susceptibility to scleractinian corals. *Journal of Experimental Marine Biology and Ecology*, *91*(3), 199–215. https://doi.org/10.1016/0022-0981(85)90176-5
Santos, T., Pérez-Tris, J., Carbonell, R., Tellería, J. L., & Díaz, J. A. (2009). Monitoring the performance of wild-born and introduced lizards in a fragmented landscape: Implications for ex situ conservation programmes. *Biological Conservation*, *142*(12), 2923–2930. https://doi.org/10.1016/j.biocon.2009.07.017
Santosa, Y., Taqiuddin, Mustari, A. H., & Rahman, D. A. (2012). Cohabitation Study of the Leaf Monkey and Bornean White-Bearded Gibbons in Gunung Palung National Park, West Kalimantan. *HAYATI Journal of Biosciences*, *19*(3), 115–123. https://doi.org/10.4308/hjb.19.3.115
Sayer, J. A. (1977). Conservation of large mammals in the Republic of Mali. *Biological Conservation*, *12*(4), 245–263. https://doi.org/10.1016/0006-3207(77)90045-3
Schmidt, P. M., McCleery, R. A., Lopez, R. R., Silvy, N. J., & Schmidt, J. A. (2010). Habitat succession, hardwood encroachment and raccoons as limiting factors for Lower Keys marsh rabbits. *Biological Conservation*, *143*(11), 2703–2710. https://doi.org/10.1016/j.biocon.2010.07.016
Schuette, P., Creel, S., & Christianson, D. (2013). Coexistence of African lions, livestock, and people in a landscape with variable human land use and seasonal movements. *Biological Conservation*, *157*, 148–154. https://doi.org/10.1016/j.biocon.2012.09.011

Scoleri, V. P., Johnson, C. N., Vertigan, P., & Jones, M. E. (2020). Conservation trade-offs: Island introduction of a threatened predator suppresses invasive mesopredators but eliminates a seabird colony. *Biological Conservation*, *248*, 108635. https://doi.org/10.1016/j.biocon.2020.108635

Shakya, S., Weintraub, P. G., & Coll, M. (2009). Effect of pollen supplement on intraguild predatory interactions between two omnivores: The importance of spatial dynamics. *Biological Control*, *50*(3), 281–287. https://doi.org/10.1016/j.biocontrol.2009.04.012

Simon, T., Pinheiro, H. T., & Joyeux, J.-C. (2011). Target fishes on artificial reefs: Evidences of impacts over nearby natural environments. *Science of The Total Environment*, *409*(21), 4579–4584. https://doi.org/10.1016/j.scitotenv.2011.07.057

Southwell, C., Emmerson, L., Takahashi, A., Barbraud, C., Delord, K., & Weimerskirch, H. (2017). Large-scale population assessment informs conservation management for seabirds in Antarctica and the Southern Ocean: A case study of Adélie penguins. *Global Ecology and Conservation*, *9*, 104–115. https://doi.org/10.1016/j.gecco.2016.12.004

Speed, C. W., Cappo, M., & Meekan, M. G. (2018). Evidence for rapid recovery of shark populations within a coral reef marine protected area. *Biological Conservation*, *220*, 308–319. https://doi.org/10.1016/j.biocon.2018.01.010

Spitzer, R., Coissac, E., Felton, A., Fohringer, C., Juvany, L., Landman, M., Singh, N. J., Taberlet, P., Widemo, F., & P.G.M. Cromsigt, J. (2021). Small shrubs with large importance? Smaller deer may increase the moose-forestry conflict through feeding competition over Vaccinium shrubs in the field layer. *Forest Ecology and Management*, *480*, 118768. https://doi.org/10.1016/j.foreco.2020.118768

Steinmetz, R., Seuaturien, N., & Chutipong, W. (2013). Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. *Biological Conservation*, *163*, 68–78. https://doi.org/10.1016/j.biocon.2012.12.016

Suazo, A. A., Fauth, J. E., Roth, J. D., Parkinson, C. L., & Stout, I. J. (2009). Responses of small rodents to habitat restoration and management for the imperiled Florida Scrub-Jay. *Biological Conservation*, *142*(10), 2322–2328. https://doi.org/10.1016/j.biocon.2009.05.008

Suski, J. G., Swan, C. M., Salice, C. J., & Wahl, C. F. (2018). Effects of pond management on biodiversity patterns and community structure of zooplankton in urban environments. *Science of The Total Environment*, *619–620*, 1441–1450. https://doi.org/10.1016/j.scitotenv.2017.11.153

Tarjuelo, R., Concepción, E. D., Guerrero, I., Carricondo, A., Cortés, Y., & Díaz, M. (2021). Agri-environment scheme prescriptions and landscape features affect taxonomic and functional diversity of farmland birds. *Agriculture, Ecosystems & Environment*, *315*, 107444. https://doi.org/10.1016/j.agee.2021.107444

Taylor, M. D., Laffan, S. W., Fairfax, A. V., & Payne, N. L. (2017). Finding their way in the world: Using acoustic telemetry to evaluate relative movement patterns of hatchery-reared fish in the period following release. *Fisheries Enhancement*, *186*, 538–543. https://doi.org/10.1016/j.fishres.2016.07.003

Teck, S. J., Lorda, J., Shears, N. T., Bell, T. W., Cornejo-Donoso, J., Caselle, J. E., Hamilton, S. L., & Gaines, S. D. (2017). Disentangling the effects of fishing and environmental forcing on demographic variation in an exploited species. *Biological Conservation*, *209*, 488–498. https://doi.org/10.1016/j.biocon.2017.03.014

Thorsen, M., Shorten, R., Lucking, R., & Lucking, V. (2000). Norway rats (Rattus norvegicus) on Frégate Island, Seychelles: The invasion; subsequent eradication attempts and implications for the island's fauna. *Biological Conservation*, *96*(2), 133–138. https://doi.org/10.1016/S0006-3207(00)00059-8

Tian, C., Liao, P.-C., Dayananda, B., Zhang, Y.-Y., Liu, Z.-X., Li, J.-Q., Yu, B., & Qing, L. (2019). Impacts of livestock grazing, topography and vegetation on distribution of wildlife in Wanglang National Nature Reserve, China. *Global Ecology and Conservation*, *20*, e00726. https://doi.org/10.1016/j.gecco.2019.e00726

Toledo-Guedes, K., Sanchez-Jerez, P., Benjumea, M. E., & Brito, A. (2014). Farming-up coastal fish assemblages through a massive aquaculture escape event. *Marine Environmental Research*, *98*, 86–95. https://doi.org/10.1016/j.marenvres.2014.03.009

Traba, J., Casals, P., Broto, F., Camprodon, J., Giralt, D., Guixé, D., Mechergui, R., Rios, A., Sales, S., Taull, M., Ammari, Y., Solano, D., & Bota, G. (2016). Coexistence and habitat partitioning at micro- and macro-scales of rodent species in a North African desert (Bou-Hedma National Park, Tunisia). *Journal of Arid Environments*, *131*, 46–58. https://doi.org/10.1016/j.jaridenv.2016.04.002

Tsegaye, D., Moe, S. R., & Haile, M. (2009). Livestock Browsing, Not Water Limitations, Contributes to Recruitment Failure of Dobera glabra in Semiarid Ethiopia. *Rangeland Ecology & Management*, *62*(6), 540–549. https://doi.org/10.2111/08-219.1

Tuboi, C., & Hussain, S. A. (2019). Determination of resource based stocking density of wild ungulates living in the floating meadows of Keibul Lamjao National Park, India. *Acta Ecologica Sinica*, *39*(3), 242–249. https://doi.org/10.1016/j.chnaes.2018.11.008

van Beeck Calkoen, S. T. S., Mühlbauer, L., Andrén, H., Apollonio, M., Balčiauskas, L., Belotti, E., Carranza, J., Cottam, J., Filli, F., Gatiso, T. T., Hetherington, D., Karamanlidis, A. A., Krofel, M., Kuehl, H. S., Linnell, J. D. C., Müller, J., Ozolins, J., Premier, J., Ranc, N., … Heurich, M. (2020). Ungulate management in European national parks: Why a more integrated European policy is needed. *Journal of Environmental Management*, *260*, 110068. https://doi.org/10.1016/j.jenvman.2020.110068

van Keeken, O. A., van Hoppe, M., Grift, R. E., & Rijnsdorp, A. D. (2007). Changes in the spatial distribution of North Sea plaice (Pleuronectes platessa) and implications for fisheries management. *Proceedings of the Sixth International Symposium on Flatfish Ecology, Part I*, *57*(2), 187–197. https://doi.org/10.1016/j.seares.2006.09.002

Van Nieuwenhove, G., Bezdjian, L. P., Schliserman, P., Aluja, M., & Ovruski, S. M. (2016). Combined effect of larval and pupal parasitoid use for Anastrepha fraterculus (Diptera: Tephritidae) control. *Biological Control*, *95*, 94–102. https://doi.org/10.1016/j.biocontrol.2016.01.004

Wallach, A. D., Murray, B. R., & O'Neill, A. J. (2009). Can threatened species survive where the top predator is absent? *Biological Conservation*, *142*(1), 43–52. https://doi.org/10.1016/j.biocon.2008.09.021

Wallgren, M., Skarpe, C., Bergström, R., Danell, K., Bergström, A., Jakobsson, T., Karlsson, K., & Strand, T. (2009). Influence of land use on the abundance of wildlife and livestock in the Kalahari, Botswana. *Journal of Arid Environments*, *73*(3), 314–321. https://doi.org/10.1016/j.jaridenv.2008.09.019

Walsh, S. J., Simpson, M., & Morgan, M. J. (2004). Continental shelf nurseries and recruitment variability in American plaice and yellowtail flounder on the Grand Bank: Insights into stock resiliency. *Proceedings of the Fifth International Symposium on Flatfish Ecology, Part II*, *51*(3), 271–286. https://doi.org/10.1016/j.seares.2003.10.003

Walton, M. E., Le Vay, L., Lebata, J. H., Binas, J., & Primavera, J. H. (2007). Assessment of the effectiveness of mangrove rehabilitation using exploited and non-exploited indicator species. *Biological Conservation*, *138*(1), 180–188. https://doi.org/10.1016/j.biocon.2007.04.012

Wang, T., Andrew Royle, J., Smith, J. L. D., Zou, L., Lü, X., Li, T., Yang, H., Li, Z., Feng, R., Bian, Y., Feng, L., & Ge, J. (2018). Living on the edge: Opportunities for Amur tiger recovery in China. *Biological Conservation*, *217*, 269–279. https://doi.org/10.1016/j.biocon.2017.11.008

Wang, T., Feng, L., Yang, H., Han, B., Zhao, Y., Juan, L., Lü, X., Zou, L., Li, T., Xiao, W., Mou, P., Smith, J. L. D., & Ge, J. (2017). A science-based approach to guide Amur leopard recovery in China. *Special Issue on China's Biodiversity Conservation*, *210*, 47–55. https://doi.org/10.1016/j.biocon.2016.03.014

Wangdi, T., Tobgay, S., Dorjee, K., Dorji, K., & Wangyel, S. (2019). The distribution, status and conservation of the Himalayan Musk Deer Moschus chrysogaster in Sakteng Wildlife Sanctuary. *Global Ecology and Conservation*, *17*, e00466. https://doi.org/10.1016/j.gecco.2018.e00466

Wolfenden, A., Jones, C. G., Tatayah, V., Züel, N., & de Kort, S. R. (2015). Endangered pink pigeons treat calls of the ubiquitous Madagascan turtle dove as conspecific. *Animal Behaviour*, *99*, 83–88. https://doi.org/10.1016/j.anbehav.2014.10.023

Zhang, M., Zhang, X., Zhang, P., Liu, Y., An, J., Wang, D., Cai, Z., & Hou, R. (2021). Natural reproductive performance is associated with captive management in adult male giant pandas. *Applied Animal Behaviour Science*, *240*, 105353. https://doi.org/10.1016/j.applanim.2021.105353

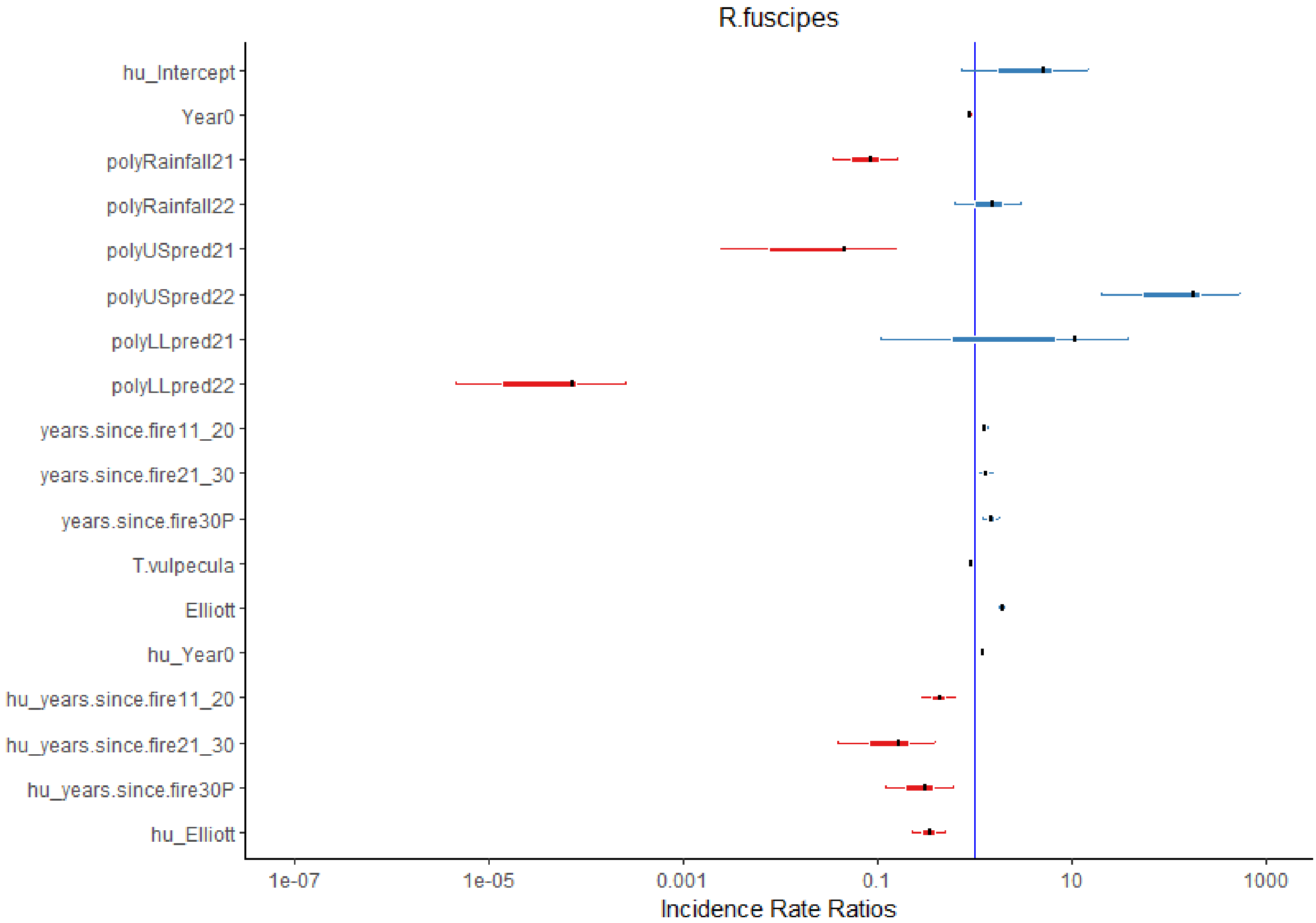
Zielinski, W. J., Tucker, J. M., & Rennie, K. M. (2017). Niche overlap of competing carnivores across climatic gradients and the conservation implications of climate change at geographic range margins. *Biological Conservation*, *209*, 533–545. https://doi.org/10.1016/j.biocon.2017.03.016

Zuccarino-Crowe, C. M., Taylor, W. W., Hansen, M. J., Seider, M. J., & Krueger, C. C. (2016). Effects of lake trout refuges on lake whitefish and cisco in the Apostle Islands Region of Lake Superior. *Journal of Great Lakes Research*, *42*(5), 1092–1101. https://doi.org/10.1016/j.jglr.2016.07.011

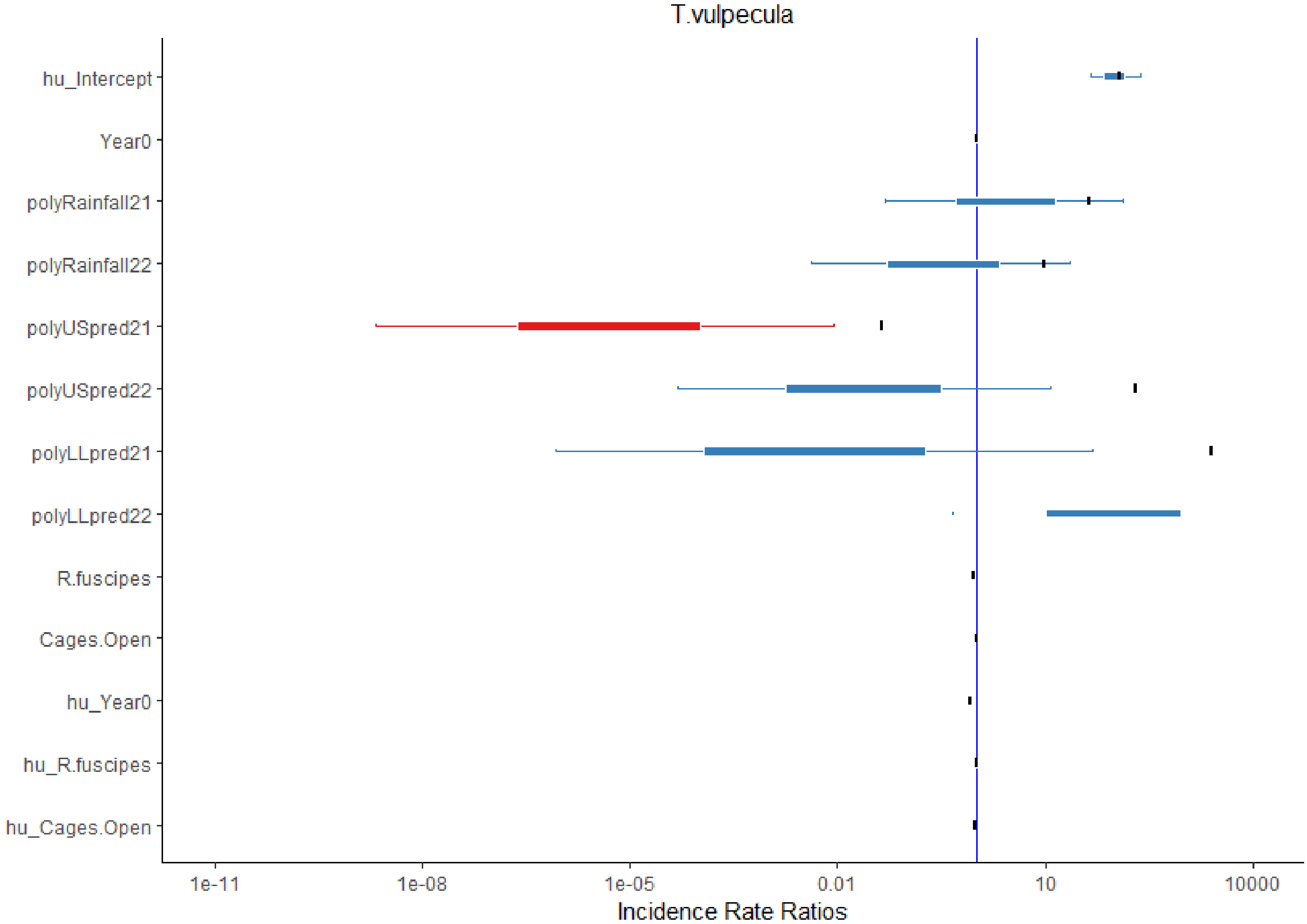
Appendix B

Appendix for Chapter 3

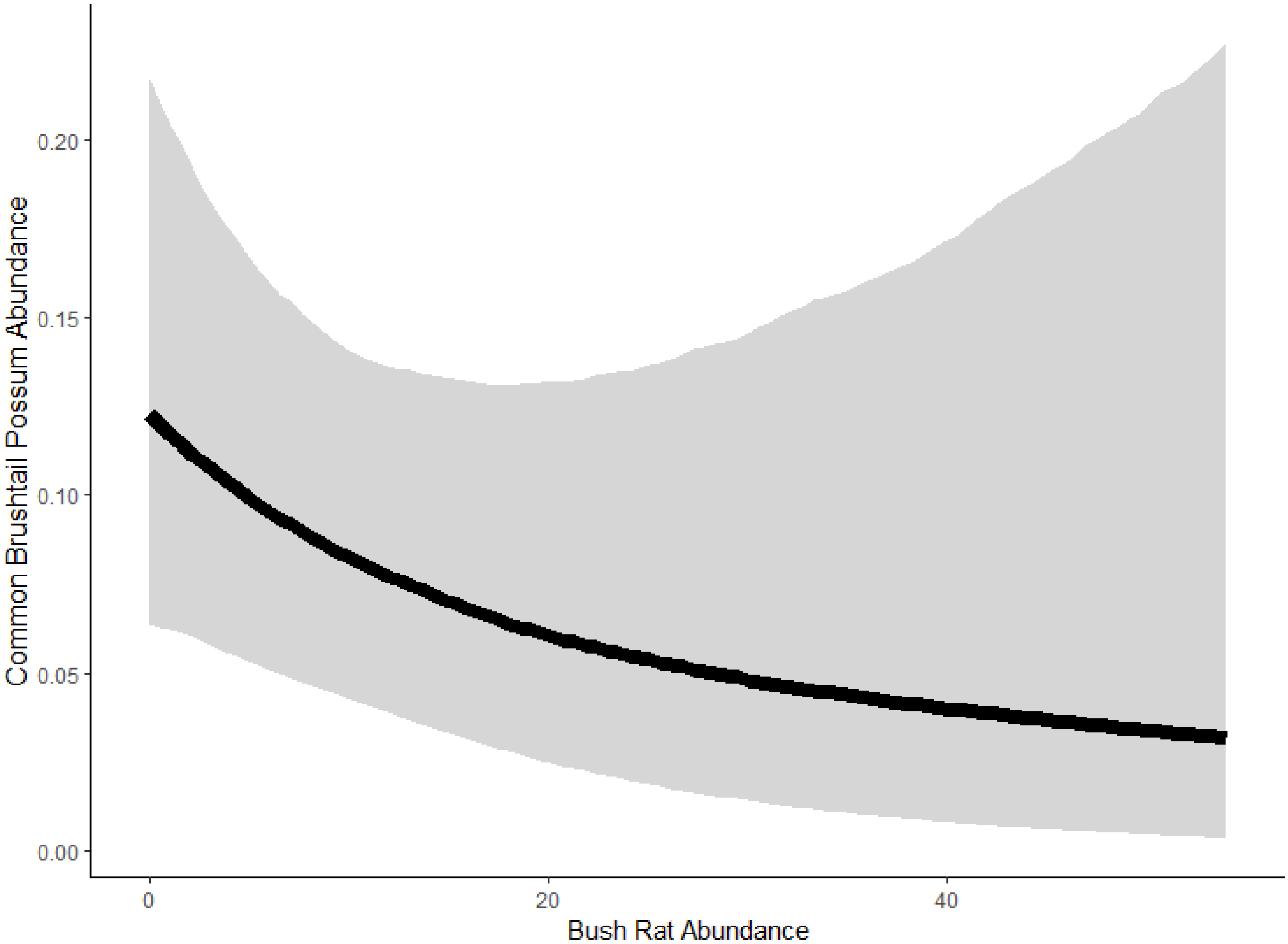
Appendix B.1. The forest plot of bush rat model 4. The blue vertical line represents the zero-effect line. Red horizontal lines on the negative side of the scale represent negative effects, blue horizontal lines on the positive side of the scale represent positive effects. The black dot represents the posterior mean. Lines that cross the zero-effect line represent non-significant results. The names for the variables match to the names used within the models, with variables including "hu_" representing variables in the hurdle model (Table 3-1).



Appendix B.2. The forest plot of common brushtail possum model 10. Red horizontal lines on the negative side of the scale represent negative effects, blue horizontal lines on the positive side of the scale represent positive effects. The black dot represents the posterior mean. Lines that cross the zero-effect line represent non-significant results. The names for the variables match to the names used within the models, with variables including “hu_” representing variables in the hurdle model (Table 3-2).



Appendix B.3. The unconditional change in the abundance of common brushtail possums in response to the increasing abundance of bush rats. The shaded regions represent the 95% credible intervals.



Appendix C

Appendix for Chapter 4

Appendix C.1. The top variations of the 5 models within 2 AICc scores. The variable names match what was presented in Table 4-1. The ΔAICc column represents the difference from the top-ranking model. The response variable with an asterix (*) represents the model variable that was selected as the most parsimonious (i.e., simplest of the model variations within 2 AICc scores of the best fitting model). This model variation was the best fitting for all models except Model 4 (TV_time).

Response	***Model Format***	***AICc***	***ΔAICc***
Model 1			
*RF_count	~ TV_count + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall Zi = TV_count + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall	166504.2	0.00
RF_count	~ TV_count + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall + years.since.fire Zi = TV_count + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall	166504.7	0.49
RF_count	~ TV_count + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall + TWI Zi = TV_count + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall	166506.0	1.86
RF_count	~ TV_count*Bin.Type + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall Zi = TV_count + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall	166506.0	1.87
Model 2			
*RF_time	~ TV_count*Bin.Type + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall	455450.8	0.00
RF_time	~ TV_count*Bin.Type + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall + TWI	455452.7	1.84
RF_time	~ TV_count*Bin.Type + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall + years.since.fire	455452.8	2.00
Model 3			
*TV_count	~ RF_count*Bin.Type + RF_time*Bin.Time + Time.Since.Rat + Illumination + Rainfall, Zi = RF_count*Bin.Type + RF_time*Bin.Type + Time.Since.Rat + Illumination + Rainfall	120179.3	0.00
TV_count	~ RF_count*Bin.Type + RF_time*Bin.Time + Time.Since.Rat + Illumination + Rainfall + TWI, Zi = RF_count*Bin.Type + RF_time*Bin.Type + Time.Since.Rat + Illumination + Rainfall	120179.9	0.64
TV_count	~ RF_count*Bin.Type + RF_time*Bin.Type + Time.Since.Rat + Illumination + Rainfall + TWI + years.since.fire, Zi = RF_count*Bin.Type + RF_time*Bin.Type + Time.Since.Rat + Illumination + Rainfall	120180.3	0.97
TV_count	~ RF_count*Bin.Type + RF_time*Bin.Type + Time.Since.Rat + Illumination + Rainfall + years.since.fire, Zi = RF_count*Bin.Type + RF_time*Bin.Type + Time.Since.Rat + Illumination + Rainfall	120181.0	1.72

Model 4			
TV_time	~ RF_count*Bin.Type + RF_time*Bin.Type + Time.Since.Rat*Bin.Type + Illumination + Rainfall + TWI	481635.9	0.00
*TV_time	~ RF_count*Bin.Type + RF_time*Bin.Type + Time.Since.Rat*Bin.Type + Illumination + Rainfall	481637.0	1.06
TV_time	~ RF_count*Bin.Type + RF_time*Bin.Type + Time.Since.Rat*Bin.Type + Illumination + Rainfall + TWI + years.since.fire	481637.1	1.18
TV_time	~ RF_count*Bin.Type + RF_time*Bin.Type + Time.Since.Rat*Bin.Type + Illumination + Rainfall + years.since.fire	481637.8	1.92
Model 5			
*RF_eat	~ TV_count + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall	446516.6	0.00
RF_eat	~ TV_count + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall + TWI	446518.6	1.95
RF_eat	~ TV_count + TV_time*Bin.Type + Time.Since.Possum*Bin.Type + Illumination + Rainfall + years.since.fire	446518.6	1.99

Appendix C.2. The summary GLMM results for model 1 (number of bush rat visits as the response variable). Term is the variable of interest (Table 3.1), estimate is the estimated mean, std.error is the standard error. The confidence levels correspond to the lower and upper 95% confidence intervals. The wrap.facet column informs whether the variable was in the conditional or zero-inflated steps of the model.

term	estimate	std.error	conf.low	conf.high	p.value	wrap.facet
scale(TV_count)	-0.186	0.005	-0.195	-0.177	0	conditional
scale(TV_time)	-0.023	0.002	-0.027	-0.019	1.06E-32	conditional
Bin.Typesmall	-0.154	0.291	-0.725	0.4168	0.596	conditional
scale(Time.Since.Possum)	-0.073	0.004	-0.080	-0.065	3.01E-75	conditional
scale(Illumination)	-0.118	0.002	-0.123	-0.114	0	conditional
scale(rainfall)	-0.185	0.003	-0.190	-0.180	0	conditional
scale(TV_time):Bin.Typesmall	0.0145	0.006	0.004	0.026	0.007	conditional
Bin.Typesmall:scale(Time.Since.Possum)	0.083	0.005	0.073	0.094	7.96E-55	conditional
scale(TV_time)	-0.448	0.055	-0.557	-0.339	6.90E-16	zero_inflated
Bin.Typesmall	1.676	1.455	-1.176	4.527	0.249	zero_inflated
scale(Time.Since.Possum)	-6.079	0.455	-6.972	-5.186	1.29E-40	zero_inflated
scale(Illumination)	0.096	0.038	0.022	0.170	0.011	zero_inflated
scale(rainfall)	0.531	0.035	0.463	0.599	3.87E-53	zero_inflated
scale(TV_count)	-1.262	0.055	-1.370	-1.154	1.15E-116	zero_inflated
scale(TV_time):Bin.Typesmall	0.356	0.082	0.196	0.516	1.27E-05	zero_inflated
Bin.Typesmall:scale(Time.Since.Possum)	5.061	0.491	4.098	6.024	6.96E-25	zero_inflated

Appendix C.3. The summary GLMM results for model 2 (length of bush rat visits as the response variable). Term is the variable of interest (Table 3.1), estimate is the estimated mean, std.error is the standard error. The confidence levels correspond to the lower and upper 95% confidence intervals.

term	estimate	std.error	conf.low	conf.high	p.value
scale(TV_count)	-0.117	0.010	-0.136	-0.097	4.76E-33
Bin.Typesmall	-0.133	0.138	-0.404	0.138	0.336
scale(TV_time)	0.173	0.006	0.1617	0.184	7.00E-197
scale(Time.Since.Possum)	0.092	0.011	0.070	0.113	3.49E-17
scale(Illumination)	0.024	0.007	0.011	0.037	0.0002
scale(rainfall)	-0.059	0.006	-0.072	-0.047	2.16E-21
scale(TV_count):Bin.Typesmall	0.219	0.032	0.155	0.282	1.30E-11
Bin.Typesmall:scale(TV_time)	-0.143	0.012	-0.167	-0.119	1.64E-32
Bin.Typesmall:scale(Time.Since.Possum)	-0.094	0.014	-0.122	-0.066	4.47E-11

Appendix C.4. The summary GLMM results for model 3 (number of possum visits as the response variable). Term is the variable of interest (Table 3.1), estimate is the estimated mean, std.error is the standard error. The confidence levels correspond to the lower and upper 95% confidence intervals. The wrap.facet column informs whether the variable was in the conditional or zero-inflated steps of the model.

term	**estimate**	**std.error**	**conf.low**	**conf.high**	**p.value**	**wrap.facet**
scale(RF_count)	-0.111	0.008	-0.127	-0.096	2.19E-45	conditional
Bin.Typesmall	-1.165	0.755	-2.644	0.315	0.123	conditional
scale(RF_time)	-0.130	0.006	-0.142	-0.118	2.40E-104	conditional
scale(Time.Since.Rat)	-0.050	0.002	-0.054	-0.045	2.22E-93	conditional
scale(Illumination)	0.075	0.005	0.066	0.084	3.21E-59	conditional
scale(rainfall)	-0.052	0.005	-0.062	-0.042	4.09E-23	conditional
scale(RF_count):Bin.Typesmall	-0.066	0.023	-0.112	-0.020	0.005	conditional
Bin.Typesmall:scale(RF_time)	0.131	0.013	0.106	0.155	3.31E-25	conditional
scale(RF_count)	-0.417	0.063	-0.540	-0.293	3.81E-11	zero_inflated
Bin.Typesmall	2.315	1.161	0.039	4.592	0.046	zero_inflated
scale(RF_time)	0.033	0.038	-0.042	0.108	0.386	zero_inflated
scale(Time.Since.Rat)	-5.275	0.384	-6.028	-4.522	6.72E-43	zero_inflated
scale(Illumination)	0.524	0.037	0.451	0.597	7.26E-45	zero_inflated
scale(rainfall)	1.275	0.031	1.214	1.335	0	zero_inflated
scale(RF_count):Bin.Typesmall	1.962	0.164	1.641	2.283	4.38E-33	zero_inflated
Bin.Typesmall:scale(RF_time)	-0.178	0.069	-0.314	-0.043	0.010	zero_inflated
Bin.Typesmall:scale(Time.Since.Rat)	0.143	0.875	-1.573	1.859	0.870	zero_inflated

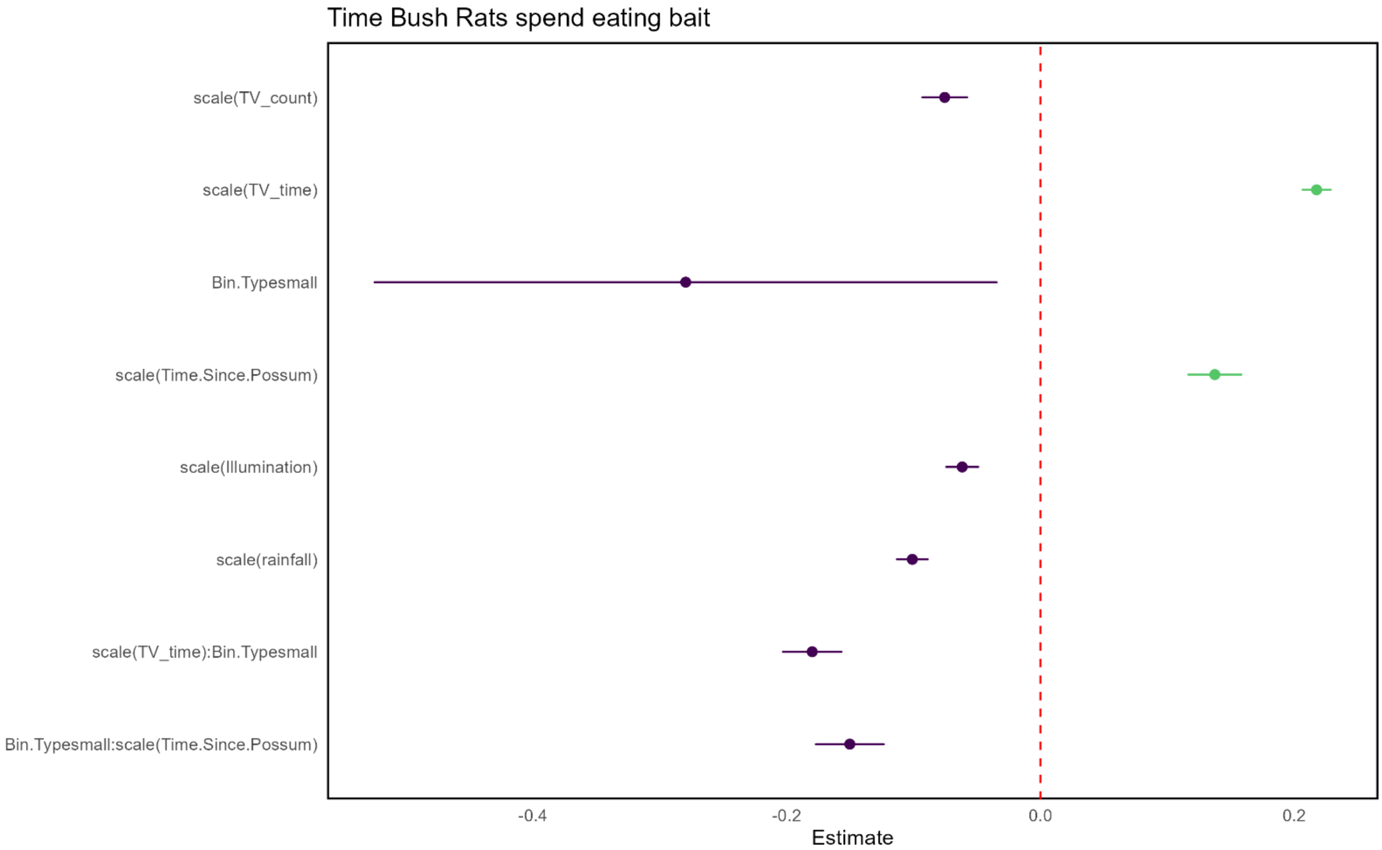
Appendix C.5. The summary GLMM results for model 4 (length of possum visits as the response variable). Term is the variable of interest (Table 3.1), estimate is the estimated mean, std.error is the standard error. The confidence levels correspond to the lower and upper 95% confidence intervals.

term	estimate	std.error	conf.low	conf.high	p.value
scale(RF_count)	-0.026	0.011	-0.047	-0.005	0.017
Bin.Typesmall	-0.126	0.140	-0.401	0.148	0.367
scale(RF_time)	0.174	0.006	0.162	0.187	2.72E-168
scale(Time.Since.Rat)	-0.077	0.007	-0.090	-0.064	9.10E-32
scale(Illumination)	-0.158	0.007	-0.173	-0.143	2.77E-99
scale(rainfall)	-0.104	0.007	-0.118	-0.091	8.43E-49
scale(RF_count):Bin.Typesmall	0.060	0.035	-0.008	0.129	0.084
Bin.Typesmall:scale(RF_time)	-0.115	0.017	-0.149	-0.081	2.39E-11
Bin.Typesmall:scale(Time.Since.Rat)	0.094	0.014	0.066	0.121	2.11E-11

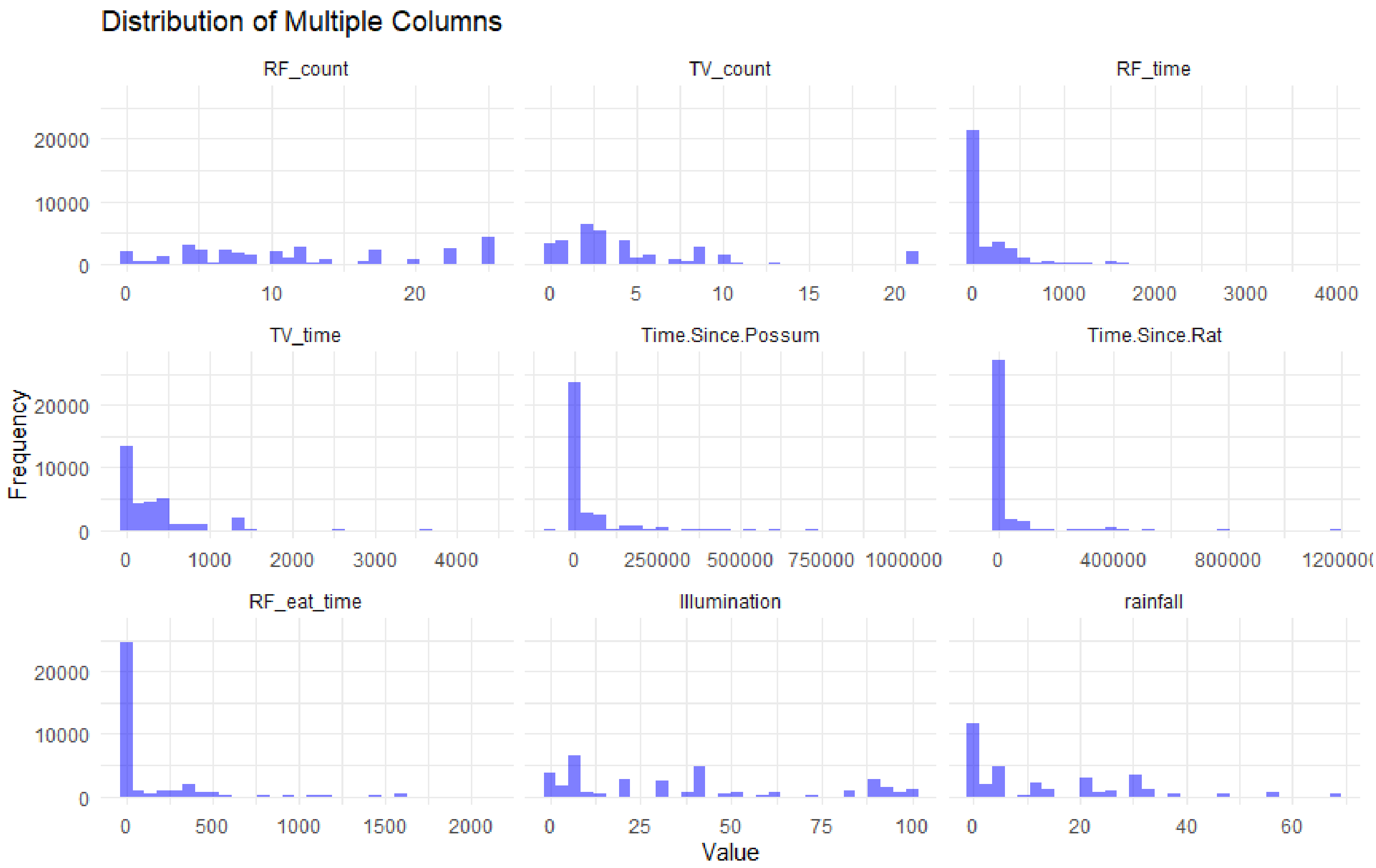
Appendix C.6. The summary GLMM results for model 5 (length visits when bush rats are eating bait as the response variable). Term is the variable of interest (Table 3.1), estimate is the estimated mean, std.error is the standard error. The confidence levels correspond to the lower and upper 95% confidence intervals.

term	estimate	std.error	conf.low	conf.high	p.value
scale(TV_count)	-0.075	0.009	-0.093	-0.058	3.45E-17
scale(TV_time)	0.218	0.006	0.207	0.229	0
Bin.Typesmall	-0.280	0.125	-0.525	-0.035	0.025
scale(Time.Since.Possum)	0.137	0.011	0.117	0.158	2.03E-38
scale(Illumination)	-0.062	0.006	-0.074	-0.049	4.94E-22
scale(rainfall)	-0.101	0.006	-0.113	-0.089	1.17E-61
scale(TV_time):Bin.Typesmall	-0.180	0.012	-0.203	-0.157	3.46E-53
Bin.Typesmall:scale(Time.Since.Possum)	-0.150	0.014	-0.177	-0.124	2.38E-28

Appendix C.7. Forest plots of the best fitting subsets of model 5 (length visits when bush rats are eating bait as the response variable), showing the effect sizes and confidence intervals. Estimates in purple show negative effects and estimates in yellow show positive effects. Error bars are the 95% confidence intervals, and bars that cross the vertical prediction line demonstrate non-significant effects.



Appendix C.8. A set of histogram plots detailing the spread of the raw data for each of the continuous selected variables (*RF_count, RF_time, TV_count, TV_time, Time.Since.Possum, Time.Since.Rat, RF_eat_time, Illumination, rainfall*).



Appendix D

Appendix for Chapter 5

Appendix D.1. The number of samples collected by species, age, sex, and vegetation type.

Bush Rat		Possum	
Total	78		57
		Sex	
Male	27	Male	23
Female	39	Female	31
Not Recorded	12	Not Recorded	3
		Age	
Adult	46	Adult	50
Juvenile	9	Juvenile	1
Subadult	14	Subadult	3
Not Recorded	9	Not Recorded	3
		Habitat	
Casuarina	0	Casuarina	4
Forest	20	Forest	32
Heathland	4	Heathland	2
Rainforest	11	Rainforest	4
Scrubland	3	Scrubland	1
Sedgeland	6	Sedgeland	0
Shrubland	19	Shrubland	8
Woodland	15	Woodland	6

Appendix D.2. The list of identified diet items, separated by plant, invertebrate, and fungi, detailing the level of resolution we were able to identify diet items to (i.e., species, genus, order).

Plant		**Invertebrate**		**Fungi**	
Species	**Level**	**Species**	**Level**	**Species**	**Level**
Avena	genus	Arthropoda	phylum	*Hysterangium*	genus
Fabaceae	family	*Rhithrogena hageni*	species	*Russula vinaceocuticulata*	species
Poales	order	Neuroptera	order	*Hysterangium pterosporum*	species
Acacia	genus	Sciaridae	family	*Chondrogaster pachysporus*	species
Schelhammera undulata	species	*Pheidole*	genus	*Mesophellia oleifera*	species
Proteaceae	family	Coleoptera	order	*Cortinarius*	genus
Orchidaceae	family	Hymenoptera	order	*Scleroderma*	genus
Poaceae	family	Diptera	order	*Russula floriformis*	species
Bossiaea	genus	*Anonychomyrma*	genus	*Protoglossum niphophilum*	species
Apiaceae	family	Phoridae	family	*Mesophellia*	genus
Patersonia glabrata	species	Araneae	order	*Thaxterogaster dulciorum*	species
Pittosporaceae	family	*Olios*	genus	*Russula*	genus
Pinus	genus	*Symplecta pilipes*	species	*Timgrovea*	genus
Rutaceae	family	Hemiptera	order	*Russula purpureoflava*	species
Oleaceae	family	*Solenopsis*	genus	*Cortinarius clelandii*	species
Rubiaceae	family	*Apis mellifera*	species	*Russula foetens*	species
Dracaena	genus	Cecidomyiidae	family	*Austrogautieria*	genus
Glycine	genus	*Diplonevra*	genus	*Hallingea*	genus
Elaeocarpus	genus	*Camponotus intrepidus*	species	*Chondrogaster*	genus
Eustrephus latifolius	species	Chloropidae	family	*Malajczukia amicorum*	species
Viola	genus	*Diarsia intermixta*	species	*Cortinarius beeverorum*	species
Zoysia macrantha subsp. walshii	species	*Persectania ewingii*	species	*Gymnomyces*	genus
Asparagus aethiopicus	species	*Idiodes apicata*	species	*Russula sinuata*	species
Liparophyllum exaltatum	species	Tetranychidae	family	*Arcangeliella claridgei*	species
Acacia nematophylla	species	*Ixodes holocyclus*	species	*Gyroporus*	genus

Crassula	genus	Braconidae	family	*Octaviania tasmanica*	species
Casuarina	genus	*Mimaglossa nauplialis*	species	*Inocybe bulbinella*	species
Smilax	genus	*Sphaleractis eurysema*	species	*Fistulinella*	genus
Myrtaceae	family				
Spiranthes sinensis var. amoena	species				
Asparagales	family				
Acacia bellula	species				
Cinnagrostis viridis	species				
Asteraceae	family				
Caryophyllales	order				
Eucalyptus vernicosa	species				

Appendix D.3. The Principal Component Analysis (PCA) plots detailing the clustering of samples based on if they are either bush rats or possums to demonstrate the similarities between the diets of each species. Each point represents an individual animal's diet, with colours and shapes indicating if the animal is a bush rat or possums. The axis (PC1 and PC2) represents the first two principal components, highlighting the main sources of variation in the dataset. (a) The overall PCA, with PC1 explaining 24.1% of the variance, and PC2 explaining 16.6% of the variance. (b) The plant diet PCA, with PC1 explaining 40.5% of the variance, and PC2 explaining 16.4% of the variance. (c) The invertebrate diet PCA, with PC1 explaining 33.4% of the variance, and PC2 explaining 22.3% of the variance. (d) The fungi diet PCA, with PC1 explaining 53.3% of the variance, and PC2 explaining 9.7% of the variance.