Bringing Back the Bettong:
Reintroducing ecosystem engineers for restoration in Box-Gum grassy woodland

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Cover image: ‘Bettong and Early Nancies’ by Emily Birks, Ink on Paper, 2018

Candidate's 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.

Catherine Ross

Catherine Elizabeth Ross Date: 7 Feb 2020

Photo by Jimmy Walsh, featuring Balbo the Bettong from the Woodlands and Wetlands Trust

Preface

This thesis is submitted as a ‘thesis by publication’, and consists of an extended context statement (Chapter 1) followed by five chapters (2-6) that are presented as papers which are either published, in review, or in preparation for publication in scientific journals. The chapters are designed to be independent and will therefore inevitably contain some repetition as well as slight differences in formatting to align with different journal styles. The publication details of each chapter are as follows:

2. Ross, C.E., Barton, P.S., McIntyre, S., Cunningham, S.A. & Manning, A.D., 2017. Fine-scale drivers of beetle diversity are affected by vegetation context and agricultural history. *Austral Ecology*, 42(7), 831–843.
3. Ross, C.E., Munro, N.T., Barton, P.S., Evans, M.J., Gillen, J., Macdonald, B.C.T., McIntyre, S., Cunningham, S.A. & Manning, A.D., 2019. Effects of digging by a native and introduced ecosystem engineer on soil physical and chemical properties in temperate grassy woodland. *PeerJ*, 7, p.e7506.
4. Ross, C.E., McIntyre, S., Barton, P.S., Evans, M.J., Cunningham, S.A. & Manning, A.D., 2020. A reintroduced ecosystem engineer provides a germination niche for native plant species. *Biodiversity and Conservation*, 29, 817-837
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While all the chapters have involved contributions from other collaborators, the majority of the work is my own. This includes most of the literature searches, experimental design, field data collection, analysis and interpretation, and writing. My supervisors Professor Adrian Manning, Dr Sue McIntyre, Dr Philip Barton and Professor Saul Cunningham provided valuable guidance and assistance throughout the process and provided feedback on each chapter. Prof. Manning instigated and designed the Mulligans Flat Goorooyarroo Woodland Experiment, which provides the framework for all my work. I used some existing data in Chapters 2 and 3 that were collected by Prof. Manning, Dr Barton, Dr McIntyre, and Dr Nicola Munro before my project started. Dr John Gillen and Dr Ben Macdonald assisted with the processing and analysis of soil samples for Chapter 3. Dr Barton, Dr Maldwyn J. Evans and the late Dr Jeff Wood provided statistical advice on various parts of the experimental design and data analysis. Dr Evans also conducted some of the statistical analyses, particularly those in R. The ideas presented in Chapter 6. were developed at a workshop held at the ANU in November 2017. I organised and facilitated the workshop with the help of Dr Sue McIntyre and wrote the paper, but all the participants contributed to the ideas and provided feedback on the manuscript.

Field work and seed collection were carried out under ACT Government licence number PL201569 under section 273 of the Nature Conservation ACT 2014. This research forms part of the Mulligans Flat–Goorooyarroo Woodland Experiment (Australian Research Council Linkage LP0561817, LP110100126, LP140100209), a partnership between The Australian National University, the Australian Capital Territory Government and James Cook University. During my candidature I was supported by an Australian Government Research Training Program (RTP) Scholarship, and an additional scholarship top-up from the ARC (LP140100209). I also received research grants from the Holsworth Foundation and the Lesslie Foundation.

Artist Interludes

Throughout my candidature, I collaborated with several artists who created artwork based on my research. I found this to be a very rewarding part of my PhD experience, so I wanted to showcase these artworks in my thesis. Between each chapter I have included an ‘artist interlude’, with a brief description of the piece and my experience working with the artist.

Acknowledgements

I acknowledge the Ngunnawal people, the traditional owners of the land where Mulligans Flat and Goorooyarroo Nature Reserves now exist, and pay my respects to their elders past, present and emerging. Thank you for allowing me to work on your beautiful country, and for sharing your knowledge and stories.

Huge thanks to my fantastic supervisors, Adrian Manning, Sue McIntyre, Philip Barton, and Saul Cunningham. I could not have asked for better supervisors, and your support and guidance through this process has been amazing.

I could not have done any of this without the ANU Mulligans Flat team – Jenny Newport, Helen Crisp, Nicki Munro, Will Batson, John Evans, and of course the other PhD and Honours students. When I started my PhD I was the only current student working at Mulligans Flat, but over the years the team has grown to include Belinda, Tim, Brittany, Kiarrah, Rachael, Shoshana and Yaana. You have all made the PhD experience (including the 2am starts!) so much more fun, and I truly feel like I have made friends and collaborators for life.

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Thanks to the Fenner School administrative and field services staff. Also thanks to the Research Training team at ANU, for the opportunity to compete in the 3 Minute Thesis, one of the most rewarding experiences of my PhD, and for providing resources, workshops, and personal support that really helped me get through my thesis. Thank you to the Woodlands and Wetlands Trust, and to the ACT Government staff for supporting all our research, keeping everything running smoothly and safely, and providing opportunities to connect and communicate with the public. Thanks to Greening Australia for keeping me employed, and for answering all my random questions about seeds!

I would also like to acknowledge financial support from the Australian Government Research Training Scholarship, the Australian Research Council, the Holsworth Foundation, and the Lesslie Foundation.

During my PhD I had the opportunity to collaborate with several artists and art projects – James Houlcroft, Emily Birks, Ceilidh Dalton, Jimmy Walsh (ANU Science) and Rachael Robb. Thank you for giving me new perspectives and insights, it was truly a pleasure to work with such talented people and to see the beautiful work you created. I have included some of these artworks in this thesis, with the kind permission of the artists.

The PhD experience can be very isolating, but I have been lucky to have amazing support and friendship from other PhD students and post-docs - Kat Ng, David Johnson, Steph Pulsford, Edwina Fingleton-Smith, Federico Davila, Nicole Hansen, Richard Beggs, Carl Tidemann, Monique Retamal, Katie Moon, Marwan El Hassan, Kelly Dixon, Pandora Holliday, Donna Belder, Shana Nerenburg, Claire Foster, Helen King, Ayako Kawai and many others.

To my parents, thank you for giving me my love of learning and nature. You taught me the wonder of the world, and to never stop asking questions. Thank you to my sister Alex and my wonderful friends for listening to my endless complaining and blabbing about bettongs. Thanks to my dog Tonks for the joy and cuddles. And finally, the biggest thanks go to my husband Dougall. We have gone through a lot in the last five years, and you have been the most amazing support through it all. You’ve read drafts, come to presentations, shared my joy in the good times and been a shoulder to cry on when things got hard. I honestly could not have done it without you, and I’m so lucky to have you.

Abstract

The grassy woodlands of eastern Australia have declined in their range by more than 95% through clearing and fragmentation. This decline has coincided with the loss of many digging or soil-foraging species that are considered to be 'ecosystem engineers' because of their role in biopedturbation and effects on other species and processes. Ecosystem engineers are therefore a priority for reintroduction to restore biodiversity and ecosystem function. However, there are gaps in our knowledge of how digging animals affect their environment and potential impacts on recipient ecosystems. The aim of this thesis was to examine the impact of the eastern bettong (*Bettongia gaimardi*) on ecosystem processes, following their reintroduction to a fenced reserve. It consists of five chapters that explore different aspects of this topic and the implications for management and conservation.

Chapter 2 examines biodiversity patterns as a backdrop to bettong reintroduction in a Box-Gum grassy woodland. We found that beetle assemblages differed in their composition among distinct ground-layer plant communities at log and tree microhabitats, while beetle communities in open microhabitats were more uniform. Sites with evidence of prior agricultural use also had altered beetle communities. These findings demonstrate the fine-scale structure of the grassy woodland ecosystem as a mosaic of plant and insect communities.

Chapter 3 investigates the structural and abiotic effects of bettong and rabbit foraging pits. I found that bettong pits filled in faster than rabbit pits due to their deeper and narrower shape. I did not find any consistent effect on soil nutrients in foraging pits, unlike similar studies in arid areas. Bettong pits reduced daily temperature fluctuations compared to the soil surface. I therefore concluded that in mesic environments, the structural effects of digging may be more important than changes in soil nutrients.

Chapter 4 tests the hypothesis that bettong foraging pits provide favourable conditions for seed germination compared to the soil surface. I found that seedling abundance was almost doubled in pits compared to the soil surface. Responses differed between species and years, with native species responding more strongly to the presence of pits than exotic species in the first year. The response was also stronger in denser grassland, suggesting that the driving mechanism for the increased germination is the creation of gaps and reduced competition from the grass canopy.

Chapter 5 examines the impact of bettongs on a native geophyte, the early nancy (*Wurmbea dioica*). I found that bettongs consumed 13-24% of the plants that emerged each year, resulting in a decline in the *Wurmbea* population over 5 years. However, there was a shift in the population demographics toward younger plants, which may suggest that bettong digging increased recruitment and a possible feedback mechanism. Similar interactions between digging animals and geophytes have been described internationally, but this is the first study in Australia.

Finally, Chapter 6 synthesises research on soil-disturbing ecosystem engineers in Australia. I argue that the goals of species reintroductions are often poorly defined, leading to missed opportunities for research and potential negative outcomes. I discuss the factors that should be considered when reintroducing ecosystem engineers and provide a framework for clarifying the goals of species reintroductions.

The outcomes of my research suggest that reintroducing extirpated ecosystem engineers may contribute to restoration of grassy woodlands, but they may also have unexpected consequences. Translocations should therefore consider both trophic and engineering effects and be prepared to monitor and manage unexpected outcomes. These findings will inform management of sanctuaries and translocations and contribute to restoration efforts in grassy woodlands in Australia and worldwide.

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Chapter 1:
Extended Context Statement

He only says, 'Good fences make good neighbors.'
Spring is the mischief in me, and I wonder
if I could put a notion in his head:
'Why do they make good neighbors?'...
...Before I built a wall I'd ask to know
what I was walling in or walling out,
and to whom I was like to give offense.
Something there is that doesn't love a wall,
that wants it down…

– Robert Frost, Mending Wall

Over the last few decades, fences have become an increasingly important tool in conservation globally (Innes et al., 2012; Legge et al., 2018; Malpas et al., 2013; Massey et al., 2014; Somers and Hayward, 2012). This is especially the case in Australia, where introduced predators have been the main cause of over 30 mammal extinctions, and severe declines of many other species (Woinarski et al., 2015). This has led to the establishment of fenced reserves where feral cats, foxes and other introduced species have been removed. These 'sanctuaries' have allowed the protection and reintroduction of at least 32 threatened species (Legge et al., 2018). Some of these species are known as 'ecosystem engineers' because they have important roles in maintaining ecosystem health and function (Jones et al., 1994; Martin, 2003), and it is thought that reintroducing them could contribute to restoration (Byers et al., 2006; Fleming et al., 2014; Law et al., 2017; Manning et al., 2015). However, there is still much uncertainty about the impacts of ecosystem engineers, particularly across environmental gradients or spatial and temporal scales (Coggan et al., 2018). The ecosystems to which species are being (re)introduced are often highly threatened or degraded themselves, so bringing these animals back could have unexpected consequences (Harris et al., 2013). There is therefore a need for more studies of reintroductions carried out within an experimental framework to allow learning and to inform adaptive management (Manning et al., 2009).

In this thesis I explore the broader issues around returning ecosystem engineers to their former ecosystems, using the reintroduction of the eastern bettong (*Bettongia gaimardi*) to a fenced sanctuary in south-eastern Australia as a case study. Like other soil-foraging mammals, bettongs are considered to be ecosystem engineers because of their role in soil turnover (Fleming et al., 2014), and this was a large part of the rationale behind the selection of the species for reintroduction (Manning et al., 2011). The reintroduction was conducted within the context of a long-term restoration experiment, providing the opportunity to explore ecosystem impacts that would not be possible outside predator-proof fences. This is the first study on the re-establishment of a locally extinct ecosystem engineer and its role in restoring critically endangered box-gum grassy woodlands.

This context statement provides background information, research aims, and a summary of each chapter, along with a brief discussion of the overall implications of my research.

1.1 *Ecosystem engineering*

The term 'ecosystem engineer' was coined in 1994 by Jones *et al.* (Jones et al., 1994). They defined the term as follows:

> 'Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and create habitat.'

Ecosystem engineers can be categorised into two groups, 'autogenic' and 'allogenic'. Examples of autogenic engineers include trees or corals, which alter or create habitat structure with their own bodies. On the other hand, allogenic engineers modify the environment through their behaviour (Jones et al., 1994). The best-known example of this is the beaver, which alters hydrology and creates extensive wetland systems through building dams (Naiman et al., 1988; Stringer and Gaywood, 2016). Ecosystem engineering is generally thought to increase heterogeneity and species richness at the landscape scale (Davidson and Lightfoot, 2008; Eldridge and Whitford, 2009; Romero et al., 2015; Wright et al., 2006, 2002), however there may also be negative effects on certain species or at certain scales (Jones et al., 1997).

Jones *et al.* (2010) introduced a framework for understanding the effects of ecosystem engineers (Figure 1). In this framework, the engineer creates a structural change, which leads to abiotic change, which in turn causes biotic change. It is important to note that at any stage in this process there may be feedback to the engineer itself, either positive or negative. For example, beavers build dams that then provide shelter, but the area may become degraded with use over time and eventually be abandoned (Wright et al., 2004). However, it is possible that the engineer may not be affected at all by the engineering.

I have used the model developed by Jones et al. (2010) as a basis for understanding how digging animals such as the bettong act as ecosystem engineers. However, this model does not include a number of important factors which also need to be considered. For example, effects of ecosystem engineers are likely to differ depending on environmental context and spatial or temporal scale (Crain and Bertness, 2006; Hastings et al., 2007). The overall impact of any engineering process will depend on the decay and recovery rate i.e. how long it takes for the engineered structure or area to return to its former state (Wright et al., 2004). The model also does not include other interactions between the engineer and the ecosystem, such as trophic or other non-trophic effects, although several other studies have attempted to integrate engineering and trophic effects (e.g. Wilby *et al.* 2001; Sanders *et al.* 2014).

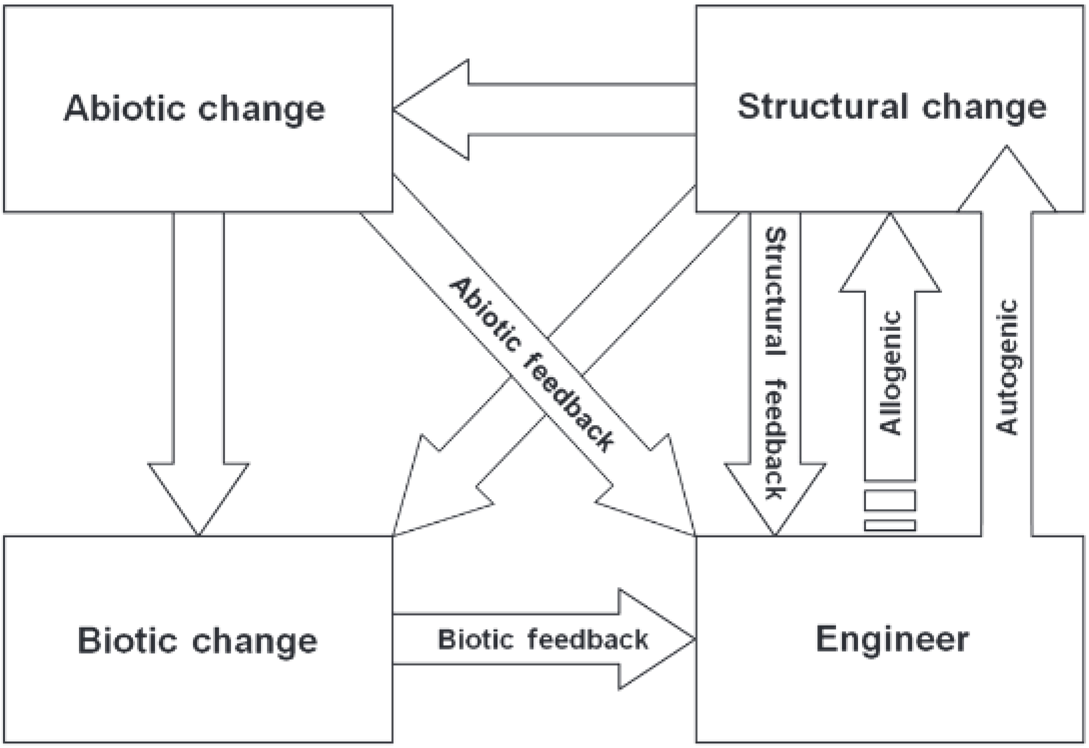


Figure 1. *Conceptual framework for understanding the structural, abiotic and biotic effects of ecosystem engineers* (Jones et al., 2010)

1.1.1 Digging animals as ecosystem engineers

Digging or soil-foraging vertebrates are considered to be important ecosystem engineers because of their role in soil turnover, and have received a lot of attention and research worldwide, particularly in arid and semi-arid regions (Coggan et al., 2018; Davidson et al., 2012; Kinlaw, 1999; Mallen-Cooper et al., 2019; Platt et al., 2016; Whitford and Kay, 1999). Examples include prairie dogs (*Cynomys spp.*) (VanNimwegen et al., 2008), plateau zokors, (*Myospalax fontanierii*) (Zhang et al., 2003), aardvark (*Orycteropus afer*) (Haussmann et al., 2018), badgers (*Taxidea taxus*) (Eldridge and Whitford, 2009), rabbits (*Oryctolagus cuniculus*) (Gálvez-Bravo et al., 2011), pocket gophers (Geomyidae) (Reichman and Seabloom, 2002), and mole rats (Bathyergidae) (Hagenah and Bennett, 2012), to name just a few.

In Australia, digging animals are found in most ecosystems, and have been shown to have significant effects on a range of ecosystem processes (Eldridge and James, 2009; Fleming et al., 2014; Martin, 2003). For example, burrows and foraging pits increase soil turnover and water infiltration and create patches of higher fertility (Davies et al., 2019; Eldridge et al., 2012, 2010;

James et al., 2009), collect litter and increase decomposition rates (Decker et al., 2019; Valentine et al., 2017). They also create a more mesic microclimate and provide habitat for other species (Dawson et al., 2019; Eldridge et al., 2015; Grossman et al., 2019; Hofstede and Dziminski, 2017; Read et al., 2008), and provide a germination niche for plants (Dodd, 2009; James et al., 2010; Pyrke, 1994; Ross et al., 2020; Valentine et al., 2018). However, most of these studies were undertaken in arid or semi-arid systems, and relatively little is known about the role of digging animals in other environmental contexts (e.g. temperate or tropical environments) (Coggan et al., 2018).

1.1.2 Using ecosystem engineers for restoration

The reintroduction of ecosystem engineers has been suggested as a potential tool for restoring degraded ecosystems (Byers et al., 2006). For example, the reintroduction of beaver (*Castor spp.*) to parts of Europe has had significant impacts on waterways, increasing plant diversity and habitat heterogeneity (Law et al., 2017; Stringer and Gaywood, 2016; Wright et al., 2002). Wild boar (*Sus scrofa*) have also been reintroduced to Britain after an absence of over 700 years, with widespread effects on soils and ground-layer vegetation (Sandom et al., 2013a, 2013b; Sims et al., 2014). Aldabran giant (*Aldabrachelys gigantea*) and Madagascan radiated (*Astrochelys radiata*) tortoises were introduced to Mauritius to replace the extinct Mauritian giant tortoise (*Cylindraspis spp.*), and have successfully reduced the abundance of exotic plants (Griffiths et al., 2010). However, there has been significant controversy around these kinds of 'rewilding' projects, with several papers encouraging caution, and warning of potential negative consequences due to a lack of clarity around the aims of rewilding and the unpredictability of how ecosystems will respond to novel species in the context of a changing environment (Hayward et al., 2019; Nogués-Bravo et al., 2016; Seddon et al., 2014). On the other hand, any disturbance will have a range of effects that can be interpreted as 'positive' or 'negative' for certain species, depending on our human values and perspectives. While there is inherent uncertainty in any restoration or rewilding project, the only way to increase our understanding, and our ability to manage undesirable outcomes, is to conduct experimental reintroductions under controlled conditions.

Many of Australia's digging animals have experienced widespread declines in their populations, and have therefore been targeted for translocation and reintroduction programs, often into fenced reserves or islands where introduced predators and other threats have been removed (Legge et al., 2018). While these translocations are usually carried out for conservation purposes, there is increasing recognition that reintroducing digging animals to areas where they have been lost could help to restore degraded ecosystems by returning missing ecosystem processes and functions (Palmer *et al.*, in review; Manning, Eldridge and Jones, 2015; Munro *et al.*, 2019). Despite this, in many cases there has been little consideration of the potential impacts of reintroduced ecosystem engineers on the recipient ecosystems, which may lead to missed opportunities for research and a failure to recognise and manage potential negative consequences. There are several recorded examples where the reintroduced digging animals have reached very high populations in the absence of predators, leading to (perceived) negative effects on vegetation and other animals (Coggan and Gibb, 2019; Linley et al., 2016; Moseby et al., 2018; Silvey et al., 2015; Verdon et al., 2016). Studies from translocations of digging animals in Australia provide an opportunity to increase our understanding of the role of ecosystem engineers and their potential to restore ecosystem processes and function, but also of the risks inherent in any reintroduction.

1.2 *The study site and species*

I conducted my field studies in two neighbouring nature reserves in the north-east of the Australian Capital Territory (A.C.T.), Mulligans Flat and Goorooyarroo, totalling 1623 ha (Figure 2). These reserves contain some of the largest remaining areas of ‘Yellow Box – Blakely’s Red Gum Grassy Woodland’, a critically endangered ecological community (Australian Government, 2006) (Figure 3). The soils and vegetation in the reserves are described in Lepschi (1993) and McIntyre *et al.* (2010). Box-Gum Grassy Woodland occurs on the lower slopes, dominated by Blakely’s Red Gum (*Eucalyptus blakelyi*) and Yellow Box (*E. melliodora*) and interspersed with patches of open grassland, while the upper slopes are dry sclerophyll forest. The reserves have a history of livestock grazing, fertilisation and timber removal, which has resulted in soil degradation, loss of species (particularly ground-layer plant species) and introduced weeds (McIntyre et al., 2010). While these threats were removed when the reserves were created, large populations of rabbits (*Oryctolagus cuniculus*) and eastern grey kangaroos (*Macropus giganteus)* maintained a high grazing pressure, preventing recovery of the ground-layer vegetation (McIntyre et al., 2017, 2010). The climate of the region is classified as temperate, with an average annual rainfall of 636.2mm, mean maximum temperature (January) of 28.5°C and mean minimum temperature (July) of 0.0°C (Bureau of Meteorology, 2020).

1.2.1 The Mulligans Flat Goorooyarroo Woodland Experiment

This research forms part of the Mulligans Flat Goorooyarroo Woodland Experiment (MFGOWE), a long-term ecological experiment in south-eastern Australia. It was established to provide an ‘outdoor laboratory’ for research on restoration of grassy woodlands (described in detail in Shorthouse et al. 2012; Manning et al. 2011). The experiment has involved the collection of long-term data on soils, vegetation, invertebrates, birds, and reptiles, as well as the application of restoration treatments including the addition of course woody debris (Figure 3a), burning, and altering macropod grazing levels. These treatments have been applied across a series of 96 one-hectare research sites (Figure 2), stratified among different vegetation types. Some aspects of this experimental design have been used in the current study, and are described in detail in the relevant chapters.

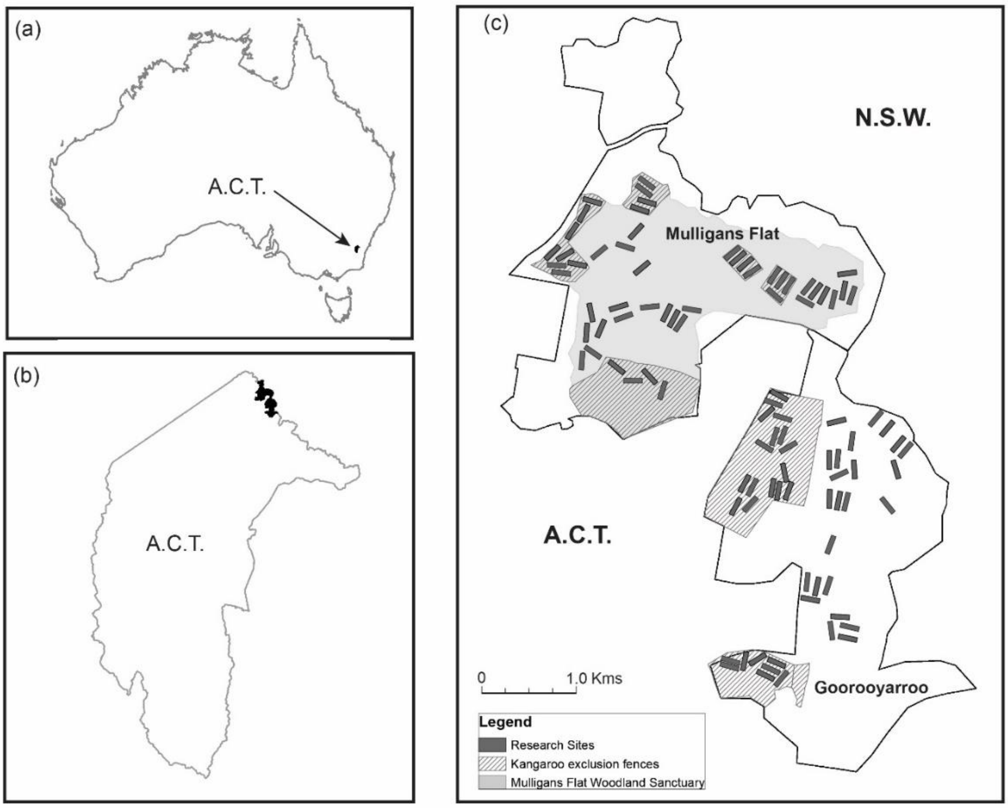


Figure 2. *Map of the Mulligans Flat Goorooyarroo Woodland Experiment (MFGOWE). The MFGOWE is located in south-eastern Australia (a), on the northern edge of the Australian Capital Territory (A.C.T.) (b). The design of the experiment (c) includes 96 one-hectare research sites, seven kangaroo exclosures (fenced areas with kangaroo populations maintained at low levels), and the Mulligans Flat Woodland Sanctuary (a 485 ha area surrounded by a predator-proof fence). Figure created by Jenny Newport.*

Figure 3. *The Mulligans Flat Goorooyarroo Woodland Experiment. (a) Goorooyarroo Nature Reserve, typical Yellow Box – Blakely's Red Gum Grassy Woodland with added course woody debris treatment. Credit: Philip Barton (b) Mulligans Flat Woodland Sanctuary, with predator-proof fence. Credit: Woodlands and Wetlands Trust https://mulligansflat.org.au/*

In addition, the MFGOWE has undertaken the reintroduction of several locally extinct species, with the aim of restoring missing ecological functions. An exclusion fence was built in Mulligans Flat in 2009 (Figure 3b), creating a 485 ha ‘sanctuary’ from which all introduced large mammals have been removed (livestock, cats, foxes, dogs, rabbits, and hares). These reintroductions form part of the experimental framework, and were designed to trial adaptive methods to improve translocation success, but also to examine the impact of these species on other species and ecosystem processes. The species have therefore been selected for the role they are expected to play in the ecosystem, as well as their conservation status. The reintroductions to date are: brown treecreeper (*Climacteris picumnus*), eastern bettong (*Bettongia gaimardi*), New Holland mouse (*Pseudomys novaehollandiae*), bush stone-curlew (*Burhinus grallarius)* and eastern quoll (*Dasyurus viverrinus*).

1.2.2 The eastern bettong (*Bettongia gaimardi*)

The eastern bettong (also known as ‘Balbo’ in the local Ngunnawal language) is a rabbit-sized marsupial in the Potoroidae family, similar in appearance to kangaroos and wallabies (Figure 4). The species historically occurred in grassy woodlands and open forests throughout eastern Australia and Tasmania, but went extinct on the mainland in the early 1900s due to a combination of introduced predators, loss of habitat and human persecution (Rose, 1986; Short, 1998). Bettong diet (studied in Tasmanian populations) consists mainly of hypogeal fungi, but may also include roots and tubers, other plant material (e.g. stems, seeds, fruits, sap), and invertebrates (Taylor, 1992a).

The eastern bettong was reintroduced to Mulligans Flat in 2012. Thirty two individuals were trapped in Tasmania and released within the introduced predator-free sanctuary area (Batson et al., 2016). The population has been monitored regularly; it initially increased quickly and reached an estimated maximum of 192 in autumn 2016, before reaching density dependence with a population around 150 in 2018 (Manning et al., 2019).

Like other bettong species, the eastern bettong is recognised as an ecosystem engineer due to its digging behaviour (Garkaklis et al., 2003; James et al., 2009; Newell, 2008; Read et al., 2008). This engineering role was a large part of the rationale behind the selection of the species for reintroduction (Manning et al., 2011; Shorthouse et al., 2012). In the process of foraging for fungi, roots and invertebrates, eastern bettongs create small pits approximately 5 x 4cm wide and 3cm deep (Munro et al., 2019). Research at Mulligans Flat, two years after the bettong reintroduction, found that each individual bettong digs approximately 218 pits per night, or 7.8 kg of soil (Munro et al., 2019). By 2014, bettong digging accounted for 55% of all soil turnover by soil-disturbing vertebrate species combined (including rabbits, ground-foraging birds and echidnas). Bettongs were more likely to dig under trees compared to open areas and near logs, and in areas with lower kangaroo density, higher density of *Acacia sp.*, and higher levels of soil phosphorus, and were the only species that dug in the most degraded parts of the landscape (Munro et al., 2019). This suggests that the reintroduction of the bettong could reinstate missing soil processes and restore functions that cannot be replicated by other digging species.

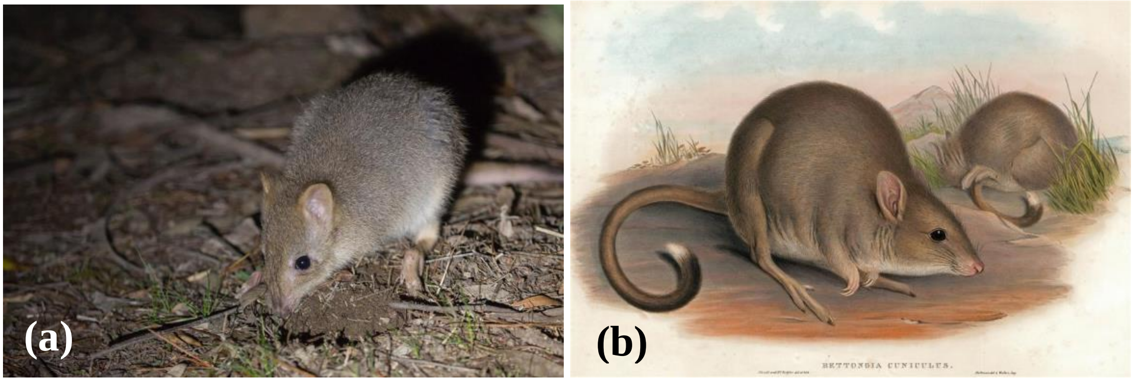


Figure 4. *The eastern bettong or Balbo (Bettongia gaimardi). (a) Eastern bettong digging a foraging pit at Mulligans Flat Woodland Sanctuary, credit Woodlands and Wetlands Trust* *https://mulligansflat.org.au/* *(b) Tasmanian jerboa kangaroo (Bettongia cuniculus) from John Gould's Mammals of Australia 1845–63, now known as the eastern bettong.*

1.3 *Research objectives*

The reintroduction of the eastern bettong to Mulligans Flat provided a unique opportunity to investigate the role of the eastern bettong as an ecosystem engineer in temperate grassy woodland. Soil-foraging species like the eastern bettong are found in many ecosystems worldwide, yet there has been relatively little research in temperate areas compared to arid and semi-arid regions (Coggan et al., 2018). Grassy woodlands once covered vast areas in south-eastern Australia and are now threatened by clearing and degradation, which has also coincided with the decline of many digging species (Fleming et al., 2014). I aimed to identify the structural, abiotic and biotic effects of the eastern bettong to inform the conservation and restoration of these ecosystems. I also aimed to investigate the interactions between trophic and engineering effects, which are not often considered together in studies of ecosystem engineering (Wilby et al., 2001).

1.4 *Chapter outlines – methodological approach and summary of outcomes*

1.4.1 Fine-scale drivers of beetle diversity are affected by vegetation context and agricultural history

Chapter 2 examined plant and insect biodiversity patterns as a backdrop to bettong reintroduction in a Box-Gum Grassy Woodland. Bettong foraging and behaviour is likely to depend on patterns of potential food resources, and several studies have shown that digging animals are likely to have impacts on invertebrate communities due to consumption as well as changes to microhabitats (Coggan and Gibb, 2019; Gibb, 2012; Silvey et al., 2015). Beetles (Coleoptera) were selected for this study because they are a known food source for the eastern bettong (Taylor, 1992a). The MFGOWE has excellent data on soils, vegetation and insects (Barton et al., 2011, 2010, 2009; McIntyre et al., 2014, 2010), providing an opportunity to examine how insect assemblages are structured by the surrounding environment. Beetles were collected using pitfall traps at three microhabitats - open grassland, logs, and under trees - within 96 one-hectare plots (Barton et al., 2011). Soils and vegetation were also surveyed systematically in each of the plots (McIntyre et al., 2010). I examined four proposed drivers of beetle communities: productivity (soil nutrients), vegetation structure, plant species richness and plant composition.

I found that soil nutrients (C, N and P) were the strongest drivers of beetle species richness and abundance at open and log microhabitat, supporting the productivity hypothesis. However, vegetation structure (tree basal area) was more important for beetle richness and abundance under trees. Beetle assemblages differed in their composition among distinct ground-layer plant communities at log and tree microhabitat, while beetle communities in open microhabitat were more uniform. Sites with evidence of prior agricultural use also had altered beetle communities, suggesting that the effects of prior land use continue to flow through from the soil to plants, and from plants to beetles, and potentially the broader ecosystem.

These findings demonstrate the fine-scale structure of the grassy woodland ecosystem as a mosaic of plant and insect communities. As bettong digging is expected to alter this fine-scale structure and create new microhabitats, understanding these interactions will inform future studies of how bettongs act as ecosystem engineers.

1.4.2 Effects of digging by a native and introduced ecosystem engineer on soil physical and chemical properties in temperate grassy woodland

Chapter 3 examined the structural and abiotic effects of bettong digging, and how these effects compare with an exotic species, the European rabbit. Rabbits are considered to be ecosystem engineers in their native range, and it has been suggested that they could act as a substitute where native engineers have been lost (Gálvez-Bravo et al., 2011; James et al., 2011). Both bettongs and rabbits create structural change to the ecosystem in the form of small foraging pits. Previous research by Munro *et al*. (2019) estimated the volume of soil moved by bettongs and rabbits in Mulligans Flat (2.85 vs 1.8 m^3/individual/year respectively), and how this disturbance is distributed across the landscape. Chapter 3 aimed to build on this work by looking at the longevity of bettong and rabbit pits (i.e. how long they take to fill in), how they affect soil chemical properties over time, and how they affect microclimatic conditions at the soil surface. Studies have shown that animal foraging pits can provide a ‘hotspot’ of productivity, due to the accumulation of nutrients (James et al., 2009; Tardiff and Stanford, 1998). Burrows and pits can also create a more mesic microclimate, providing habitat for other species (James et al., 2010; Pike and Mitchell, 2013; Read et al., 2008).

To determine the persistence and infill rate of pits, we established 170 artificial bettong and rabbit pits. The dimensions for the artificial pits were the mean length, width and depth of real pits (n = 1518 for bettongs, n = 432 for rabbits) (Munro et al., 2019). Using artificial pits allowed us to compare bettong and rabbit pits of the same age side by side. We measured the dimensions of the pits after eight months and two years. We found that after two years, only 22% of all pits were completely filled in, and that bettong pits filled in slightly faster than rabbit pits (27% and 17% filled in respectively). This difference in infill rate may be due to variation in pit morphology; bettong pits were deeper and narrower than rabbit pits and tended to become shallower and wider over time as the walls collapsed into the pit and collected litter and debris. Both pit types filled in more quickly in the first eight months, but once they had reached a depth of around 1-2 cm the rate of infill slowed, suggesting that they may persist for some time as shallow depressions. This difference in dig morphology may mean that rabbit diggings are not able to fully replicate the ecosystem engineering effects of the native bettong, and thus cannot replace their role in Australian ecosystems. In addition, any beneficial effect of rabbit digging is likely to be outweighed by their detrimental effects (Eldridge and Simpson, 2002; Johnson, 2006), and therefore efforts to understand how to bring native ecosystem engineers back would be a preferable option..

To examine the chemical changes in bettong and rabbit pits, we collected soil samples from the same artificial pits after eight months and two years, as well as controls of equivalent depth in undisturbed soil 50 cm away. We conducted analyses on chemical properties, including total nitrogen (N), total organic carbon (C), mineral nitrogen ($NO3^-$ and $NH4^+$), plant available phosphorus (P), pH and electrical conductivity (EC). While we did find some significant effects of digging on soil chemistry, we were not able to find any effects that were consistent across vegetation types, age of pits or animal species. We also looked at the effect of bettong digging on soil surface temperatures, using temperature loggers placed in freshly dug bettong pits and on the soil surface. We found that digging had a moderating effect on temperature, reducing the extremes of temperature experienced on the soil surface by up to 25°C. While bettong pits are probably too small to be thermal refugia for other vertebrates, they may provide a more favourable microclimate for plant seedlings or invertebrates by reducing exposure to desiccation or frost.

In this study, we did not find any consistent significant effects of bettong or rabbit digging on soil properties. These results differ from those found in arid ecosystems and suggest the effects of digging animals in temperate grassy woodlands are restricted to physical alteration of the soil rather than the creation of nutrient hotspots. This finding supports recent research suggesting that the effects of soil-disturbing vertebrates are more pronounced with increasing aridity (Decker et al., 2019; Mallen-Cooper et al., 2019). It also reinforces the importance of testing findings across different environmental conditions.

1.4.3 A reintroduced ecosystem engineer provides a germination niche for native plant species

In Chapter 4 I looked at the biotic effects of bettong digging, specifically whether bettong pits increase seed germination. Several studies have shown that animal foraging can provide important sites for seed germination, particularly in arid areas where pits provide a less hostile microclimate and allow organic matter and seed to accumulate (Eldridge and Mensinga, 2007; James et al., 2010, 2009). In temperate grasslands, many species rely on small gaps and disturbances for seedling establishment, and foraging pits may provide these sites (Bullock et al., 1995; Morgan, 1997). However, many exotic species also benefit from disturbance, so bettong digging might facilitate weed invasion into relatively intact grasslands (Hobbs, 1991; Larson, 2003).

To measure the responses of seedlings to bettong digging, we marked 160 natural bettong pits, with paired undisturbed control plots approximately 30 cm away. The pits were located in two grassland types, a dense grassland dominated by kangaroo grass (*Themeda triandra*), and a more open grassland dominated by wallaby grass (*Rytidosperma sp.*). We added seed of seven native forb species to half of the plots (pits and controls), to control for seed availability. We counted and identified all seedlings, both natural and planted, that had germinated in November 2016, and then returned in November 2017 to measure survival.

We found that bettong pits had almost twice as many seedlings on average, compared with an undisturbed area of the same size. Surprisingly, native species responded more strongly to pits, while exotic plants did not seem to benefit from the disturbance created by the digging and in some cases experienced a negative response compared to the controls. However, when we returned to the same pits after one year, this effect had reversed, and the pits had a greater number of exotic seedlings.

We also found a difference in the response between dense and open grassland types. While the dense grassland had fewer seedlings overall, there was a greater increase in the number of seedlings in pits (compared to controls) in the dense grassland compared to the more open grassland. This suggests that the pits create gaps in the grass canopy that would otherwise suppress germination. However, this may also create space for exotic species as well as natives. Over time, this could lead to a change in plant community composition, favouring species that benefit from the presence of digging. It also suggests the potential for bettongs or other digging animals to facilitate the restoration of plant communities, either passively by increasing germination rates of species already present, or in combination with active seed addition to reintroduce species that are missing from the seed bank.

1.4.4 Population demography of a native geophyte in response to a reintroduced ecosystem engineer

Chapter 5 explored more of the biotic effects of bettong digging, as well as the interactions with trophic effects and feedbacks. Since the reintroduction of bettongs to Mulligans Flat, they have frequently been observed digging for roots and tubers, particularly the underground corm of the early nancy (*Wurmbea dioica*), a small native lily. We were therefore interested in whether the reintroduction of bettongs was having a negative effect on the *Wurmbea* population, or if there is any evidence of a feedback effect through an increase in germination (as shown in Chapter 4). Several studies have found this type of interaction between digging mammals and geophytes (plants with underground storage organs). For example, in the Negev desert in Israel, porcupines appear to have a symbiotic relationship with several species of geophyte, some of which only regenerate from within pits, either from seed or from surviving parts of the original plant (Gutterman, 1987, 1982). In the UK, Sims *et al.* (2014) found that patches of bluebells quickly regenerated after being dug by boar, which was likely due to some facilitation of germination by the disturbance. By foraging for the bulbs of glacier lilies, grizzly bears create patches of bare soil and increase mineral nitrogen, improving the growth and reproduction of the lily (Tardiff and Stanford, 1998).

I monitored the *Wurmbea* population over five years from 2015-19. We chose nine sites across the reserve which had large populations of *Wurmbea* and evidence of bettong digging, with paired control sites in areas where bettongs were absent (bettong exclusion areas or outside the reserve). At each site, we marked and photographed at least 100 plants in 0.5 m^2 plots. By comparing photographs from previous monitoring sessions, we were able to follow the fate of individual plants from germination to flowering and seeding and record the number that were eaten or buried by bettongs.

Each year, between germination and flowering (July-September), bettongs consumed on average 13-24% of the *Wurmbea* plants marked at each site. This resulted in a decline in the *Wurmbea* population of 69% on average at sites where bettongs were present, which was exacerbated by several years of drought during the monitoring period. We also observed a shift in the population towards a greater proportion of young (1-leaf) plants and fewer flowering and seeding plants at sites with bettongs. We were also able to answer some important questions about *Wurmbea* life history.

This study adds to our understanding of the complex interactions of trophic and engineering effects of digging animals. Interactions between digging animals and geophytes appear to be common in many ecosystems worldwide, but this is the first to be recorded in Australia. While we were not able to confirm the hypothesis that bettong engineering increased *Wurmbea* germination, previous studies have suggested that there may be a positive effect if rainfall is sufficient. However, as droughts are expected to become more frequent and severe under future climate predictions, we may need to consider ways to manage the bettong population or protect vulnerable plant species to ensure that *Wurmbea* and other geophytes are able to persist in Box-Gum grassy woodland.

1.4.5 Soil-disturbing animals as ecosystem engineers - clarifying goals for conservation and restoration in Australia

Finally, Chapter 6 covered many of the issues that I have explored, and those that have emerged in this thesis, and provided a review of the literature as well as identifying knowledge gaps and directions for future research. As part of the research agenda for my thesis, I organised a workshop at the Australian National University in November 2017 for a group of experts in the field of ecosystem engineering, and facilitated a series of discussions on the current state of the field in Australia. Many of the ideas presented in Chapter 6 were the result of these discussions and hence the paper was written in collaboration with the other participants who provided expert advice and edited the manuscript

We explored current research on soil-disturbing engineers and their contribution to restoration in Australian ecosystems, to identify knowledge gaps and factors that should be considered when reintroducing ecosystem engineers. We found that while biopedturbation is widely accepted to be important for ecosystem function, there is still a large degree of uncertainty around the effects of digging animals, particularly across different scales and environmental gradients. We therefore have limited capacity to predict the precise effects of reintroducing ecosystem engineers, due to a lack of reference conditions and the complexity of ecological cascades and feedbacks. It is important to fill these knowledge gaps to increase our understanding of the potential impacts of ecosystem engineers and inform management.

We also discuss the benefits and limitations of sanctuaries. Sanctuaries have been shown to greatly increase the success of species translocations and offer unique opportunities for research and public engagement, but also risk disruption of the existing ecosystem if not managed appropriately. These risks may be magnified when the species being reintroduced is an ecosystem engineer that is expected to have widespread impacts on ecosystem processes and function.

Finally, we present a new framework and provide recommendations to help managers clarify their goals and identify considerations for any translocation, particularly when ecosystem engineers are involved. The aims of translocations are often poorly defined in the planning stages, making it difficult to determine success (Palmer *et al.*, in review). Ideally, all future translocations should be explicit about their goals, and put in place long-term monitoring to determine whether those goals have been met. We argue that greater consideration of species' ecological roles is required to improve outcomes for research, conservation and restoration and mitigate the potential risks.

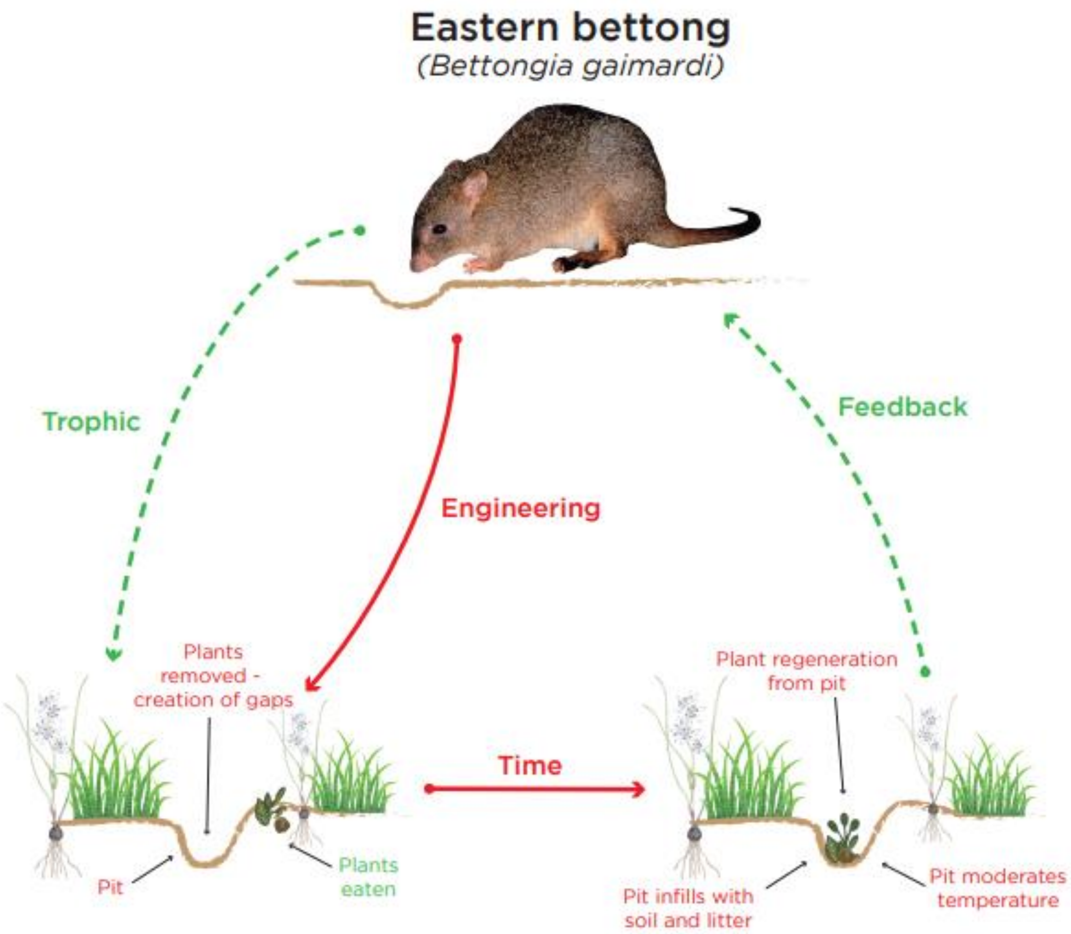
1.5 *Synthesis and research significance*

Fenced sanctuaries like Mulligans Flat provide unique opportunities to study the ecological effects of reintroductions in Australian ecosystems. The results of my experiments conducted at Mulligans Flat demonstrate that bettongs play an important role as ecosystem engineers, causing substantial structural, abiotic, and biotic changes to the ecosystem (summarised in Figure 5). These effects have the potential to restore processes that have been lost since the extinction of the bettong over a century ago. However, as with any reintroduction there may also be unintended or undesirable effects that will need to be monitored and managed in the future, such as weed invasion and impacts on other species. It is also important to recognise that the ‘desired’ state in any restoration project is strongly influenced by our own human values and preferences, particularly where there is no reference state. It is therefore vital for any reintroduction to have clearly defined goals while acknowledging these limitations and are conducted within experimental frameworks that allow learning and adaptive management.

The results of Chapter 2 highlight the importance of differences among microhabitats in determining patterns of diversity, and that these differences can only be detected when sampling occurs at the appropriate scales. This will provide a basis for future studies to investigate the impacts of bettongs on invertebrate communities at Mulligans Flat, but this was not within the scope of my thesis. Given that bettong digging creates new microhabitats with altered structural and abiotic conditions (Chapter 3), we can expect that there will be biotic responses to these changed conditions. This thesis (Chapter 4) found that plants responded to the microhabitat created by pits, but further research will be needed to examine the effects on other taxa including microbes and invertebrates. Future studies might also look at how digging effects scale up to influence plant species recruitment and potentially whole vegetation communities over the longer term.

Most studies of digging animals to date have been conducted in arid or semi-arid biomes where resources such as water and soil nutrients are limited. In these systems it appears that pits assist with resource accumulation. However, there is growing evidence that the effects of ecosystem engineers are less pronounced in temperate climates (Decker et al., 2019; Mallen-Cooper et al., 2019; Romero et al., 2015). Crain and Bertness (2006) suggest that the mechanisms of ecosystem engineering may be different in mesic environments, where reduction of competition is more important than amelioration of environmental stress. My results support this hypothesis, suggesting that the creation of gaps and reducing competition among plants is more important than the creation of nutrient ‘hotspots’ (Chapters 3 and 4). This finding adds to our understanding of the mechanisms driving the effects of digging across different environmental conditions.

I found that bettong foraging pits can have a positive effect on seedling germination and survival, particularly for native plant species (Chapter 4). This is an important finding and can



Engineering effects: →

Structural change
- 'Leaning cone' shaped pit with spoil heap
- ~2.8 m³ soil turnover/individual/year
- Remove or bury existing plants/soil crust
- Create gaps and bare ground
- Pits last 2+ yrs. (differ from rabbit pits in morphology and infill rates)

Abiotic change
- Moderate diurnal temperature range up to 25⁰C
- Soil nutrients – inconsistent effects

Biotic change
- Increase germination, esp. native species
- Change plant composition

Trophic effects: →

- Herbivory → Structural change
- 13-24% of *Wurmbea dioica* population eaten annually
- Change plant population demographics
- Change plant composition

Feedback ▪▪▪▪▪▪▪▪▶

- Biotic feedback via trophic effects
- Interaction with certain food plants e.g. *Wurmbea dioica*

***Figure* 5.** *Conceptual model of engineering and trophic effects of bettongs, and summary of thesis findings. Digging by soil-foraging animals has both trophic and engineering effects through the consumption of plants, fungi or insects (trophic) and the creation of pits (engineering). I have shown that over time, these pits change the structure of the soil surface, moderate extremes of temperature and provide a germination niche for plant seedlings. There may also be trophic feedback to the bettong as they either deplete or increase their own food source.*

inform conservation and restoration of grassy ecosystems worldwide. Many digging animals are highly threatened, so it is vital that we recognise their importance and prioritise their conservation where they are still present. Current grassland restoration techniques are often very invasive (e.g. scalping) and therefore not appropriate for relatively high-quality sites, so the reintroduction of digging animals may be an effective way to increase heterogeneity and diversity, perhaps in conjunction with other methods such as seed addition. During my candidature I co-supervised an honours student who found that artificial pits were able to replicate the positive effects of bettong digging on seed germination (Robb *et al*., unpublished data). This may be a viable option in areas where digging animals are not present and reintroduction is not possible, but further research will be required to implement this on a larger scale.

My work also highlighted the importance of understanding both the trophic and engineering effects of reintroduced species, and how these are likely to interact (Chapter 5). As in the case of the relationship between digging animals and geophytes, trophic and engineering effects may be closely linked (Figure 5), however many studies of ecosystem engineering do not take this into account (Prugh and Brashares, 2012; Sanders et al., 2014; Wilby et al., 2001). While the engineering effects of bettong digging are likely to be positive in terms of increasing seedling germination (Chapter 4), this is offset by potentially negative trophic effects on certain plant species through consumption (Chapter 5.). I found that at current population levels, the bettongs are apparently contributing to a decline in the population of a native geophyte, which was exacerbated by severe drought conditions. This result contrasts with a study of porcupines in the Negev desert, which found that consumption of geophytes had little effect on overall plant populations compared to the increase in germination as a result of digging (Wilby et al., 2001). Integrating trophic and other non-engineering effects into models of ecosystem engineering is vital to fully understand the impacts of engineers on ecosystems (Sanders et al., 2014).

What bettongs eat may also determine where and how much they dig, and this is likely to change between seasons and years depending on food availability (Taylor, 1992b, 1992a). While the diet of eastern bettongs in Tasmania has been studied previously, we know very little about the diet of the reintroduced population in Mulligans Flat. A study is currently underway using high-throughput DNA sequencing methods to examine the contents of bettong scats collected since the reintroduction to Mulligans Flat. We hope this will allow us to identify the seasonal, climatic and population effects on bettong diet, as well as potential impacts on threatened species.

While reintroducing ecosystem engineers can be an important tool for restoration, there has been relatively little consideration of the risks of such reintroductions for the recipient ecosystem (Chapter 6). Quantifying the potential risks and impacts on other parts of the ecosystem was at the forefront of our thinking from the outset of this reintroduction. The concept of ‘rewilding’, or reintroducing species to restore ecosystems, assumes that because a species was present in the past, its return will result in positive changes (Nogués-Bravo et al., 2016). However, this is certainly not guaranteed, particularly when the species has been absent for a long time, or if the ecosystem has been significantly altered. In Australia, it has become common practice to introduce animals into fenced reserves, which provide protection from predators but limit dispersal, together creating a risk of overpopulation. As is the case at Mulligans Flat, these reserves may also contain highly sensitive, threatened or degraded ecosystems. This raises the question of if, when and how we intervene. Rewilding, by definition, aims to create ecosystems that function without human intervention, that are more ‘wild’ (Lorimer et al., 2015). Yet we have already intervened by building a fence, removing certain species and reintroducing others, and I would argue that we have an ethical responsibility to protect those species and the ecosystems in which they live. The question is ultimately one of values and judgement, but these decisions must be informed by an understanding of the consequences of our actions. Studies such as mine, and the broader long-term experiment within which it sits, are therefore vital in increasing our understanding of the complex interactions between species, processes and ecosystems.

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Artist Interlude no. 1

Co-Lab: Science Meets Street Art

James 'Houl' Houlcroft

The first artist I worked with was James 'Houl' Houlcroft, a local Canberra graffiti artist. We met through a project called Co-Lab: Science Meets Street Art, which was organised by Lee Constable as part of Science Week in 2015. The project aimed to match up scientists and street artists who would then collaborate to create a series of murals in a public space, to engage the community with research in a novel way. James created this mural in just a few hours, in front of a live audience. It was fantastic to work with James and to see him translate my research into his own unique and quirky style. The mural shows a bettong as an 'ecosystem engineer', with high-vis vest and holding rolled up plans. Surrounding the bettong are early nancy (*Wurmbea dioica*) flowers and seedlings, one of the bettongs' favourite foods.

Chapter 2:

Fine-scale drivers of beetle diversity are affected by vegetation context and agricultural history

Ross, C.E., Barton, P.S., McIntyre, S., Cunningham, S.A. & Manning, A.D., 2017. Fine-scale drivers of beetle diversity are affected by vegetation context and agricultural history. *Austral Ecology*, 42(7), pp.831–843.

2.1 *Abstract*

Environmental gradients have been shown to affect animal diversity, but knowledge of fine-scale drivers of insect diversity is, in many cases, poorly developed. We investigated the drivers of beetle diversity and composition at different microhabitats, and how this may be mediated by past agricultural activities. The study was undertaken in temperate eucalypt grassy woodland near Canberra, south-eastern Australia, with a 200-year history of pastoral land use. We sampled beetles using pitfall traps at three microhabitats (open grassland, logs and under trees). We analysed the effects of soil properties, vegetation structure, and plant composition on beetle composition, and compared beetle responses among the microhabitats. We found that microhabitat was a strong determinant of the way beetle communities responded to their environment. Soil nutrients (C, N and P) were the strongest drivers of beetle species richness, abundance and composition at open and log microhabitat, however vegetation structure (tree basal area) was more important for beetle richness, abundance and biomass under trees. We also found significant differences in beetle composition among distinct ground-layer plant communities at log and tree microhabitat. We show that prior agricultural land use, particularly fertilization, has altered soil and plant communities, and that these effects continue to flow through the system affecting beetle assemblages. These findings have implications for future management of microhabitat structures in temperate grassy woodlands with a history of agricultural use.

Keywords: Australia, eucalypt, grassy woodland, insect, microhabitat, soil nutrients.

2.2 *Introduction*

Environmental gradients are important drivers of variation in biodiversity (Rosenzweig 1995; Gaston 2000). A range of biotic and abiotic factors have been shown to affect animal diversity, but are typically examined at the broader scale of patches or landscapes, where gradients may be profound due to underlying climatic, geological, or vegetation differences. While this approach is appropriate for generating knowledge of broader patterns of diversity (Hawkins et al. 2003; Jetz & Fine 2012; Luo et al. 2012), insects and other invertebrates interact with habitat at much finer scales (Cole et al. 2010; Hortal et al. 2010), and this necessitates finer scale approaches. Further complication arises when fine-scale patterns are considered in the context of larger scale gradients such as broader vegetation composition, productivity, disturbance, or land use. Previous research has identified the strong role of microhabitat and fine-scale environmental variation on insect diversity and composition (Niemelä et al. 1996; Koivula et al. 1999; Barton et al. 2009, 2010), yet there is still much to learn about how microhabitat structures, such as logs and individual trees, might moderate the influence of broader-scale environmental gradients on insect assemblages.

There are many hypotheses in the literature regarding the most influential factors in determining insect diversity and abundance in grasslands, such as productivity, vegetation structure, plant species richness and plant composition (reviewed by Joern & Laws 2013). Of course, these hypotheses are not independent; plant structure and species richness are both attributes of the plant community, which is also influenced by a range of factors including productivity. The productivity hypothesis predicts that diversity increases with higher productivity, usually indicated by elevated soil nutrients (Nitrogen, Phosphorus). Several studies have found that high productivity increases arthropod abundance (Siemann 1998; Borer et al. 2012), but this does not always translate to an increase in species richness, and in some cases soil nutrient enrichment has been shown to have a negative effect on plant and arthropod species richness (Haddad et al. 2000; Simons et al. 2014).

Vegetation structure and structural heterogeneity are widely considered to be important for insect diversity and are often used as surrogates for vegetation composition (Lawton 1983; Dennis et al. 2001; Schwab et al. 2002; Tews et al. 2004). For example, grasslands with greater structural height have been shown to support greater diversity of arthropods (Morris 2000; Kruess & Tscharntke 2002), while biomass accumulation (e.g. as a result of fire or grazing exclusion) can have a negative impact on plant species richness in grasslands (Oba et al. 2001; Lunt & Morgan 2002; Bhattarai et al. 2004). Trees and logs have been identified as ‘keystone structures’ in many ecosystems because they have a disproportionately large contribution to ecosystem functioning relative to their biomass (Harmon et al. 1986; Manning et al. 2006), and there is growing recognition of their importance to insect communities (Barton et al. 2009, 2011).

Given that many insects depend directly on plants for food or habitat it is expected that plant richness and composition should have a strong influence on insect assemblages. Many studies have found a positive relationship between plant and insect species richness (Murdoch et al. 1972; Siemann et al. 1998; Haddad et al. 2001, 2009), however this relationship is less clear for non-herbivorous species (De Bruyn et al. 2001). Others have also found strong relationships between insect assemblages and plant community composition (McCracken 1994; Koricheva et al. 2000; Blake et al. 2003; Foord et al. 2003; Schaffers et al. 2008; Torma et al. 2014).

Although there are many published studies on arthropod diversity in grasslands (e.g. see review by Joern & Laws 2013), the sampling methods often do not allow for analysis that distinguishes the small scale at which these species interact with their environment (Mehrabi et al. 2014). This is because habitats, as they are perceived by humans and other large animals, occur on a scale of tens of meters or more. Yet at smaller scales they can contain distinctive features or physical structures that reoccur throughout the community; we refer to these features as microhabitats. Many studies of grassland invertebrates worldwide have been carried out in treeless grasslands. However, in our study area, open grassy areas are interspersed with variably spaced trees that provide shade and can shed large amounts of litter (McElhinny et al. 2010).

These trees also drop coarse woody debris and fallen logs that provide vital habitat for many species and also influence the surrounding soils and vegetation (Harmon et al. 1986; Barton et al. 2009; Goldin & Hutchinson 2013; Manning et al. 2013; Goldin & Brookhouse 2015).

In this study, we examined the factors influencing diversity and species composition of ground active beetles within two neighbouring nature reserves in south-eastern Australia, which support temperate eucalypt grassy woodland and dry sclerophyll forest. The reserves have a 200-year history of agricultural management including clearing, grazing and pasture development, which has had an impact on the soils and native vegetation (McIntyre et al. 2010, 2014), but unknown effects on the beetle community.

We therefore asked the following question: *what effect do the vegetation and soils have on beetle diversity and composition at different microhabitats?* To answer this question, we analysed data on ground active beetles collected from three microhabitat types – open grassland, near logs and under trees. We then used both univariate and multivariate statistical methods to examine the relationships between the beetle community and the vegetation and soils, and how these differed among microhabitats. Beetles preferring any of these microhabitat types may respond differently to the surrounding soils and vegetation. For example, we may expect beetles living in open grasslands to be more strongly influenced by the plant diversity and composition of the ground-layer vegetation, while beetles living at logs or under trees may respond more to soil nutrient levels or vegetation structural attributes. We used these analyses to examine a second question: *how have past agricultural practices, as mediated by changes in soil fertility and vegetation composition, influenced beetle diversity and composition?* A better understanding of how previous land management, vegetation and microhabitat effects impact the beetle communities may inform future management of the remaining remnants of eucalypt grassy woodland in order to maximize beetle diversity.

2.3 *Materials and methods*

2.3.1 Study area and experimental design

Our study was conducted in the Mulligans Flat – Goorooyarroo Woodland Experiment (Manning et al. 2011; Shorthouse et al. 2012). The experiment consists of two adjacent reserves in the Australian Capital Territory – Mulligans Flat Nature Reserve (683 ha established in 1994) and Goorooyarroo Nature Reserve (702 ha established in 2006). In each reserve, 48 1-ha ‘sites’ (200 m 9 50 m) were permanently marked with posts at each end, resulting in a total of 96 sites across the two reserves. The vegetation survey and soil sampling were undertaken systematically across each site, while the beetles were sampled at three microhabitat types within each site, which we describe in detail below.

2.3.2 Vegetation surveys and soil sampling

We surveyed ground-layer vegetation at each of the 96 1-ha sites in late spring 2007. In each of the 96 sites, 30 quadrats (0.5 9 0.5 m) were placed systematically across each site. The BOTANAL method (T'Mannetje & Haydock 1963; Tothill et al. 1992) was used to record dominant species and estimate total ground-layer biomass and species abundance in each quadrat. Data were aggregated at the 1-ha site scale. The methods and results of this survey are detailed in McIntyre et al. (2010). Average total ground-layer biomass was 549 kg ha^{-1} and ranged from 204 to 2352 kg ha^{-1}. A total of 102 species of native plants and 69 exotic species were recorded in the top six most abundant species in each quadrat. In each 1-ha site, the average number of recorded species was 35 (plant species counts for each site were calculated as the total number of ranked species and as such can only be used as a relative measure and is not a reflection of total species richness). We calculated tree basal area in each 1-ha site by measuring the DBH of all trees (eucalypt and non-eucalypt) greater than 2 cm DBH (Manning et al., unpubl. data, 2016).

The 96 1-ha sites were classified using a Bray-Curtis dissimilarity measure based on species composition (McIntyre et al. 2010). Six emergent floristic groups were identified which are summarized in Table 1, with the groups arranged from high to low productivity. Only four sites were classified as Group 5, so for this study we combined it with Group 2, the most similar group determined by the dendrogram presented in McIntyre et al. (2010). Groups 1 and 6 had elevated levels of N and P and were dominated by exotic pasture species, from which we infer that these sites are likely to have a history of fertilization. It is also worth noting that although high soil nutrients are often associated with high plant biomass, this was not always the case. The sites with the lowest nutrient levels (Group 3) also had the highest biomass due to the presence of *Joycea pallida* which forms large tussocks and is associated with soils naturally low in nutrients (J. pallida is now included in the genus *Rytidosperma* (Linder et al. 2010), however we continue to use the former name to differentiate between groups characterized by other *Rytidosperma* spp., from which it differs ecologically).

We quantified soil chemistry from soil samples collected in late summer 2008. A single soil core (depth 10 cm, diameter 20 mm, total volume 32 cm^3) was taken from each of the 30 quadrats in every site and combined to give a single site-level sample. Analysis was performed by the Victorian Department of Primary Industries Laboratory, Werribee, Victoria. A complete description of all analyses and methods used is available in McIntyre et al. (2010). For this study only available phosphorus (Colwell), total nitrogen (%), total carbon (%) and C:N ratio were used. The numeric variables are summarized in Table 2.

***Table 1**: Floristic groups characterized by dominant species, soil attributes and total biomass, (adapted from McIntyre et al. 2010). Groups are arrayed from high- to low-productivity (left-right). These groups were used as a multistate explanatory variable in the analyses. Group 5 was combined with Group 2 to create five groups/states in all further analyses.*

Group number	1	6	4	2 (and 5)	3
Dominant species	*Phalaris* – fertilized	*Rytidosperma* spp. – fertilized	*Themeda* – lawn	*Rytidosperma* spp. - lawn	*Joycea* – large tussocks
No. sites	10 sites	11 sites	16 sites	46 sites	13 sites
Available P (mg.kg^{-1})	13	7	8.6	5.4	5.4
Nitrate N (mg.kg^{-1})	7.4	5.9	0.8	1.1	0.7
C:N ratio	17.4	17	17.6	20.2	22.8
Biomass (kg.ha^{-1})	817	351	353	422	1346

***Table 2:** Plant and soil attributes measured at 96 1-ha sites used as explanatory variables for the analysis of beetle occurrences.*

	Total carbon (%)	**Total nitrogen (%)**	**Available phosphorus (mg.kg^{-1})**	**C:N ratio**	**Plant biomass (kg.ha^{-1})**	**Plant species count**	**Tree basal area (cm^2)**
Range	1.5 – 4.7	0.07 – 0.3	<4 - 23	14.8 – 31.5	204 - 2352	22 - 52	9870 - 235963
Mean	2.7	0.14	7	19.5	569	35.6	78832

2.3.3 Beetle sampling

We sampled beetles from all 96 1-ha sites (method described in Barton et al. 2009). Within each site, beetles were sampled at three different microhabitat types – at the base of a tree, near a log or in the open. ‘Tree’ habitat was located in the leaf litter under the canopy of a yellow box (*Eucalyptus melliodora*) or Blakely’s red gum (*Eucalyptus blakelyi*) with a diameter at breast height (DBH) of more than 0.25 m. ‘Log’ habitat was located adjacent to logs >0.1 m in diameter and >1 m in length. Open habitat was located in grassland beyond the drip-line of any tree canopy, and >10 m from any log. Sample locations were chosen within a 25 m radius of the permanent marker posts at each end of the site. In Mulligans Flat reserve, all three microhabitat types were sampled at both ends of the site, whereas in Goorooyarroo reserve log and open habitat were sampled at one end and a log and a tree habitat were sampled at the other end. In some cases, where we could not locate a suitable tree or log within 25 m of the marker post, that microhabitat was not sampled.

At each sample location, two pitfall traps were placed 1 m apart, and opened for 3 weeks during early autumn 2007. Traps consisted of 200 mL plastic jars dug in flush with the soil surface, each with 100 mL of polypropylene glycol as a preservative. No barriers were placed near traps to increase capture rates. We excluded from analysis any traps disturbed by large mammals. We sorted adult beetles from the pitfall collections, identified them to family using keys to the Australian beetle fauna (Lawrence & Britton, 1991; Lawrence et al. 1999) and then identified to genus (where possible) and morphospecies (Oliver & Beattie 1996; Pik et al. 1999). Morphospecies were verified by expert taxonomists at the Australian National Insect Collection.

The various limitations of pitfall traps, and their advantages, are well established in the literature (e.g. Melbourne 1999). In particular, trap captures are known to reflect both the density and activity of individuals, and are influenced by differences in habitat structure that could facilitate or impede the movement of individuals. Further, there may be some accidental captures of transient species not associated with the target microhabitat. With this in mind, we improved the robustness of our data and comparability among the three microhabitat types in two ways: (i) we used two traps at each microhabitat, and then pooled these data to increase total captures, and (ii) we excluded singleton species from our data prior to compositional analysis to reduce the chance of rare species inflating among-sample differences.

In total, our sampling consisted of a total of 980 pitfall traps – 362 samples at logs, 305 at trees and 313 in the open. 5693 individual beetles from 210 morphospecies belonging to 34 families were collected (Appendix S1). Note that at the time of sampling (i.e. late summer), hot and dry conditions result in fewer active arthropods; however this is also likely to lead to greater fidelity to habitat type as there is no dispersal or reproductive movements.

For each morphospecies, we measured total body length (mm, excluding appendages), and then converted this to biomass (mg) using a generalized formula applicable to the Coleoptera (Hodar 1996). Biomass is a good indicator of comparative productivity in studies of terrestrial arthropod ecology (Saint-Germain et al. 2007).

2.3.4 Statistical analysis

2.3.4.1 Variation in plant and soil variables

We first used Principal Component Analysis (PCA) to examine the main gradients of variation in soil and plant attributes between sites. This analysis uses an orthogonal transformation of multiple possibly correlated variables to identify new compound axes of variation that explain the largest possible variance in the dataset (Pearson 1901). We performed a PCA on a correlation matrix of seven plant and soil variables measured at each site (Table 2).

2.3.4.2 Beetle diversity – species richness, abundance and biomass

We first summarized the beetle data by plotting mean species richness, abundance and biomass for each microhabitat and floristic group. We then used all-subsets generalized linear regression models to identify which combination of variables best explained beetle abundance, species richness and biomass (our response variables). The eight explanatory variables comprised seven plant and soil attributes (Table 2), and the floristic groups (Table 1). This was done separately for the three microhabitat types (open, log and tree). The best models were selected using the Schwarz Information Criterion (SIC), which takes into account both the statistical goodness of fit and also the degrees of freedom in the model, so that models with fewer variables are preferred (Schwarz 1978). We used a general model with Poisson distribution and log link function. We also explored the possible effect of the spatial grouping of our sites within polygons by running additional GLMMs that included sites within polygons as a random effect. We fixed the dispersion parameter at 1 to estimate the variance component of the random effect, but found that this effect was small compared with its standard error, and the magnitude and order of the fixed effects changed very little, and therefore it is not included in final models.

2.3.4.3 Beetle community composition

Since we had multiple beetle samples for each microhabitat within a site, comparisons with variables measured at site-scale may overestimate statistical power. In our univariate analyses we avoided this by first examining the importance of this nested design by testing for random effects. However, multivariate methods do not allow for this, so instead we summed each pair of pitfall traps in order to get a single 'site-level' value for each microhabitat within each site. In the cases where there were two pairs of pitfall traps for each microhabitat (one in each plot), one pair was deleted at random. Some sites had only one pitfall for a particular microhabitat, so those sites were deleted altogether. Of the 96 sites, this left 92 site-level samples for open grassland, 90 for logs and 91 for trees. The beetle abundances were then converted to presence-absence data so that the results were not influenced by the few very abundant species.

Following this treatment of our data, we next used three different multivariate approaches to examine the plant and soil factors affecting the composition of the beetle community at each microhabitat. First, we used Canonical Correspondence Analysis (CCA) to examine the relationship between the beetle community composition and the plant and soil variables (Ter Braak 1986). This technique is a constrained ordination, which allowed us to visualize the main gradients of variation in the beetle community associated with our seven explanatory variables (Table 1). We repeated the CCA analyses using the floristic groups as the constraining factor. In both sets of CCAs, the three microhabitats were analysed separately (Figure. 2). Second, we used multi-response permutation procedures (MRPP; Zimmerman et al. 1985) to test if there were significant differences in beetle community composition comparing the five floristic groups.

MRPP is a non-parametric method that makes pairwise comparisons of within and between a priori group distances (Bray-Curtis).

Third, we used Mantel and partial Mantel tests to determine the relative correlations between the plant community or soil nutrient levels and the beetle community. This technique tests for correlation between two dissimilarity matrices, and the partial Mantel uses partial correlation conditioned on a third matrix. This method is often used to control for similarity in species composition due to sites being closer together (spatial autocorrelation) (Legendre & Troussellier 1988). For this analysis we used the full plant species matrix rather than the five floristic groups used previously. The beetle and plant data were transformed to presence-absence, and the soil variables (carbon, nitrogen, phosphorus and C:N ratio) were standardized to remove the large variation in scale of measurement. We used a Mantel test to look directly for spatial autocorrelation among sites for each of our beetle community (Bray-Curtis distance measure), plant community (Bray-Curtis) and soil nutrients (Euclidean) datasets. We then used the partial Mantel test to compare the beetle and plant community while controlling for spatial autocorrelation. We also compared the soil nutrients with the beetle and plant communities, again while controlling for spatial autocorrelation.

We used the statistical software GENSTAT 16 (VSN International 2016) to conduct the PCA and GLMs, PCORD (MjM Software Design 2016) was used for the MRPP, and R (The R Project for Statistical Computing 2016) was used for the CCA and Mantel tests.

2.4 *Results*

2.4.1 Correlations among plant and soil variables

The first three axes in the PCA explained 80% of the total variation among sites (Table 3). PC1 was positively correlated with carbon, nitrogen and phosphorus and explained 43% of the variation. PC2 (21%) was negatively correlated with the C:N ratio and tree basal area, and PC3 (16%), was positively correlated with plant biomass and negatively with plant richness. These three gradients – from low to high nutrients (PC1), from few trees to many trees (i.e. grassland to woodland) (PC2) and from low ground-layer plant richness and high biomass through to high richness and low biomass (PC3) – describe much of the environmental variation that is observed in the reserves. These axes broadly align with three possible drivers of insect diversity identified in the introduction, that is, productivity, plant richness and vegetation structure.

2.4.2 Beetle diversity – species richness, abundance and biomass

Beetle species richness and biomass were highest in the tree microhabitat and lowest in the open, whereas beetle abundance was highest in the open. Floristic Group 6 (*Rytidosperma* spp. – fertilized) generally had the highest beetle species richness, abundance and biomass (Figure. 1).

Table 3: *Results of Principal Component Analysis showing percentage variation explained by the three components and correlation coefficients for the seven soil and plant variables with each component. The environmental variables most strongly correlated with each axis are shown in bold.*

	PC1	**PC2**	**PC3**
Percentage total variation explained	42.5%	21.3%	15.8%
Correlation with soil and plant variables			
Carbon %	**0.49**	-0.30	0.02
Nitrogen %	**0.56**	0.04	-0.06
Phosphorus (available)	**0.51**	0.06	0.17
C:N	-0.40	**-0.50**	0.20
Plant biomass (ground layer)	-0.04	0.11	**0.74**
Plant richness (ground layer)	-0.09	0.10	**-0.61**
Tree basal area (cm^2)	0.12	**-0.79**	-0.10

The results of the GLMs are presented in Table 4; in most cases there were several models with very similar SIC scores, so all models within 2 points of the lowest SIC score have been presented. The goodness of fit (R^2) was generally low, with most models explaining less than 10% of the variation. In the open microhabitat, beetle richness and abundance responded negatively to soil nutrients (particularly Carbon) and were positively related to plant richness. Floristic group also had a strong effect on beetle biomass in the open, with the highest beetle biomass occurring in Group 6. At logs, beetles responded positively to Nitrogen and Phosphorus, and beetle biomass was best explained by the C:N ratio (or Carbon and Nitrogen together). Tree basal area was also important for beetles collected at logs and trees; interestingly, beetle richness, abundance and biomass were all higher at sites with low tree basal area (i.e. where there were fewer trees).

2.4.3 Beetle community composition

In our CCA analysis, the variation explained by all soil and plant variables combined was 9.7%, 9.2% and 8.6% for open, log and tree microhabitat respectively, and the global model was significant for log and tree but not open (see Appendix S2). For all microhabitats, floristic group had a significant effect on beetle composition and explained more variation than any other single variable (see Appendix S2). At logs and open microhabitat, none of the individual variables were significant (marginal significance with all other variables included as covariables), whereas tree basal area and ground-layer plant biomass were significant at trees (Figure. 2b, d, e, and Appendix S2).

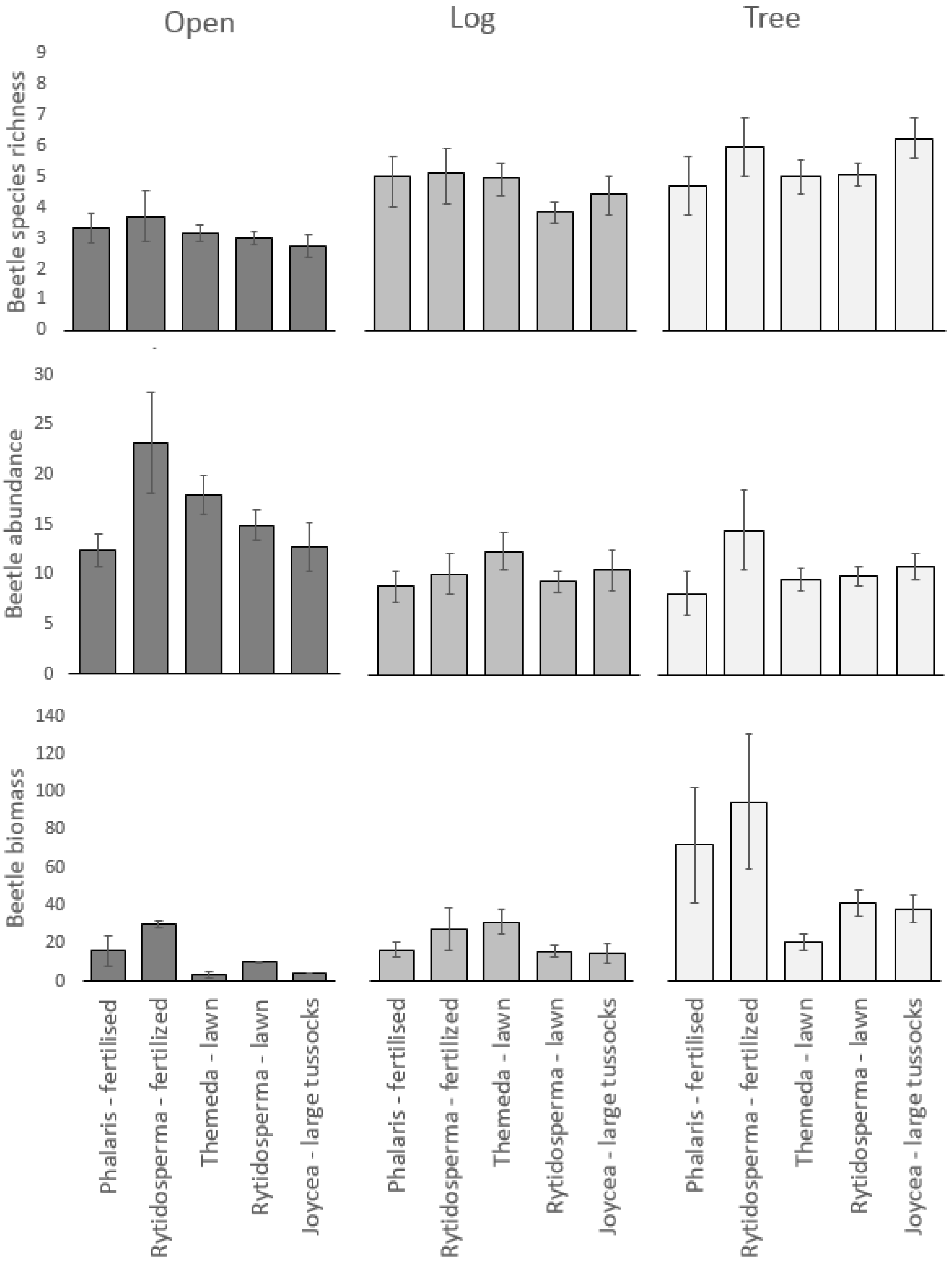


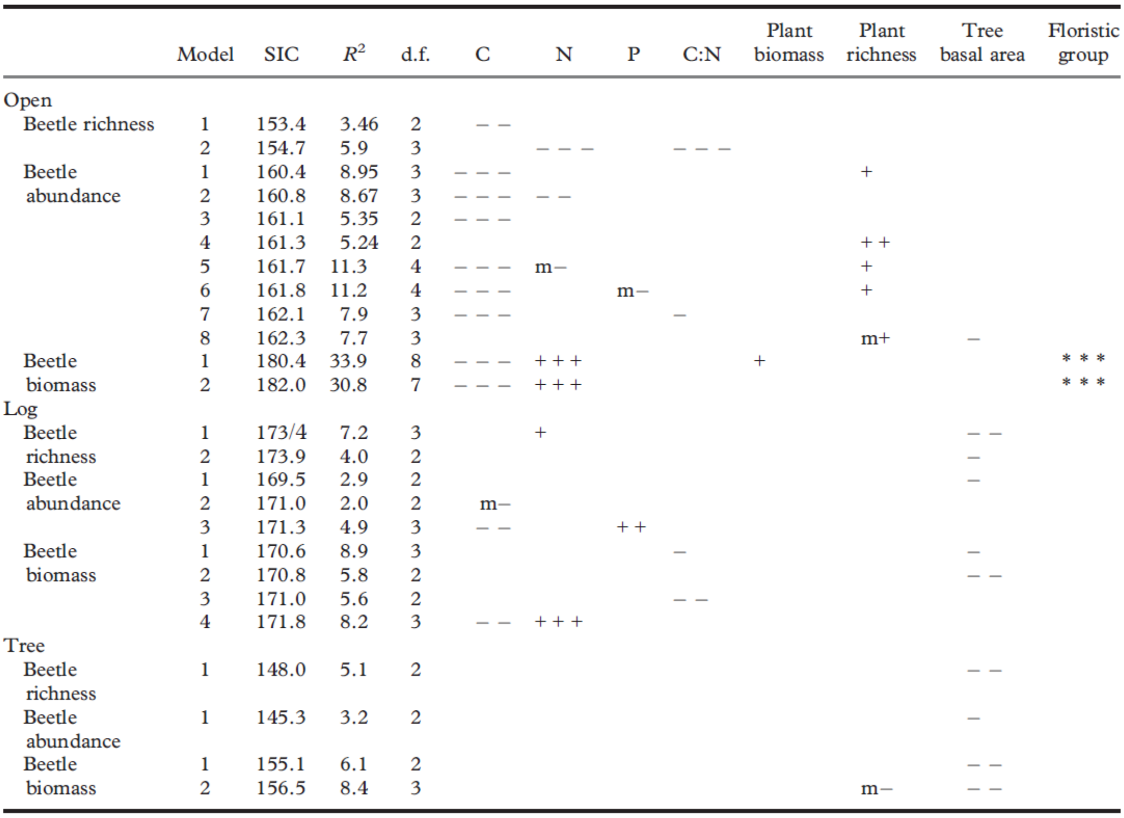
Figure 1*: Means of beetle species richness, abundance and biomass by microhabitat and floristic group. Floristic groups arranged in order of decreasing productivity (see Table 1).*

Each of the five ground layer plant communities were associated with distinct beetle communities at the log and tree microhabitats, but at open microhabitat the beetle communities were less distinct (Figure 2a, c, e). Across all microhabitats, sites in floristic Group 2 (*Rytidosperma* spp. – lawn) tended to cluster in the centre of the ordination; this was the largest group containing almost half the sites. In the open, the most distinct groups were 1 and 6 (dominated by *Phalaris* and *Rytidosperma* spp. respectively), which both had evidence of fertilization and high levels of N and P. Groups 3 and 4 (*Joycea* and *Themeda* respectively) overlapped with Group 2 in the open, but were distinctly different at the log and tree sites.

The most common beetle across all microhabitats and floristic groups was a species of Latridiidae (*Cortinicara sp*.), however it was most associated with open sites and floristic group 4 (Appendix S1). Several other common taxa tended to be associated with low productivity sites (floristic group 3), for example, Anthicidae (*Formicomus sp*. and *Tomoderus sp*.) and Elateridae (*Agrypnus sp*.), whereas the Staphylinidae (e.g. *Polylobus sp*. and *Atheta sp*.) and Coccinelidae (e.g. *Diomus sp*.) tended to prefer high productivity sites (floristic group 6).

Our MRPP analysis revealed there were significant differences in beetle composition between floristic groups at log and tree microhabitat, but none at open microhabitat, which reflected the results of the ordination (Appendix S3). The two groups most similar to each other were 1 and 6, which were also found to have similar floristic composition in McIntyre et al. (2010).

Table 4*: Summary of results from All Subsets Regression - generalized linear models for beetle richness, abundance and biomass at log, tree and open habitats. Best models selected using Schwartz Information Criterion (SIC); all models within 2 points of the lowest SIC score are presented. Direction (+ or −, * for categorical variables) and significance (0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘m*’ 0.1 ‘ ’ 1) of variables included in each model are shown.*



	Model	SIC	R^2	d.f.	C	N	P	C:N	Plant biomass	Plant richness	Tree basal area	Floristic group
Open												
Beetle richness	1	153.4	3.46	2	− −							
	2	154.7	5.9	3		− − −		− − −				
Beetle abundance	1	160.4	8.95	3	− − −					+		
	2	160.8	8.67	3	− − −	− −						
	3	161.1	5.35	2	− − −							
	4	161.3	5.24	2						+ +		
	5	161.7	11.3	4	− − −	m−				+		
	6	161.8	11.2	4	− − −		m−			+		
	7	162.1	7.9	3	− − −			−				
	8	162.3	7.7	3						m+	−	
Beetle biomass	1	180.4	33.9	8	− − −	+ + +			+			* * *
	2	182.0	30.8	7	− − −	+ + +						* * *
Log												
Beetle richness	1	173/4	7.2	3		+					− −	
	2	173.9	4.0	2							−	
Beetle abundance	1	169.5	2.9	2							−	
	2	171.0	2.0	2	m−							
	3	171.3	4.9	3	− −		+ +					
Beetle biomass	1	170.6	8.9	3				−			−	
	2	170.8	5.8	2							− −	
	3	171.0	5.6	2				− −				
	4	171.8	8.2	3	− −	+ + +						
Tree												
Beetle richness	1	148.0	5.1	2							− −	
Beetle abundance	1	145.3	3.2	2							−	
Beetle biomass	1	155.1	6.1	2							− −	
	2	156.5	8.4	3						m−	− −	

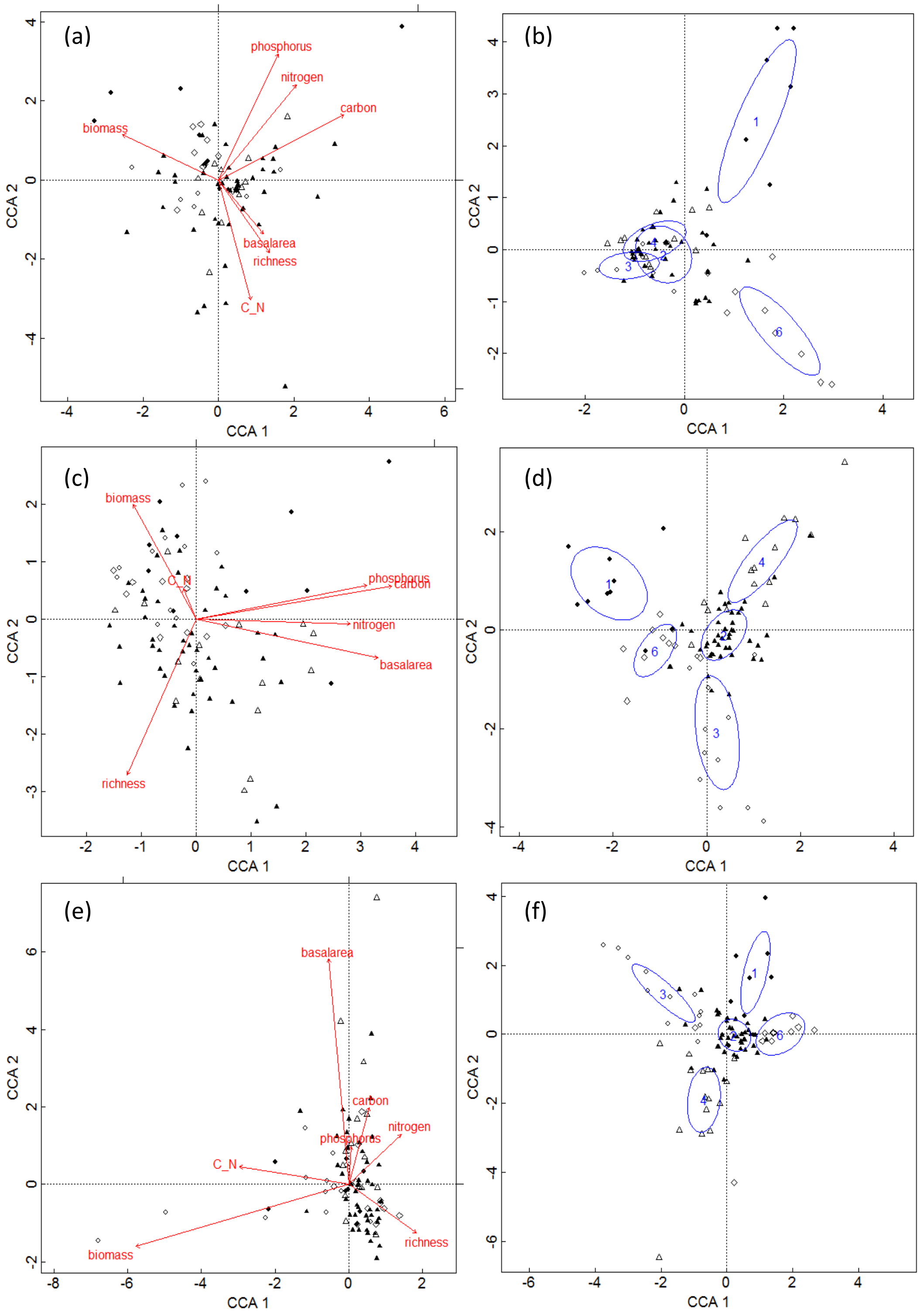


Figure 2: *Canonical correspondence analysis (CCA) of the beetle community composition for open (a, b), log (c, d) and tree (e, f) microhabitat and constrained by plant and soil variables (a, c, e) or floristic groups (b, d, f). Each point represents the beetle community at one site, and sites with a more similar beetle community are placed closer together on the ordination. Arrow direction indicates the correlation between the seven explanatory variables and the CCA axes, and arrow length represents the strength of the relationship with the beetle community. Ellipses indicate one standard deviation from the centroid of the five floristic groups.*

Table 5*: Summary of results of Mantel and partial Mantel tests for correlations between the beetle community (abundance transformed to presence-absence), plant community, soil nutrients (C, N, P, C:N, standardized) and location (spatial proximity). Significant (P<0.05) values shown in bold, n/a = not applicable as scales of measurement differ.*

	Log	**Open**	**Tree**	**Site**
Mantel test				
1st matrix vs 2nd matrix				
Beetles vs Location	r = 0.01, **P = 0.005**	r = 0.01, P = 0.39	r = 0.08, **P = 0.007**	n/a
Plants vs Location	n/a	n/a	n/a	r = 0.25, **P = 0.001**
Soils vs Location	n/a	n/a	n/a	r = 0.23, **P = 0.001**
Partial Mantel test				
1st matrix vs 2nd matrix/ controlling for 3rd matrix				
Beetles vs Plants/Location	r = 0.04, P = 0.18	r = 0.06, P = 0.11	r = 0.12, **P = 0.004**	n/a
Beetles vs Soil/Location	r = -0.04, P = 0.77	r = -0.07, P = 0.87	r = -0.09, P = 0.98	n/a
Plants vs Soil/Location	n/a	n/a	n/a	r = 0.15, **P = 0.002**

The Mantel test indicated there was significant spatial autocorrelation in beetle composition among sites at log (P = 0.005) and tree microhabitats (P = 0.007), but not among sites in the open (Table 5). Using a partial Mantel test to control for this spatial autocorrelation, we found a significant relationship between the beetles and plants (P = 0.004), but only for the tree microhabitat. In other words, tree sites that had a more similar beetle community also had a more similar plant community, but this was not the case for the log and open sites. At the site level, partial Mantel tests found a significant relationship between the plant community and the soil nutrients (P = 0.002), even after controlling for spatial autocorrelation. However, there was no direct relationship between the beetle community and the soils at any of the microhabitat types.

2.5 *Discussion*

We found that beetle communities collected from different microhabitats responded very differently to gradients in the surrounding environment. Soil nutrients had the strongest effect on beetle species richness, abundance and biomass, while vegetation composition had an effect on beetle community composition. Our results provide evidence that the impacts of past agricultural management, particularly fertilization, continue to flow through the system, affecting soils, plants and the beetle community for decades after nutrient inputs cease.

2.5.1 Effects of soil and vegetation attributes on beetle diversity and composition

In general, soil nutrients tended to be the most important factors influencing beetle species richness, abundance, biomass, and composition, indicating that many beetles preferred sites with high phosphorus and low carbon levels. However, for beetles collected at trees the most important factor was the site level tree basal area, which had a negative effect on beetle richness, abundance and biomass. This finding seems counterintuitive, but tree basal area was positively correlated with soil carbon (see Appendix S4) so this may be an expression of the same preference for high productivity sites. It could also be due to a reduction in light intensity under a dense canopy. Although a few very large trees can result in a high basal area measurement, high basal area usually indicates more trees per site (see Appendix S4). Densely packed trees are likely to be smaller and thus produce less litter than large, widely spaced trees (McElhinny et al. 2010), and litter depth is an important factor for those beetles living under trees (Barton et al. 2010). So, regardless of whether beetles were collected in the open or at logs or trees, overall they seem to prefer higher productivity sites with fewer, larger trees. This has implications for tree management in the reserves, where dense regeneration of small trees has become widespread due to the removal of grazing and lack of fire. Adaptive management experiments with thinning dense regeneration, to encourage the growth of larger trees (Allen et al. 2002; Dwyer et al. 2010) and provide additional coarse woody debris, could be considered to increase beetle diversity.

Surprisingly, plant species richness only had a significant effect on beetle abundance at open sites, and ground-layer plant biomass was not included in any of the best models. This is interesting because many studies in other ecosystems have shown that plant biomass and species richness have an impact on insect diversity (Murdoch et al. 1972; Siemann 1998; Siemann et al. 1998; Haddad et al. 2001, 2009; Wenninger & Inouye 2008). This may be due to the fact that there was not a clear linear relationship between plant biomass and soil nutrients. The highest biomass sites (Group 3, Table 1) were dominated by *Joycea*, a large tussock grass that grows on very nutrient poor soils but produces large amounts of unpalatable biomass. The general lack of a relationship between plant and beetle diversity might also be explained by the fact that our species counts were only an indicator of total plant diversity, and the trophic diversity of our beetle community. Koricheva et al. (2000) found that only highly specialized herbivorous groups were affected by plant species richness, and associations between predaceous and saprophagous species with the plant community are expected to be weaker (see also Torma et al. 2014). Targeted sampling of foliage-dwelling insects might be necessary to find a similar result.

Several studies in the Northern Hemisphere have found that soil conditions had a strong influence on ground beetles (Carabidae) (Eyre et al. 1990; Luff et al. 1992; McCracken 1994; Sanderson et al. 1995; Blake et al. 2003). We found that while soil nutrients were the most important factors affecting beetle diversity, there was no relationship between soil nutrients and beetle community composition (after controlling for spatial autocorrelation). Again, this may be explained by the fact that our study included a wide range of trophic groups and feeding behaviours, some of which may be more reliant on the soil conditions than others. It is also important to point out that the soil sampling was carried out at the site scale, and the beetles may well respond to localized differences in soil conditions at the microhabitat scale. However, soil nutrients did have a significant effect on the plant composition, suggesting an indirect effect of soils on beetle composition via the plant community. This is explored further in the following section.

2.5.2 Effects of floristic group and plant community on beetle diversity and composition

While floristic group identity was not included in the best models for beetle species richness or abundance, it is interesting to note that when floristic group was in the model the R2 was significantly improved. This indicates that floristic group was able to explain some of the observed variation, but in combination with other variables it did not significantly improve the models overall.

Several previous studies have found strong relationships between plant and arthropod composition, and were able to identify distinct arthropod communities corresponding with different vegetation types (Blake et al. 2003; Foord et al. 2003; Torma et al. 2014). We also found distinct differences in beetle community composition between floristic groups. As described by McIntyre et al. (2010), the floristic groups were defined by their similarity in plant species composition, and corresponded well with the different management histories within the reserves. In particular, sites in Groups 1 and 6 had elevated N and P levels indicating a history of fertilization, and had distinct plant communities dominated by exotic pasture grasses such as *Phalaris sp.* and exotic annuals such as *Trifolium sp.* These sites had higher beetle biomass, and their plant and beetle communities were more similar to each other than to any other groups (Figure. 2; Appendix S3). There were also differences in the beetle community between other floristic groups, but only at log and tree microhabitat, indicating that the beetles living at logs and under trees were responding to the plant species present in the surrounding area while beetle communities in the open were more homogeneous. These results suggest that the management history of a site not only influences the plant community but that this management legacy flows through to the beetle community, and that this is mediated by microhabitat.

This flow-through effect was also evident from the results of the partial Mantel test. After controlling for spatial autocorrelation, there was no direct relationship between soil nutrients and beetle composition. However, there was a significant relationship between soil nutrients and the plant community composition, and between the plant and beetle communities (at trees only), indicating that the plant composition may be directly affecting the beetle community in a way not explained by soil properties (Figure 3). This matches observations by Schaffers et al. (2008), who found that the plant community was a better predictor of arthropod assemblage composition than all other environmental and structural attributes combined. They hypothesized that the plant community is able to combine and integrate the effects of environmental and structural variables, as well as having direct effects on the arthropod community. This suggests the broader context of plant community is a key factor for considering fine-scale insect diversity patterns.

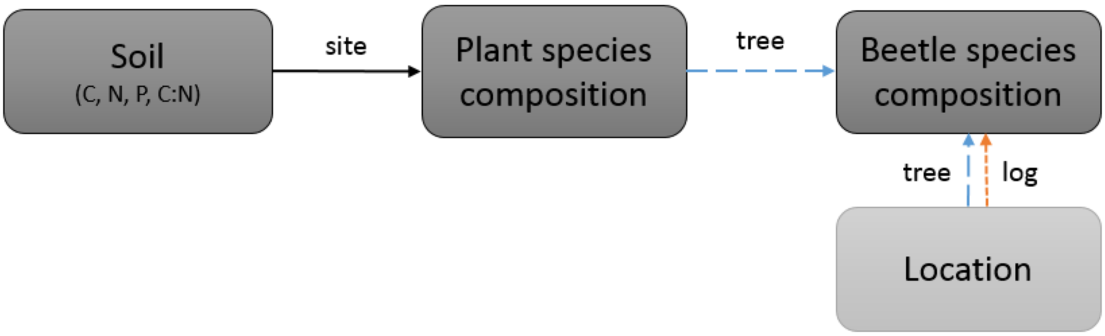


Figure 3: *The flow-through effects of management history on soils, plants and beetles, based on results of Mantel and partial Mantel tests (Table 5). After controlling for spatial autocorrelation (at logs and trees), there was a significant relationship between the soil nutrients and the plant species composition, and between the plant and beetle community (at trees only), but no direct relationship between the soil and beetles.*

2.5.3 Effects of microhabitat on beetle diversity and composition

We found that microhabitat was a very important factor in determining beetle diversity, abundance and biomass. In this study, the open sites had the highest beetle abundance and biomass, but low species richness and were dominated by a single species of Latridiidae. The MRPP and Mantel tests failed to find any patterns in beetle composition at open sites, indicating that open sites had a more homogeneous beetle composition across sites (Table 5, Appendix S3). On the other hand, the log and tree sites had higher species richness per sample, and there was more variation in the beetle composition between samples. This indicates that logs and trees increase heterogeneity and diversity in the beetle community, which agrees with previous findings by Barton et al. (2010, 2011) and supports current management recommendations such as addition of coarse woody debris (Harmon et al. 1986; McWinn & Crossley 1996; Manning et al. 2013; Craig et al. 2014) and protection of scattered trees (Manning et al. 2006; Frizzo & Vasconcelos 2013) to improve biodiversity in degraded grassy woodlands.

Further, we found that microhabitat had a very strong effect on how the beetle community responds to larger scale environmental gradients. Beetles collected at open and log sites were strongly influenced by soil nutrients, whereas beetles under trees were more responsive to tree basal area and the plant community. This finding fills an important knowledge gap of drivers of insect diversity, especially in environments more complex than simple grasslands (Joern & Laws 2013).

2.6 *Conclusions*

The results of this study highlight the importance of differences among microhabitats in determining patterns of beetle diversity, and that these differences can only be detected when sampling occurs at the appropriate scales (Mehrabi et al. 2014). The beetle community responded differently to the soils and vegetation depending on microhabitat and whether we were looking at beetle species richness, abundance, biomass or composition. Studies which use only one measure of diversity, or which sample at larger scales, are therefore likely to miss these potentially critical drivers of insect biodiversity.

We examined four proposed drivers of beetle communities: productivity, vegetation structure, plant species richness and plant composition. Soil nutrients were the strongest drivers of beetle species richness and abundance at open and log microhabitat, supporting the productivity hypothesis. However, vegetation structure (tree basal area) was more important for beetles under trees. Plant species richness was only important for beetle abundance in the open, but there was a strong relationship between the plant and beetle community composition. These findings build on the literature reviewed by Joern and Laws (2013), and are therefore relevant to studies of insect diversity in grassy ecosystems worldwide.

We also found that sites with higher soil nutrients and particular floristic composition (i.e. reflecting a history of fertilization) had distinct beetle communities, suggesting that the effects of prior land use continue to flow through from the soil to plants, and from plants to beetles, and potentially the broader ecosystem. By showing that the effects of previous land use on insects can depend on their microhabitat use, we unravel some of the complexity of insect diversity at small spatial scales.

2.7 *Acknowledgements*

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Adam Slipinski (CSIRO). The plant survey was funded though the National Heritage Trust Program (Project 18150) and the Caring for our Country Initiative (Project 2705) with the support of the ACT Natural Resource Management Council. Jeff Wood, Claire Foster and Ding Li Yong assisted with statistical analysis. The authors declare that they have no conflict of interest. This article does not contain any studies with human participants or animals performed by any of the authors.

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Chapter 2: Supplementary material

Appendix S1: Summary of beetle families

Appendix S2: Canonical correspondence analysis (CCA) results

Appendix S3: MRPP results

Appendix S4: Relationship between tree basal area and number of stems or soil carbon

Appendix S1: *Summary of beetle families – number of morphospecies from each family, and number of individual beetles from each of the microhabitats (open, log, tree) and floristic groups (1, 2, 3, 4, 6).*

Family	**No. species**	**Individuals by microhabitat**			**Individuals by floristic group**				
		Open	**Log**	**Tree**	**1**	**2 (+5)**	**3**	**4**	**6**
Anobiidae	9	15	81	137	12	98	20	73	30
Anthicidae	8	110	233	95	25	202	98	78	35
Bostrichidae	2	5	-	4	-	3	-	-	-
Bothrideridae	4	-	2	7	1	5	-	1	2
Brentidae	1	-	1	-	1	-	-	-	-
Byrrhidae	2	7	5	1	3	5	6	-	-
Cantharidae	1	2	17	86	23	59	8	12	3
Carabidae	16	16	40	42	4	47	13	28	6
Cerambycidae	1	-	1	-	-	1	-	-	-
Chrysomelidae	12	23	39	4	9	18	20	9	10
Cleridae	2	-	-	3	-	2	-	-	-
Coccinellidae	13	42	81	134	25	130	32	16	54
Colydiidae	2	1	8	1	2	1	6	1	-
Corylophidae	3	5	74	38	14	50	14	22	17
Curculionidae	23	58	68	82	36	100	12	45	15
Dermestidae	1	-	2	-	-	1	-	-	1
Elateridae	14	16	115	195	13	168	96	37	12
Histeridae	1	-	-	1	-	-	-	1	-
Hybosoridae	4	5	12	18	1	8	15	9	2
Latridiidae	7	2024	662	279	177	1360	379	683	366
Melyridae	1	2	1	1	1	2	-	-	1
Mordellidae	1	-	-	1	-	1	-	-	-
Mycetophagidae	2	1	11	15	3	11	4	6	3
Nitidulidae	6	11	4	5	-	9	3	7	1
Phalacridae	1	-	-	2	1	-	1	-	-
Pselaphidae	8	30	27	21	3	38	7	21	9
Scarabaeidae	17	25	20	54	12	43	11	22	11
Scirtidae	1	4	1	-	1	-	4	-	-
Scydmaenidae	3	14	12	10	1	10	7	11	7
Sphindidae	1	2	3	3	1	-	1	5	1
Staphylinidae	22	49	98	319	75	284	60	125	97
Tenebrionidae	10	-	13	13	3	10	2	7	4
Trogidae	3	1	1	13	-	9	-	-	6
Trogossitidae	1	-	1	-	-	-	1	-	-
unknown	7	3	2	3	1	-	5	1	1
Total	**210**	**2471**	**1635**	**1587**	**448**	**2675**	**825**	**1220**	**694**

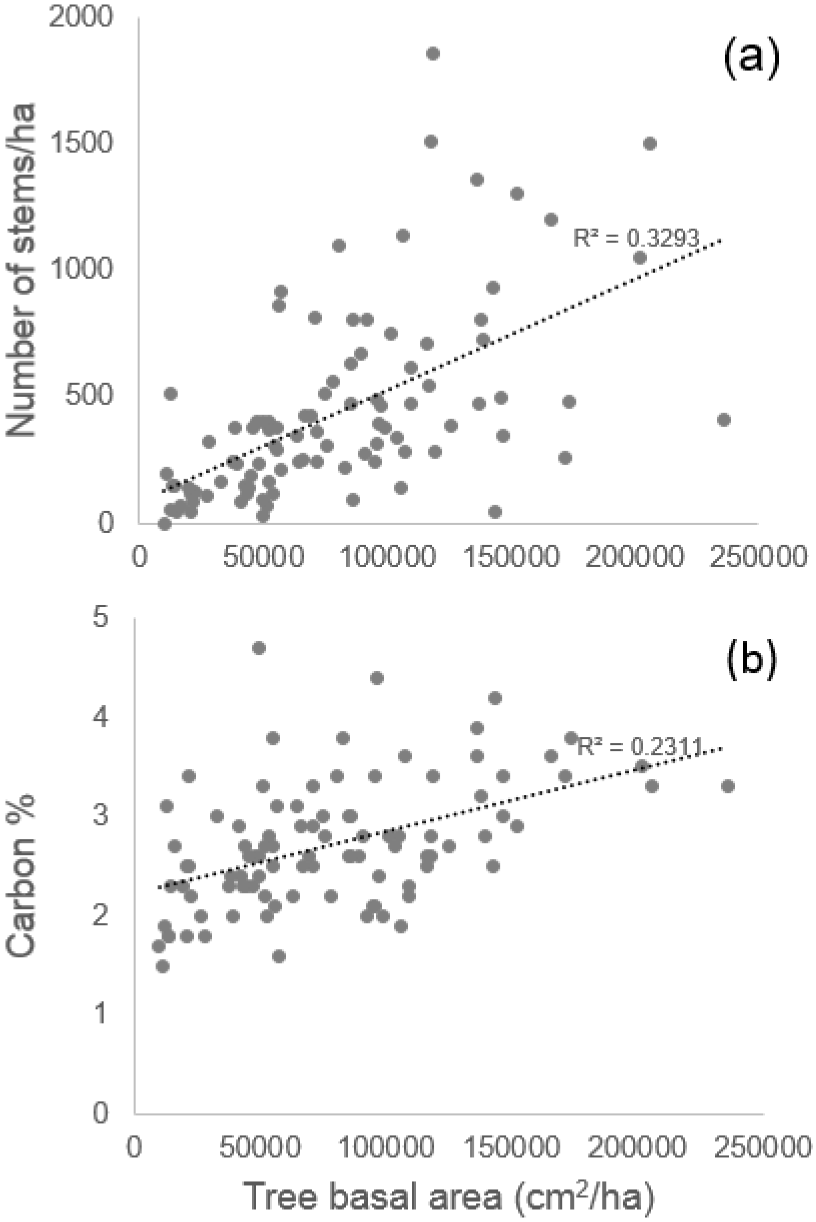
Appendix S2: *Summary of Canonical correspondence analysis (CCA) of the beetle community composition for open (1), log (2) and tree (3) microhabitat and constrained by (a) plant and soil variables or (b) floristic groups. Percentage of the total variation explained by each model are presented, along with significance values for the models and marginal significance for each variable. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.*

	% variation explained	**F**	**Pr(>F)**	
(1) CCA Open				
(a) Soil and plant variables	9.72	1.29	0.13	
Tree basal area		1.39	0.15	
Plant richness		1.17	0.57	
Plant biomass		1.35	0.22	
Carbon		1.31	0.20	
Nitrogen		1.29	0.24	
Phosphorus		1.03	0.83	
C:N		1.31	0.26	
(b) Floristic group	6.01	1.39	**0.02**	*
(2) CCA Log				
(a) Soil and plant variables	9.23	1.19	**0.002**	**
Tree basal area		1.21	0.09	.
Plant richness		1.08	0.28	
Plant biomass		1.22	0.10	.
Carbon		1.20	0.09	.
Nitrogen		1.17	0.12	
Phosphorus		1.05	0.38	
C:N		1.18	0.16	
(b) Floristic group	5.26	1.18	**0.008**	**
(3) CCA Tree				
(a) Soil and plant variables	8.63	1.12	**0.05**	*
Tree basal area		1.28	**0.04**	*
Plant richness		1.18	0.09	.
Plant biomass		1.45	**0.02**	*
Carbon		0.82	0.9	
Nitrogen		0.86	0.88	
Phosphorus		0.89	0.83	
C:N		0.91	0.70	
(b) Floristic group	5.35	1.22	**0.002**	**

Appendix S3: *Summary of MRPP analyses showing pairwise comparisons of beetle community composition between five floristic groups. Numbers are p-values (significant values <0.05 shown in bold) indicating whether between group distance was greater than within group distances.*

OPEN	**1**	**2**	**3**	**4**
2	0.28			
3	0.26	0.27		
4	0.24	0.52	0.54	
6	0.31	0.11	0.19	0.09
LOG	1	2	3	4
2	0.03			
3	0.28	0.10		
4	0.26	0.35	0.20	
6	0.61	0.03	0.19	0.02
TREE	1	2	3	4
2	0.80			
3	0.08	0.01		
4	0.17	0.11	0.06	
6	0.68	0.40	0.01	0.08

Appendix S4: *Relationship between tree basal area and number of stems (a) or soil carbon (b).*



Artist Interlude no. 2

‘What’s in your bag?’

ANU Science

In 2018, the ANU Science communications team produced a social media campaign inviting researchers to reveal ‘what’s in your bag?’ I had great fun trying to explain the purpose of all these weird items, and even got to hang out with Balbo the Bettong! My favourite item is the egg ring, which happens to be about the average size of a bettong digging so it was perfect for giving a consistent area to count seedlings. I used the coloured disks to mark plants – they are actually sheep ear tags, but the hole in the middle makes them perfect to slip over a tiny plant without damaging it so we could record their location in a photo. I love this image as a reminder of the months of fieldwork and countless hours of kneeling to identify thousands of seedlings during my PhD.

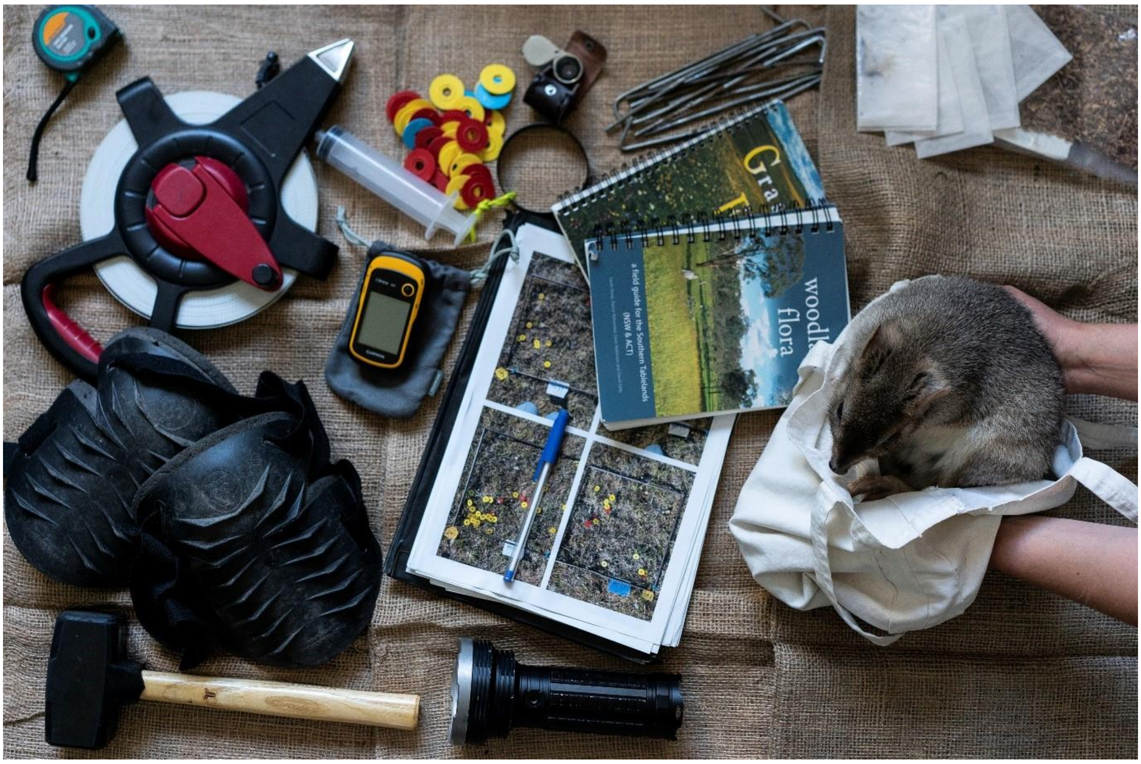


Photo by Jimmy Walsh, featuring Balbo the Bettong from the Woodlands and Wetlands Trust

Chapter 3:

Effects of digging by a native and introduced ecosystem engineer on soil physical and chemical properties in temperate grassy woodland

Ross, C.E., Munro, N.T., Barton, P.S., Evans, M.J., Gillen, J., Macdonald, B.C.T., McIntyre, S., Cunningham, S.A. & Manning, A.D., 2019. Effects of digging by a native and introduced ecosystem engineer on soil physical and chemical properties in temperate grassy woodland. *PeerJ*, 7, p.e7506.

3.1 *Abstract*

Temperate grasslands and woodlands are the focus of extensive restoration efforts worldwide. Reintroduction of locally extinct soil-foraging and burrowing animals has been suggested as a means to restore soil function in these ecosystems. Yet little is known about the physical and chemical effects of digging on soil over time and how these effects differ between species of digging animal, vegetation types or ecosystems. We compared foraging pits of a native reintroduced marsupial, the eastern bettong (*Bettongia gaimardi*) and that of the exotic European rabbit (*Oryctolagus cuniculus*). We simulated pits of these animals and measured pit dimensions and soil chemical properties over a period of two years. We showed that bettong and rabbit pits differed in their morphology and longevity, and that pits had a strong moderating effect on soil surface temperatures. Over 75% of the simulated pits were still visible after two years, and bettong pits infilled faster than rabbit pits. Bettong pits reduced diurnal temperature range by up to 25ºC compared to the soil surface. We did not find any effects of digging on soil chemistry that were consistent across vegetation types, between bettong and rabbit pits, and with time since digging, which is contrary to studies conducted in arid biomes. Our findings show that animal foraging pits in temperate ecosystems cause physical alteration of the soil surface and microclimatic conditions rather than nutrient changes often observed in arid areas.

Keywords: Eastern bettong, European rabbit, ecosystem engineer, soil nutrients, grassland, grassy woodland, digging

3.2 *Introduction*

Temperate grasslands and woodlands are among the most threatened biomes worldwide due to widespread clearing and degradation from land use changes and inappropriate management (Hoekstra et al., 2004). Loss of species has both accompanied and contributed to this degradation, including soil-foraging and burrowing animals that play a role in soil turnover. Some of these animals are considered to be ‘ecosystem engineers’ because their digging behaviour has cascading effects on soil function and associated biota (Jones, Lawton & Shachak, 1994; Berke, 2010). Most knowledge of the role of digging animals in ecosystems has been developed from arid environments (Coggan, Hayward & Gibb, 2018). This leaves little understanding of their role in many other ecosystems, and their potential use for ecosystem restoration (Byers et al., 2006; Manning, Eldridge & Jones, 2015).

Ecosystem engineers structurally alter their environment, which in turn leads to changes in abiotic and biotic conditions (Jones et al., 2010). In the case of digging animals, the creation of pits and burrows can increase soil moisture and infiltration (Laundre, 1993; Garkaklis, Bradley & Wooller, 1998; Eldridge, 2009; Eldridge et al., 2012a; Valentine et al., 2017), reduce soil bulk density (Canals, Herman & Firestone, 2003; Cuevas et al., 2012; Travers et al., 2012), moderate extremes of temperature (Gutterman, 1997; Eldridge & Mensinga, 2007; James, Eldridge & Moseby, 2010), mix the soil profile and trap plant litter and seeds (Martin, 2003; Eldridge & Mensinga, 2007; James, Eldridge & Hill, 2009).

Several studies have found that digging animals can also change the chemistry of soils, but these effects are highly variable. Some nutrients (e.g. carbon, nitrogen, ammonium, nitrate, phosphorus and sulphur) may be higher in pits because of collection of organic matter (Tardiff & Stanford, 1998; James, Eldridge & Hill, 2009; Eldridge et al., 2012b; Travers et al., 2012), increased microbial activity and decomposition (Eldridge et al., 2015, 2016; Valentine et al., 2017), or removal of plants which would otherwise use the nutrients (Canals, Herman & Firestone, 2003). In contrast, some studies have found a reduction in certain nutrients in pits, perhaps as a result of leaching due to increased water infiltration (Garkaklis, Bradley & Wooller, 2003; Eldridge & Mensinga, 2007), and others have found no effect (Groot Bruinderink & Hazebroek, 1996). A recent global meta-analysis of the effects of digging animals on soil found they significantly increased soil N and P, but there was no overall effect for C or pH (Mallen-Cooper, Nakagawa & Eldridge, 2019).

Most studies of digging animals have focused on arid and semi-arid ecosystems (Whitford & Kay, 1999; Kinlaw, 1999), with few studies conducted in temperate ecosystems, particularly in Australia (Coggan, Hayward & Gibb, 2018). This is important because the effects of digging are likely to differ between arid and temperate ecosystems (Crain & Bertness, 2006). Several studies have suggested that the effects of digging animals are more pronounced in more arid or resource-poor sites (Mallen-Cooper, Nakagawa & Eldridge, 2019; Decker, Eldridge & Gibb, 2019), however Coggan, Hayward & Gibb (2016) found the opposite pattern. Further research on ecosystem engineers in temperate ecosystems is therefore required to close this knowledge gap. The total impact of an ecosystem engineer on its environment depends on both the spatial and temporal aspects of its effects (Hastings et al., 2007). However, most studies on digging animals have focused on only the spatial aspects of digging; quantifying the number and distribution of pits and how much soil is moved in a certain area (e.g. Eldridge, 2004). In contrast, fewer studies have looked at temporal aspects of digging such as the longevity or ‘decay rate’ of pits (Raynaud, Jones & Barot, 2013). How long the effects of pits persist is likely to be influenced by many factors such as vegetation, soil type, climate and topography, as well as the morphology of the pit itself (Alkon, 1999). For example, pits have been shown to infill more quickly in sandy soils (Newell, 2008) and under tree canopies (Eldridge & Kwok, 2008), while pits with larger openings collect more litter (James, Eldridge & Hill, 2009). The effects of digging on soil chemistry are also likely to change over time as organic matter accumulates and decomposes and may persist well after the physical pit is no longer visible.

In Australia, habitat loss and feral predators have caused widespread decline of many native soil-foraging and burrowing mammals (Burbidge & McKenzie, 1989), and their loss is thought to have contributed to the degradation of Australian ecosystems (Martin, 2003; Eldridge & James, 2009; Fleming et al., 2014). However, the introduced European rabbit (*Oryctolagus cuniculus*) has become widespread in most ecosystems, and it has been suggested that they could fill a similar niche (Read et al., 2008; James et al., 2011). This is because they are comparable in size and create small foraging pits similar to those of native digging animals (James et al., 2011). In their native range, rabbits are recognised as important ecosystem engineers, increasing habitat heterogeneity and plant diversity (Galvez-Bravo et al., 2011). In Australia, however, they have become extremely abundant, leading to negative impacts on soils and native vegetation (Eldridge & Myers, 2001; Eldridge & Simpson, 2002; Eldridge & Koen, 2008) and competition with native animals (Short & Smith, 1994; Short, 1998; Johnson, 2006). Rabbits also create fewer pits than other native species, and their pits tend to be shallower (James & Eldridge, 2007; James et al., 2011; Munro et al., 2019), which may have an impact on their ecological effects. To date, no studies have directly compared the physical and chemical properties of rabbit foraging pits with a native marsupial in a temperate ecosystem.

In this study, we wanted to investigate the physical and chemical effects of foraging pits of an Australian native marsupial, the eastern bettong (*Bettongia gaimardi*) and those of the introduced European rabbit. To do this, we accurately re-created pits and measured their physical dimensions and soil properties over time. We also used real bettong diggings for measuring the microclimatic effects on temperature. We posed the following questions:

1. How do the physical dimensions of artificial bettong and rabbit pits change over time?
2. Do natural bettong pits influence soil surface temperature?
3. What is the effect of artificial bettong and rabbit digging on soil chemistry within and directly beneath the pits, and how does this change over time?

We hypothesised that differences in morphology of bettong and rabbit foraging pits would result in different rates of infill over time, and that natural bettong pits would have a more mesic microclimate with a smaller diurnal temperature range compared to the soil surface. We also predicted that soil collected from within and beneath bettong pits would be distinct from rabbit pits and control (non-pit) sites, and that any effects on soil chemistry would change over time. By addressing these questions, our study provides some new insight into the role of digging mammals as ecosystem engineers in temperate ecosystems and informs the conservation and management of both native and exotic digging mammals.

3.3 *Materials and methods*

3.3.1 Study area

We conducted our study within the Mulligans Flat-Goorooyarroo Woodland Experiment, which consists of two neighbouring nature reserves on the outskirts of Canberra, south-eastern

Australia (Manning et al., 2011; Shorthouse et al., 2012). The two reserves contain important remnants of Yellow Box-Blakely's Red Gum Grassy Woodland, which is listed as a critically endangered ecological community (Australian Government, 2006). In 2009, a 485 ha predator-proof sanctuary was established in Mulligans Flat reserve to provide protection for the native wildlife and allow the reintroduction of several locally extinct species, including the eastern bettong (*Bettongia gaimardi*) which was introduced in 2012 (Batson et al., 2016). Within the sanctuary, feral predators (cats, foxes and dogs) and hares were removed, and rabbits were managed at low numbers.

3.3.2 Vegetation, soils and climate

The soils and vegetation in the reserve have been described by Lepschi (1993) and McIntyre et al. (2010). For this study we defined three structural vegetation types: 'Grassland' (dominated by *Rytidosperma sp*., with poorer soils); 'Woodland' (discontinuous eucalyptus canopy with understorey of *Themeda australis* and large tussock grass e.g. *Rytidosperma pallida*, richer soils) and 'Forest' (continuous eucalyptus canopy with sparse understorey of *Rytidosperma pallida*, with intermediate soils and thick litter layer).

Mean minimum and maximum temperatures for the hottest and coldest month are 13ºC and 28ºC (Jan) and 0ºC and 11ºC (Jul) respectively. Mean annual rainfall is 644.5 mm (1935–2017, Bureau of Meteorology, 2018). Monthly rainfall over the study period is shown in Fig. S1 (see Supplementary Materials).

3.3.3 Study design

We assessed the physical and chemical properties of artificial bettong and rabbit pits located in the three vegetation types and over time. Our study design consisted of three fenced bettong 'exclosures' (200 m x 50 m) within the reserve, with one in each of the three vegetation types. We used fenced areas where bettongs did not have access to prevent any subsequent disturbance. We marked transects with star pickets placed 50 m from one end of the exclosure extending through the middle of the site for 50 m. In the woodland site, the transect passed through a section of grassland indicating a potentially different soil type, so we extended the transect to 70 m and avoided taking soil samples from that section. In December 2014, we placed artificial pits (see below) one metre apart along the transect, alternating between bettong and rabbit pits (giving a total of 170 pits—85 bettongs and 85 rabbits). The location of each pit was marked with a peg and a metal tag. For each pit, we measured length, width and depth (at the deepest point). We placed three coloured pebbles (approx. five mm in diameter) in the bottom of each pit to mark the original depth. In August 2015 (8 months after initiation), the pits were measured again. We then took soil samples from a selection of the pits (see below). This was repeated in January 2017 (24 months after initiation).

3.3.4 Artificial pits

We created foraging pits that simulated those of bettongs and rabbits, in order to measure changes in pit dimensions (Question 1) and soil chemistry (Question 3) over time. The temperature measurements (Question 2) were taken from real bettong pits (see below). We chose to use artificial pits for two reasons, (1) to be certain of the age of the pits, which is difficult to determine for real pits, and (2) to enable side-by-side comparison of bettong and rabbit pits in the same location and under the same conditions. We created the pits by hand using a teaspoon to scrape and scoop away the soil into a 'spoil heap', imitating the action of the animal. We based the size and shape of the pits on measurements of 1,518 bettong and 432 rabbit pits, which were taken previously from the same study site (Munro et al., 2019). While the pits of both animals can vary widely, bettong pits are generally narrower and deeper than rabbit pits with a typical 'leaning cone' shape, while rabbit pits are a shallow 'bowl' shape (Fig. 1).

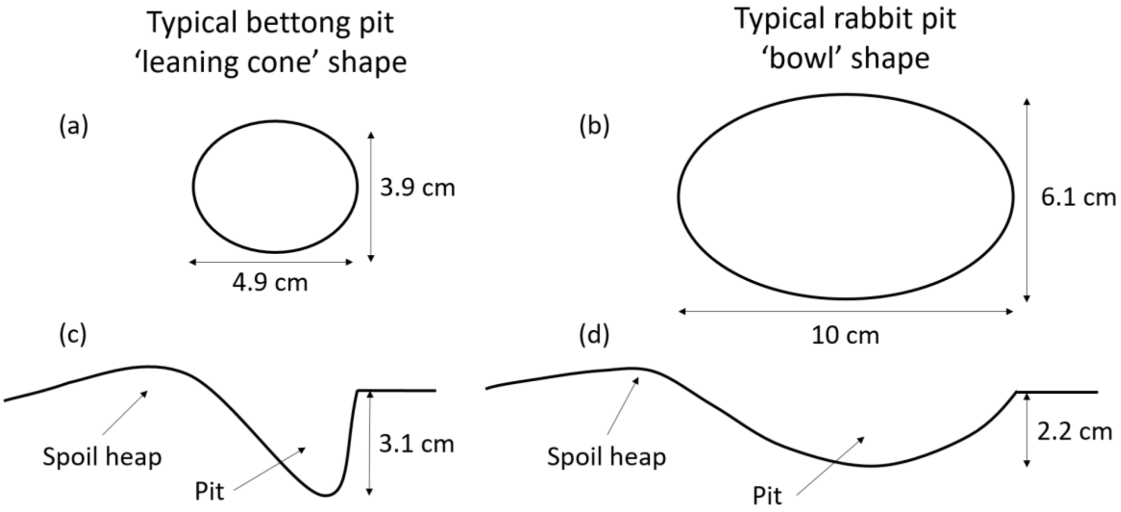


***Figure 1**. Bettong and rabbit pit dimensions. Shape and dimensions of 'typical' bettong and rabbit foraging pits shown from above (a, b) and in cross-section (c,d) (to scale). Measurements are means taken from 1518 bettong and 432 rabbit pits (Munro et al., 2019).*

3.3.5 Soil sampling

We took soil samples from six bettong and six rabbit pits in each of the three sites, at 8 months and 24 months after the pits were created (36 pits total at each sampling time). We selected the pits for sampling using a random number generator. In some cases where the pit could not be found or had been disturbed, we used the next suitable pit along the transect. Due to the destructive nature of the sampling, once a pit had been sampled, it could not be sampled again. Sampled pits were also excluded from further measurement for pit dimensions.

For the 'pit' sample, we used a small trowel to collect all the loose soil that had accumulated in the pit, down to the original depth indicated by the coloured pebbles. Any large litter was first removed from the site by gently brushing it away. We then sampled the 'under-pit' soil below the pebbles using a 50mL syringe with the end cut off, pushed into the soil at the base of the pit up to the 10 mL mark (Fig. S2). The control samples were taken from an undisturbed area approximately 50 cm further along the transect (i.e. halfway between the pits). For the ‘pit control’, we used the trowel to excavate a new depression of the same dimensions as the paired pit. We then took the ‘under-pit control’ from below the ‘pit control’ sample, using the same method as the ‘under-pit’. This gave a total of 144 samples (36 _ pit and under-pit, 36 _ pit control and under-pit control).

3.3.6 Soil analysis

Each soil sample was analysed to measure total nitrogen (N) and total organic carbon (C), mineral nitrogen ($NO3^-$ and $NH4^+$), plant-available phosphorus (P), pH and electrical conductivity (EC). The coarsely ground oven-dried soil was finely ground using a puck mill, and the organic carbon and total nitrogen content were determined using a LECO CNS 2000 (C Method 6B2 and N Method 7A5; Rayment & Higginson, 2011). These data were also used to calculate the Carbon:Nitrogen ratio (C:N). A sub-sample of each sample was used to determine soil $NO3^-$ and $NH4^+$ content using 1:10 ratio of soil to two M KCl extract. The extract was shaken for 1 h, centrifuged, and filtered prior to analysis. The $NO3^-$ and $NH4^+$ concentrations were determined by the cadmium reduction and phenate method (Rice et al., 2012) using an Autoanalyser. Soil plant-available phosphorus was extracted using the Resin P method (Tiessen & Moir, 2007) and determined using the colorimetric molybdate-ascorbic acid method (Murphy & Riley, 1962). Five grams of field soil to 25 ml DI water extract were used to determine soil pH (Method 4A1; Rayment & Higginson, 2011) and EC (Method 3A1; Rayment & Higginson, 2011).

3.3.7 Temperature measurements

To measure the effect of digging on soil surface temperatures, we selected six real bettong pits at an open grassland site in full sun, within Mulligans Flat Nature Reserve. We chose an open site to avoid variation due to shading, so the measurements are likely to represent the most extreme temperature variation experienced in the reserve. These measurements were taken from real bettong pits because we were not concerned about pit age or subsequent disturbance, but we did select pits that appeared to be fresh (i.e. no infill). Pits were randomly distributed across the site, with a minimum distance of one metre between pits. We placed six digital temperature data loggers (Maxim Integrated Thermochron iButton Device DS1921G) in the base of the pits, and six on the soil surface 20 cm from each pit. The thermometers were protected from direct sun by the grass canopy, or a thin layer of loose soil in the bottom of the pits. We set the thermometers to record every 15 min and left them out over 4 days during winter, and again during summer (25–29 Aug and 9–13 Dec 2016).

3.3.8 Data analysis

To examine the change in physical dimensions of the pits over time (Question 1), we calculated the average radius (length + width/4) and depth of bettong and rabbit artificial pits recorded at 0, 8 and 24 months. We used the ratio of depth to radius as a proxy for the change in the dimensions of the pit. We also calculated the volume of each pit, assuming a circular cone shape (pi * radius^2 * (depth/3)). We used linear mixed models to test for the interactive effects of pit age and species on the pit dimensions (depth/radius) and volume. We included vegetation type as a random effect to account for site differences. We then tested for pairwise significant differences between the different factor levels using Tukey's post-hoc test.

To measure the effect of natural bettong pits on soil surface temperatures (Question 2), we plotted the temperatures recorded inside pits and at the soil surface at 15-min intervals, with each interval averaged across the six data loggers for each treatment ('pit' and 'surface' in summer and winter). We then plotted temperatures as a boxplot to show the overall mean and range for the 4 days of data. For each data logger, we calculated the mean, maximum, minimum and range of temperatures recorded over 4 days in the field. We then conducted paired t-tests to test whether there was a difference between the pit and surface in each of summer and winter using GenStat (VSN International, 2015).

To assess the effects of artificial bettong and rabbit pits on soil chemical properties (Question 3), we first used Principal Component Analysis (PCA) to explore the correlations among all the soil variables in relation to other explanatory variables (e.g. vegetation type, age of pit, treatment). This analysis combines variables using an orthogonal transformation to identify compound axes of variation that explain the largest possible variance in the dataset (Pearson, 1901). Eight soil variables were included in the analysis: total nitrogen (N), total carbon (C), C:N ratio, nitrate and ammonium ($NO3^-$ and $NH4^+$), plant-available phosphorus (P), pH and EC. We conducted the PCA using PC-ORD (MjM Software Design, 2016).

We next used linear mixed models to test for the interactive effects of our experimental treatments on each of the eight soil variables. Our fixed effects were: *Treatment*—two levels (Treatment and Control), tests for the effect of digging with respect to a paired control (non-pit); *Pit*—two levels (Pit and Under-pit), tests for the difference between soils collected from inside and directly below the pit; *Animal*—two levels (Bettong and Rabbit), tests for the difference between pits created by bettongs or rabbits; *Age*—two levels (8 months and 24 months), tests for the difference due to the age of the pits; *Vegetation type*—three levels (Forest, Woodland and Grassland), tests for the difference due to vegetation type. We were interested in the treatment effect (treatment vs control) in each level of the interaction of age, vegetation type, animal and pit. We used *Pit number* (i.e. position along the transect) as a random effect to account for spatial autocorrelation. Our response variables were Total C (g/kg), Total N (g/kg), C:N ratio, $NH4^+$ (μg/kg), $NO3^-$ (μg/kg), P (μg/kg), EC and pH. All response variables were log transformed to achieve normal distribution, except pH. We represented the results of these nested treatment effects as effect sizes. These were extracted from the model coefficients and represent the effect of a treatment vs its corresponding control within each of the interacting effects. We used R (R Core Team, 2017) with the 'lme4' (Bates et al., 2015) package for the generalised and linear mixed models, the 'emmeans' package (Lenth, 2018) for the Tukey post-hoc test and the 'ggplot2' package (Wickham, 2009) for figure plotting (for code see Supplementary Material).

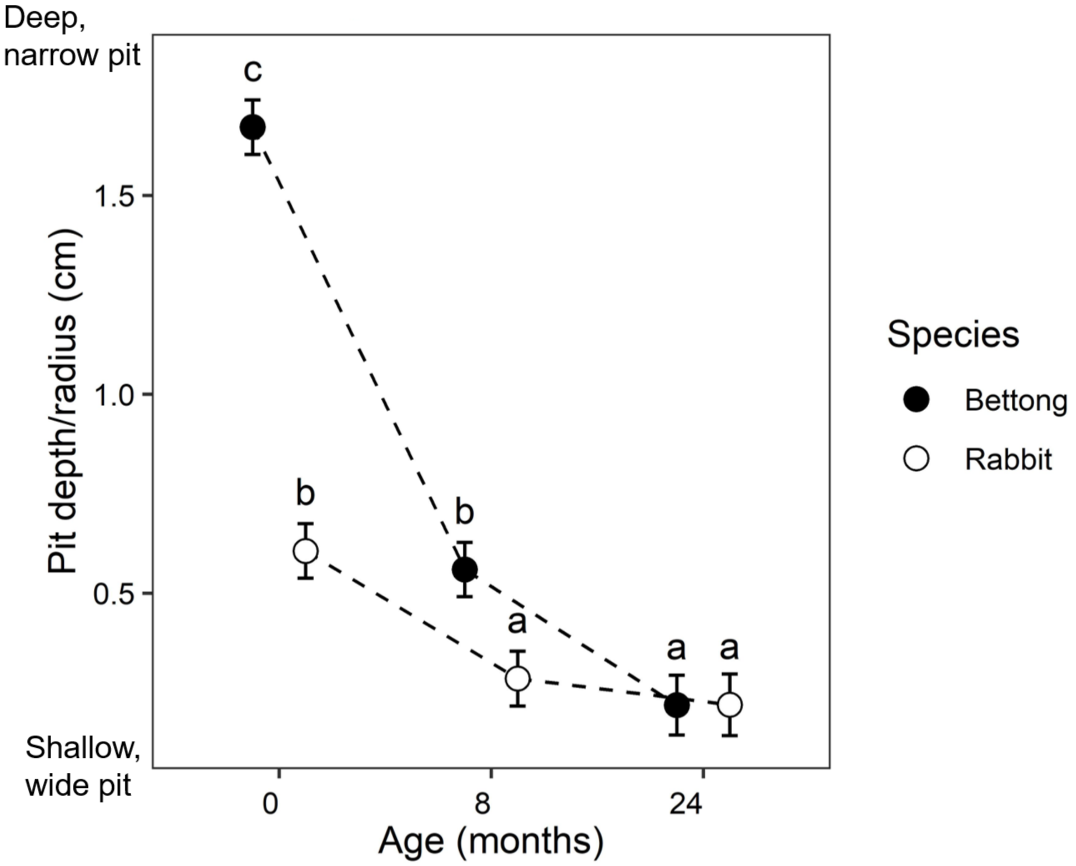


Figure 2. *Bettong and rabbit pit dimensions over time, shown as the ratio of pit depth to radius.* *Values are predicted means with standard errors based on linear mixed models. Letters (a-c) indicate pairwise significant differences based on Tukey's post-hoc test.*

3.4 ***Results***

3.4.1 Pit dimensions

We found that after 2 years, 75% of all pits were still visible. After 8 months, 5% of bettong pits were completely filled in, while only 1% of rabbit pits were full. After 24 months, 27% of bettong pits were completely full compared to 17% for rabbit pits. The results of the linear mixed models are shown in Table S1, and the results of the Tukey post-hoc tests are in Table S2. There was a significant interaction between pit age and species ($p < 0.001$) for both depth/radius and volume, indicating that the difference between the bettong and rabbit pits changed over time. At the start of the experiment (0 month), the bettong pits were deeper and narrower than rabbit pits (higher depth/radius ratio), but the rabbit pits had higher average volume due to their larger surface area (see Fig. 2; Fig. S3). At 8 months, the bettong pits had become wider and shallower as their sides collapsed, but the depth/radius ratio was still significantly higher than the rabbit pits. At this point there was no difference in volume between bettong and rabbit pits. Between 8 and 24 months, the bettong pits continued to infill at a slower rate, but there was no significant change in the rabbit pit dimensions. At 24 months there was no difference in dimensions or volume between bettong and rabbit pits.

3.4.2 Soil surface temperatures

There was no difference between the mean temperature in a bettong pit and the soil surface in either summer ($p = 0.25$) or winter ($p = 0.56$) (Fig. 3; Fig. S4). However, the pits were characterised by a significantly smaller diurnal temperature range (summer $p < 0.001$, winter $p = 0.03$). In summer, the mean maximum temperature in a pit was approximately 12ºC cooler than on the surface ($p < 0.003$), the minimum was 3ºC warmer ($p < 0.001$). In winter, the mean maximum temperature in a pit was 5ºC cooler ($p = 0.03$), and the minimum temperature was 2ºC warmer ($p = 0.02$).

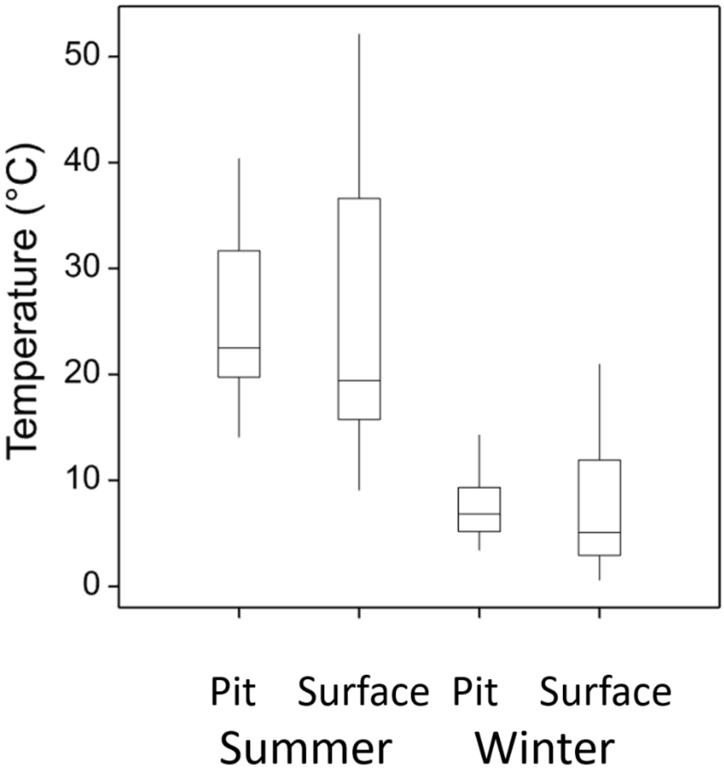


Figure 3. *Bettong pit and soil surface temperatures (°C)**.** Temperature data from bettong pits and soil surface, measured every 15 minutes over four days in summer and winter 2016.*

Table 1. *Summary table of the eight soil variables measured for all soil samples (including pit, control, under-pit, and under-pit control), and the results of Principal Components Analysis (PCA) identifying the variation accounted for by the first three axes and their correlated soil variables.*

Soil Variables	***Min***	***Max***	***Mean***	***Std. dev.***	***Correlation with PCA axis***		
					Axis 1	Axis 2	Axis 3
Total C g/kg	12.81	413.4	67.41	57.63	0.53	-0.25	-0.16
Total N g/kg	0.6	13.23	3.44	2.25	0.52	-0.20	-0.19
C:N	4.16	37.56	18.46	3.74	0.32	-0.36	-0.15
NO_3^- *µg /kg*	0.005	90.15	9.16	15.19	0.005	-0.45	0.47
NH_4^+ *µg /kg*	0.02	221.95	29.73	41.63	0.37	0.41	0.006
P µg /kg	0.02	19.49	2.49	3.49	0.09	-0.04	0.81
pH	4.16	6.38	5.17	0.53	0.15	0.56	0.11
EC	4.16	225.6	53.71	40.91	0.43	0.29	0.22
% Variance explained					34.7%	26.7%	15.2%

3.4.3 Effect of digging on soil chemistry

The PCA showed that our eight soil chemistry variables could be combined into three main axes that explained 77% of the total variation among samples (Table 1). The first axis of the PCA was correlated with C and N (Table 1), and there was a gradient along this axis by vegetation type, with the lowest levels of C and N found in the grassland sites and the highest levels in forest sites (Fig. 4B). Importantly, the PCA ordination revealed that pits were clearly separated by age along the second axis, which was positively correlated with pH and $NH4^{+}$, and negatively with $NO3^{-}$. At 8 months, soil samples had higher pH and $NH4^{+}$, whereas at 24 months the samples tended to have higher levels of $NO3^{-}$ (Fig. 4A). There were no obvious visual differences between the bettong and rabbit pits, or between the pit, under-pit and control samples in terms of their positions in ordination space.

We found some significant effects of foraging pits on soil chemistry, which are summarised in Table 2 (full results for each variable shown in Figs. S5A–S5H). The effects were dependent on vegetation type, animal, age of pit or some combination thereof, with no consistent patterns across treatments. Most of the significant effects were detected at 8 months, and rabbit pits had more significant effects than bettong pits. For example, rabbit pits in the forest vegetation type had higher levels of carbon at 8 months compared to the control (non-pit), but those in the grassland site had less (Fig. 5); whereas in the woodland, available phosphorus levels were higher in rabbit pits but lower in rabbit under-pits. At 8 months, rabbit pits in the

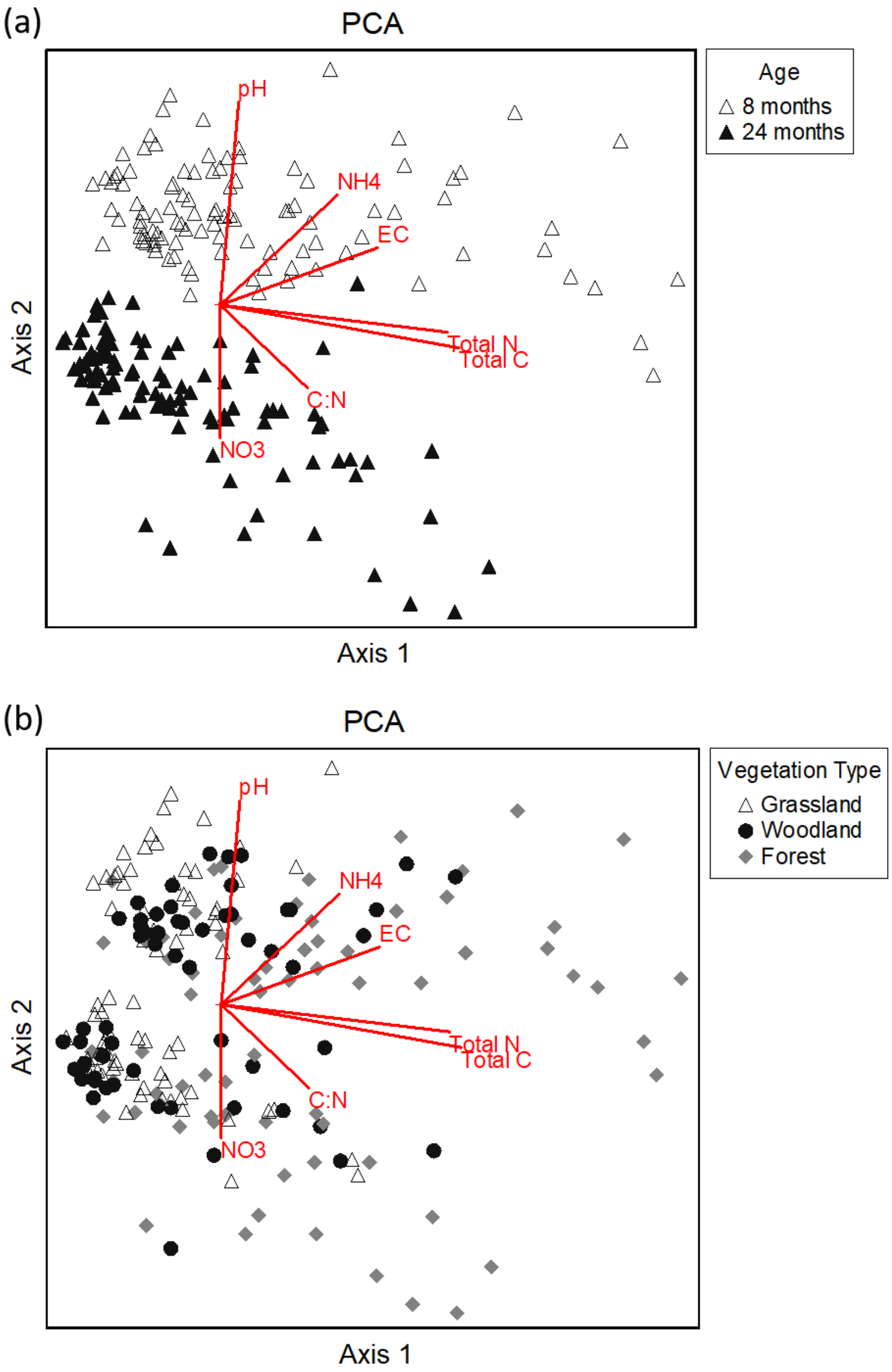


***Figure 4**. Principal component analysis. Principal Component Analysis (PCA) of all soil samples (including pit, control, under-pit, and under-pit control), coded by **(a)** the age of the pit when the samples were taken and **(b)** vegetation type. The biplot lines indicate direction and strength of correlation with the eight response variables (Total C, Total N, C:N ratio, NH_4^+, NO_3^-, P, EC and pH).*

***Table 2**. Summary of results of linear mixed models (LMM), showing effects of digging on eight soil chemistry variables. Note: only significant response variables are shown, indicating a significant digging effect when compared with paired controls (non-dig). NS indicates that there were no significant effects.*

	Forest	***Woodland***	***Grassland***
Bettong pit	8 months: ↑EC	8 months: NS	8 months: ↑pH
	24 months: NS	24 months: NS	24 months: ↑EC
Rabbit pit	8 months: ↑C ↑N	8 months: ↑P	8 months: ↓C ↓N ↑pH
	24 months: ↓EC	24 months: NS	24 months: NS
Bettong under-pit	8 months: ↑NH_4^+	8 months: NS	8 months: NS
	24 months: NS	24 months: NS	24 months: ↓EC ↓C:N
Rabbit under-pit	8 months: NS	8 months: ↓P	8 months: ↓C ↓N
	24 months: ↑EC	24 months: NS	24 months: ↑C:N

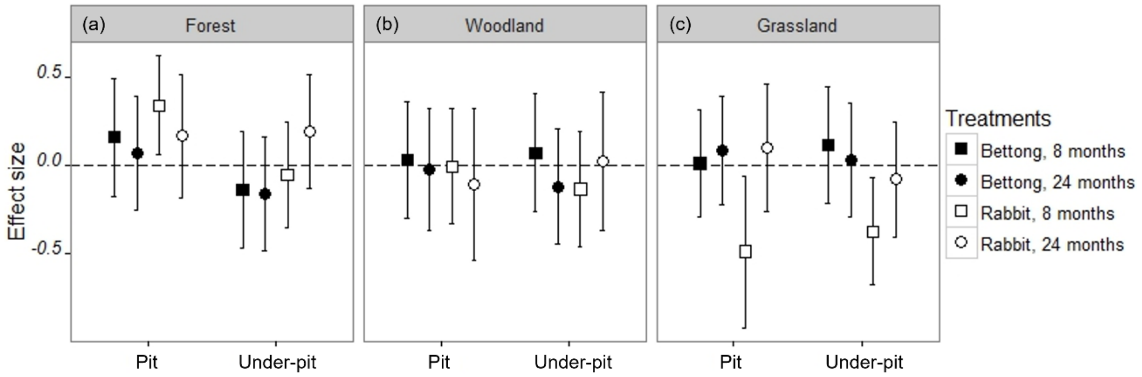


***Figure 5.** Digging effects on Total Carbon**.** Effect size plot based on linear mixed models for Total Carbon (g/kg). See Supplementary material (Figure S3a-h) for plots for the other measured soil variables (Total N, C:N ratio, NH_4+, NO_3-, P, EC and pH). These effect sizes are the coefficients of the treatment level vs the control level in the treatment variable. The effects of vegetation type, animal, age of pit and pit vs under-pit on total carbon are all accounted for and not represented in this figure. Points falling above the dotted line indicate a positive effect and below the line is a negative effect. Results are significant only where the confidence intervals do not cross the dotted line.*

grassland had higher pH, but at 24 months pH was higher in rabbit under-pits in the woodland site. At 24 months, EC in the forest was lower in rabbit pits but higher in the under-pit. There were no digging effects on any soil nutrients (C, N, $NH4^+$, $NO3^-$ and P) in bettong pits. At 8 months, bettong pits had higher pH in the grassland vegetation type. Bettong pits in the forest had higher EC at 8 months, whereas at 24 months in the grassland EC was higher in bettong pits but lower in the under-pit. In bettong under-pits, ammonium was higher in the forest site at 8 months. There was no significant difference in nitrate among the treatments.

3.5 *Discussion*

In this study we tested the hypothesis that that foraging pits of an Australian native marsupial, the eastern bettong (Bettongia gaimardi), were distinct from control (non-pit) sites and those of the introduced European rabbit in temperate grassy woodlands. We demonstrated that while bettong and rabbit pits differed in their physical effects, such as the micro-topography of the soil surface and the temperatures in the pit, they did not have a clear effect on soil chemistry. We suggest the role of digging ecosystem engineers in temperate zones may be limited to physical disturbance of the soil rather than the creation of nutrient or resource hotspots described previously in arid zone ecosystems. Our work has meaningful implications for understanding the role of ecosystem engineers in temperate ecosystems.

3.5.1 Question 1 - How do the physical dimensions of artificial bettong and rabbit pits change over time?

We found that more than 75% of all pits were still visible after 2 years. This was despite significant rainfall and flooding at around 20 months, which we expected would cause rapid infill. Both pit types filled in more quickly in the first 8 months (Fig. 2) but once they had reached a depth of around one–two cm the rate of infill levelled off, suggesting that they may persist for some time as shallow depressions. Other similar studies have reported decay rates ranging from 4 months up to 3 years depending on vegetation and soil type (Johnson, 1994; Eldridge & Kwok, 2008; Newell, 2008); however, much longer periods have been recorded (see Gutterman, 1987; Whitford & Kay, 1999). We also found that bettong pits filled in slightly faster than rabbit pits. This may be the result of different pit morphology; we observed that the steeper sides of bettong pits quickly collapsed into the hole and appeared to collect more litter and debris, whereas we observed the shallow bowl-shaped rabbit diggings tended to be washed out by wind and water.

3.5.2 Question 2 - Do natural bettong pits influence soil surface temperature?

We found that bettong digging alters physical conditions of the soil surface by moderating the diurnal temperature range up to 25ºC compared to the soil surface. Several previous studies have shown that animal burrows can provide thermal refugia for many species, particularly in arid biomes (Williams, Tieleman & Shobrak, 1999; Casas-Criville´ & Valera, 2005; Read et al., 2008; Walde et al., 2009; Pike &Mitchell, 2013). However, very few studies have measured temperatures in shallow foraging pits. Gutterman (1997) measured temperatures in porcupine pits (~10 cm deep) over a period of two days during spring and summer and found a very similar moderating effect, with daytime temperatures up to 18ºC higher on the soil surface. Eldridge & Mensinga (2007) found that echidna pits (~9 cm deep) were around 2ºC cooler than the soil surface.

3.5.3 Question 3 - What is the effect of artificial bettong and rabbit digging on soil chemistry?

We found that digging influenced soil chemistry, but the effects were not consistent across vegetation types, between bettong and rabbit diggings, or over time. We found the strongest pattern in soil chemistry to be the separation of samples by their different ages (Fig. 4A). This was not an effect of digging but occurred across all samples and was most likely due to seasonal differences in soil moisture and below-ground processes between the sampling times. The 8-month samples were taken in winter, when soil moisture was high, while the 24-month samples were taken in summer and had very low soil moisture. Moisture levels can affect soil pH, EC and particularly the relative concentration of $NH4^+$ and $NO3^-$; at high levels of soil moisture, $NO3^-$ concentration declines while $NH4^+$ increases (Zhang & Wienhold, 2002). However, the variation in soil moisture would not affect the other variables e.g. total C or N. There also appeared to be a gradient of increasing levels of C and N according to vegetation type (Fig. 4B) and reflects the greater input of organic plant litter in the woodland and forest sites compared to the grassland. The influence of pit age and vegetation type explained most of the variation in chemistry among the samples, making any differences due to digging harder to detect.

We expected that any effects of digging on soil chemistry would change over time, with some changes appearing soon after pit formation, while others may take months or years to develop as the pits fill in. We found that there were more differences in soil chemistry at 8 months after the pits were created, but most of these had disappeared by the second sampling time at 24 months. This suggests that as the pits fill in, they become less distinct from non-pit soil. However, as mentioned above, some of the age effects could have been confounded with seasonal differences. Two years may also be too short a time to observe some effects; most of the pits were not completely filled in, and rates of litter decomposition in this system can be extremely slow due to the inherent low fertility of the soils and the associated leaf traits in the vegetation (Orians & Milewski, 2007; Cornwell et al., 2008; McIntyre et al., 2010).

Our results contrast with the findings of a meta-analysis by Mallen-Cooper, Nakagawa & Eldridge (2019), which found that disturbances greater than 12 months old tended to be more distinct from undisturbed soil than fresh pits. However, ours is the only study we are aware of with repeated sampling over time, and in fact most studies used pits of unknown age. Where the age is known, there is wide variation among studies. For example Travers et al. (2012) found that after 18 months, echidna (*Tachyglossus aculeatus*) pits contained more total C and N than surface soils, whereas Garkaklis, Bradley & Wooller (2003) found a reduction in ammonium, nitrate and sulphur in 3-year-old woylie (*Bettongia penicillata*) diggings but no change in carbon, phosphorus or pH. Parsons et al. (2016) examined pygmy rabbit (*Brachylagus idahoensis*) burrows and found that duration of occupancy (1–12 years) had a limited effect on soil nutrients.

3.5.4 General discussion

Our results support, in part, the hypothesis that the importance of ecosystem engineers differs across gradients of environmental stress (Crain & Bertness, 2006). Most studies of digging animals in Australia have been in arid or semi-arid biomes (Coggan, Hayward & Gibb, 2018), and a recent global review of digging animals found that soil disturbance effects were generally stronger in more arid environments (Mallen-Cooper, Nakagawa & Eldridge, 2019). Several studies have suggested that this is due to the creation of resource ‘hotspots’, where pits collect litter and moisture and become concentrated patches of these limited resources (Eldridge & Mensinga, 2007; Eldridge & Whitford, 2009; James, Eldridge & Hill, 2009). We suggest that in our temperate woodland system, resources like water and nutrients are not as limiting and may be more evenly distributed across the landscape, so any difference between dug and un-dug patches is likely to be less pronounced. In more benign or mesic environments, competition becomes more of a limiting factor (Crain & Bertness, 2006), so the removal of existing vegetation and creation of gaps may be more important for some species (e.g. gap-dependent forbs (Grubb, 1977; Morgan, 1998)) than the provision of resources.

The eastern bettong pits measured at Mulligans Flat are also considerably smaller and shallower than the pits of other species such as the bilby or the burrowing bettong (Newell, 2008) or those of the same species recorded in Tasmanian dry sclerophyll forest (Davies et al., 2019), so they may not be as effective at incorporating organic matter into the deeper layers of soil. The reason for this difference in pit size is unclear, but could be due to differences in soil type, depth, moisture or compaction making it harder to dig, the availability of food at different depths, or the fact that bettongs and other digging animals have long been absent from the site. This would be an interesting avenue for further research.

According to the framework put forward in Jones et al. (2010), the magnitude of structural change created by an ecosystem engineer is a function of the rate of structure formation and the rate of decay i.e. how long the structure persists without maintenance. A previous study at the same site estimated the rate of digging by bettongs, rabbits and other digging animals (Munro et al., 2019). However, it was limited to a short timeframe and did not measure decay rates. Our study therefore adds to our understanding of the persistence of the effects of digging animals in ecosystems.

Pit longevity, morphology and microclimate may have other ecological implications. Studies have shown that animal diggings provide sites for seed germination, particularly in arid environments (Gutterman & Herr, 1981; James, Eldridge & Moseby, 2010; Valentine et al., 2017). While we did not investigate impacts of digs on other biota in this study, we did observe seedlings germinating in pits. James et al. (2011) found that pits of native marsupials contained 80% more seedlings than rabbit pits, which they attributed to the difference in morphology. The steeper sided bettong pits may also make it more difficult for ants to remove seeds (Radnan & Eldridge, 2017). While bettong pits are too small to provide habitat for most vertebrates, the temperature moderating effect may be important for generating heterogeneity in microclimate for seedlings, microbes and some invertebrates (Eldridge & Mensinga, 2007; James, Eldridge & Hill, 2009).We observed that pits were often free from frost in winter and appeared to retain moisture longer after rainfall events in summer. Further research is needed to confirm whether pits have an impact on seed germination and other biota in temperate grassy woodland and the mechanisms driving this effect.

It is important to note that because we used artificial pits, they may not fully replicate the effects of a real bettong or rabbit digging. Artificial pits do not capture the wide range of natural variation in size and shape, which may depend on soil type, time of year and many other factors. By using artificial pits, we expected to reduce this variation to detect differences between treatments more easily. Natural pits may also have unknown qualities, for example it has also been suggested that bettongs and other mycophagous species may be able to spread fungal spores via their noses or in their faeces (Claridge et al., 1992; Martin, 2003), and this of course cannot be replicated with artificial pits.

While rabbits are considered pests in Australia, it has been suggested that they could fill the niche created by the loss of native engineers (Read et al., 2008; James et al., 2011). We found that the morphology of bettong and rabbit diggings had an impact on their infill rate and longevity, with rabbit diggings taking longer to fill than bettong diggings. This difference in dig morphology may mean that rabbit diggings are not able to fully replicate the ecosystem engineering effects of the native bettong. Previous research by Munro et al. (2019) found that bettongs have a much higher rate of soil turnover than either rabbits or other common native species such as echidnas or ground-foraging birds (e.g. white-winged chough, *Corcorax melanorhamphos*). Rabbits have also famously shown the explosive population dynamics that sometimes occur with species introduced into a new range, with devastating impacts on native species and ecosystems (Eldridge & Simpson, 2002; Johnson, 2006). However, in areas where other native diggers have disappeared, rabbits (or other exotic species such as pigs) may be the only digging species remaining, and this should be considered before undertaking rabbit control programmes where there are no native digging species present. Ideally, replacement of introduced diggers by native diggers in an integrated restoration programme would be the preferred solution to this.

3.6 *Conclusions*

We examined the effects of foraging pits of the eastern bettong and introduced rabbits on soil physical and chemical properties in a temperate grassy woodland ecosystem. We found that pits of bettong and rabbit pits differed in theirmorphology and longevity and that bettong pits moderated daily temperature extremes. We also found that more than 75% of all pits were still visible after 2 years. However, digging did not have consistent effects on soil chemistry. These results differ from those found in arid ecosystems and suggest the effects of ecosystem engineers in temperate grassy woodlands are restricted to physical alteration of the soil rather than the creation of nutrient hotspots.

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3.8 *Additional information and declarations*

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Catherine E. Ross performed the experiments, analysed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.

- Nicola T. Munro conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, approved the final draft.
- Philip S. Barton analysed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Maldwyn J. Evans analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- John Gillen conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, approved the final draft.
- Ben C.T. Macdonald contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.
- Sue McIntyre approved the final draft.
- Saul A. Cunningham approved the final draft.
- Adrian D. Manning conceived and designed the experiments, approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The raw data and code are available in the Supplemental Files.

Supplemental Information

Supplemental information for this article can be found online at

http://dx.doi.org/10.7717/peerj.7506#supplemental-information.

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Chapter 3: Supplementary material

Figure S1: Monthly rainfall (in mm) totals for Canberra over the experimental period

Figure S2. Method used to collect ‘under-pit’ samples

Figure S3. Volume of bettong and rabbit pits over time

Figure S4. Bettong pit and soil surface temperature (°C) in summer and winter

Figure S5 (a-h). Effect size plots based on linear mixed models for all eight soil variables (Total C, Total N, C:N ratio, NH_4+, NO_3-, P, EC and pH)

Table S1. Summary of results of linear mixed models showing change in pit dimensions and volume over time

Table S2. Summary of results of Tukey’s post-hoc tests

***Figure S1**. Monthly rainfall (in mm) totals for Canberra over the experimental period (Nov 2014-Feb 2017). Artificial pits were established in December 2014, and sampling was conducted in August 2015 and January 2017 (indicated with arrows). Data sourced from the Australian Government Bureau of Meteorology (http://www.bom.gov.au/) 'Ginninderra CSIRO' weather station.*

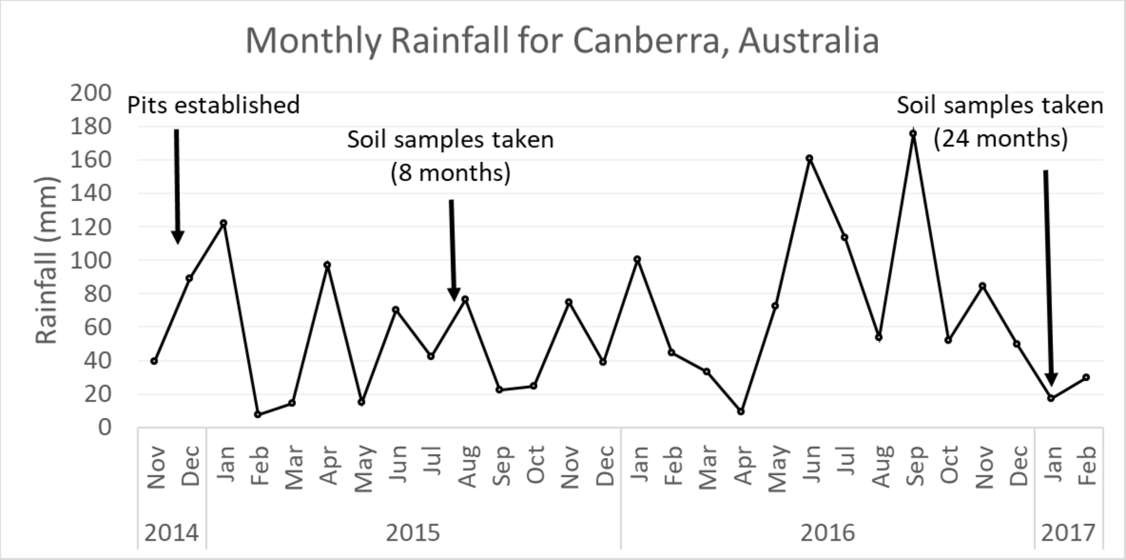


Figure S2. *Method used to collect 'under-pit' samples – a 50mL syringe with the end cut off is pushed into the soil at the base of the pit up to the 10mL mark, giving a sample of approximately 10mL.*

Figure S3. *Volume of bettong and rabbit pits over time. Values are predicted means with standard errors based on linear mixed models. Letters (a-e) indicate pairwise significant differences based on Tukey's post*-*hoc test.*

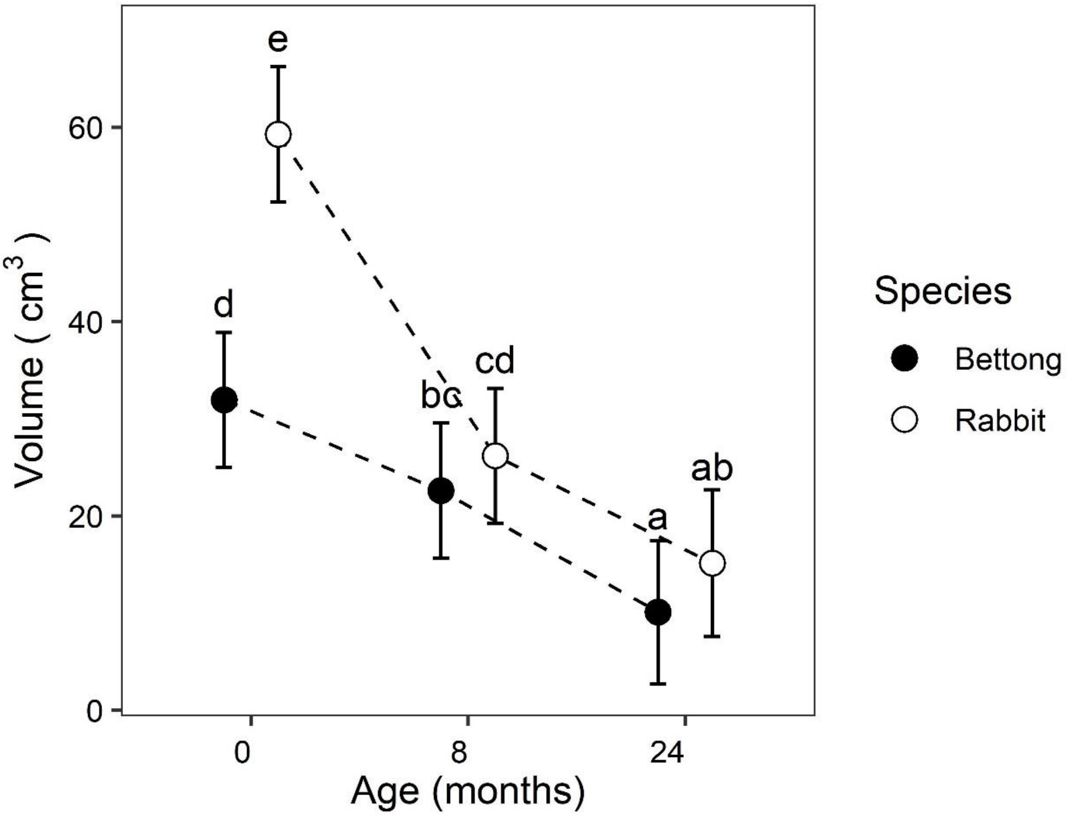


Figure S4. *Bettong pit and soil surface temperature (°C) in summer and winter. Temperature at soil surface and at bottom of bettong pits, averaged across six thermometers for each treatment. Measured every 15 minutes over four days in summer and winter 2016.*

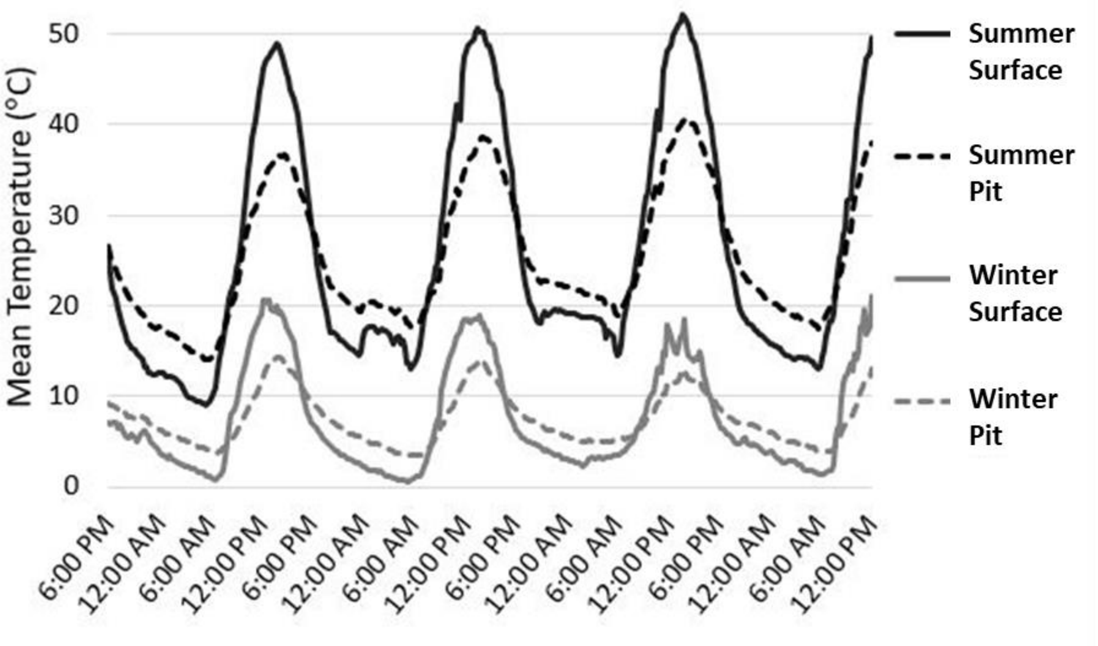
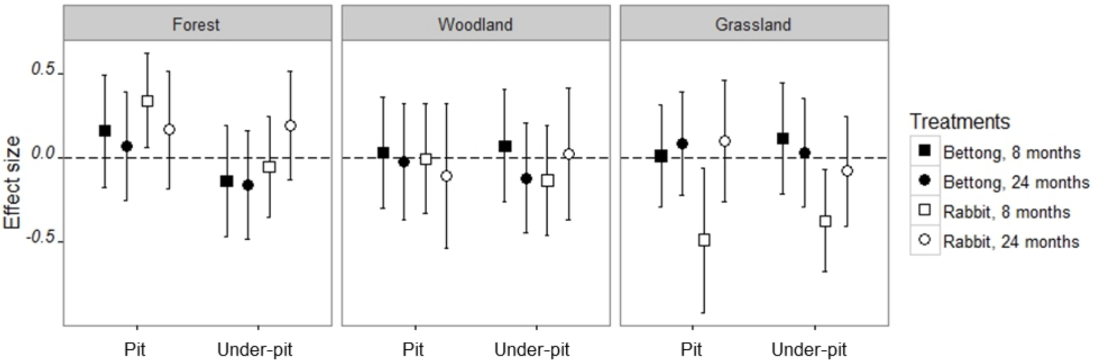
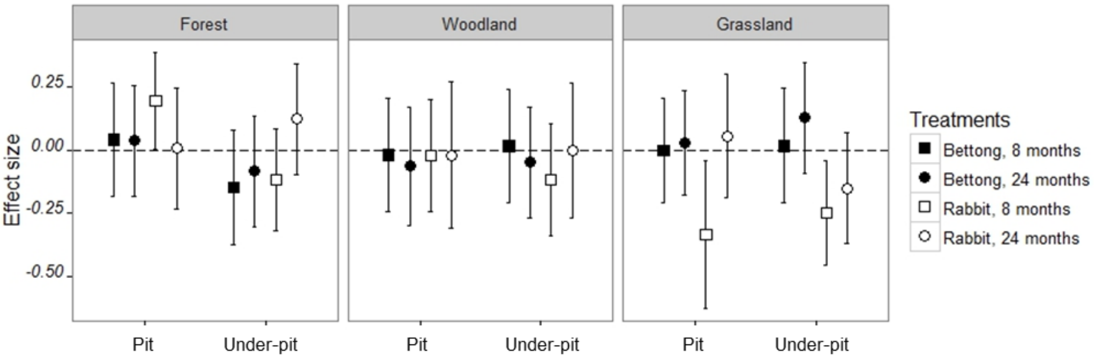


***Figure S5 (a-h)**. Effect size plots based on linear mixed models for all eight soil variables (Total C, Total N, C:N ratio, NH_4+, NO_3-, P, EC and pH). Plots show the treatment effects (pit vs non-pit) after taking into account vegetation type, animal, age of pit, and pit vs under-pit, and their interactions. Points falling above the dotted line indicate a positive effect and below the line is a negative effect. Results are significant only where the confidence intervals do not cross the dotted line.*

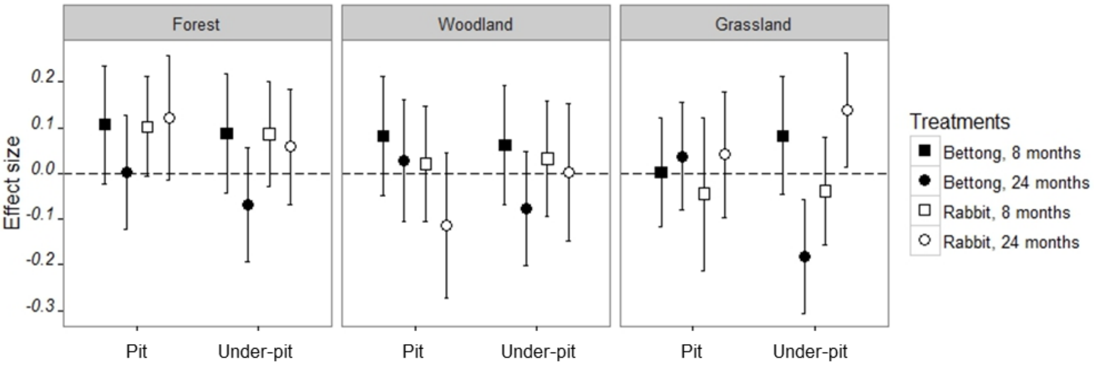
(a) Total C g/kg



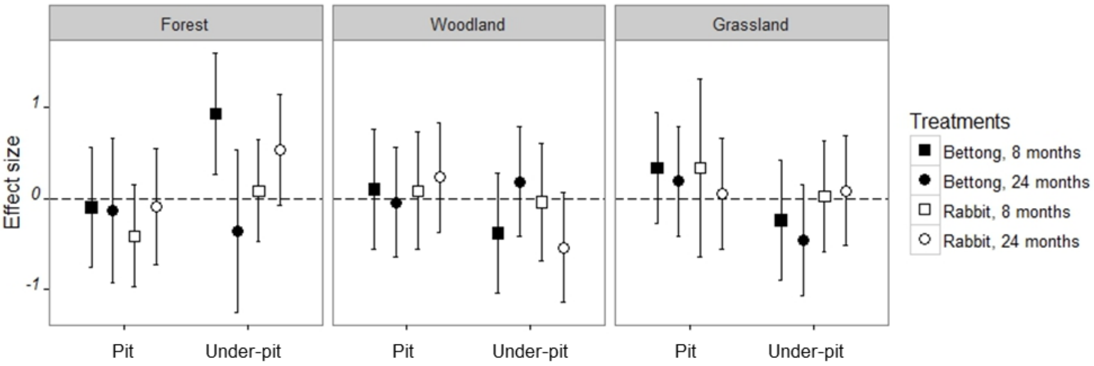
(b) Total N g/kg



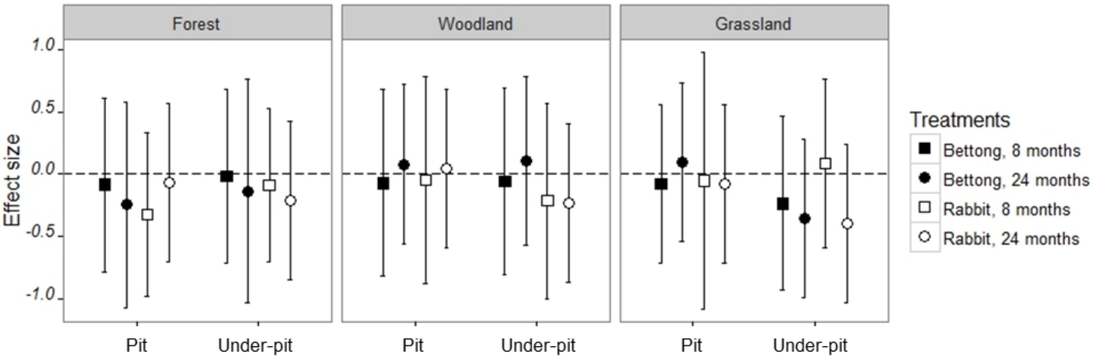
(c) C:N ratio



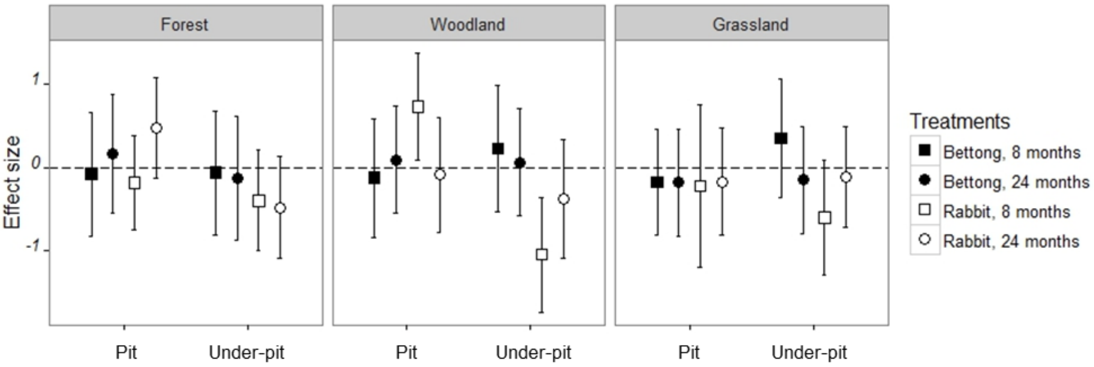
(d) NH_4^+ µg/kg



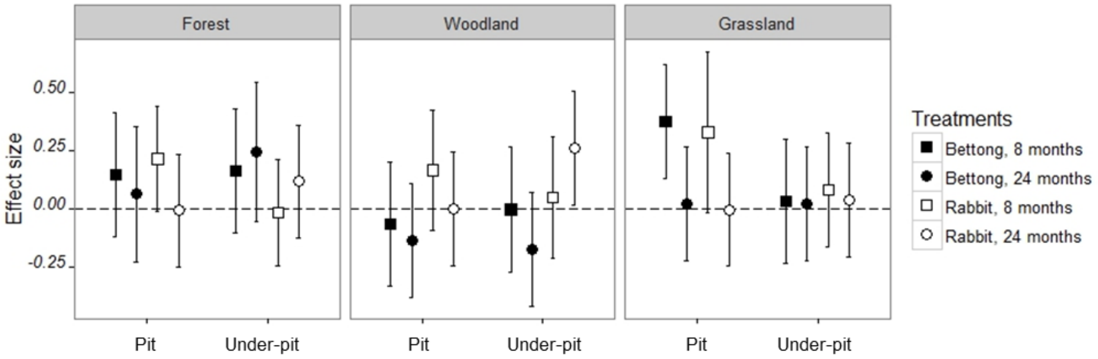
(e) NO_3^- µg/kg



(f) P µg/kg



(g) pH


Forest
Woodland
Grassland
Effect size
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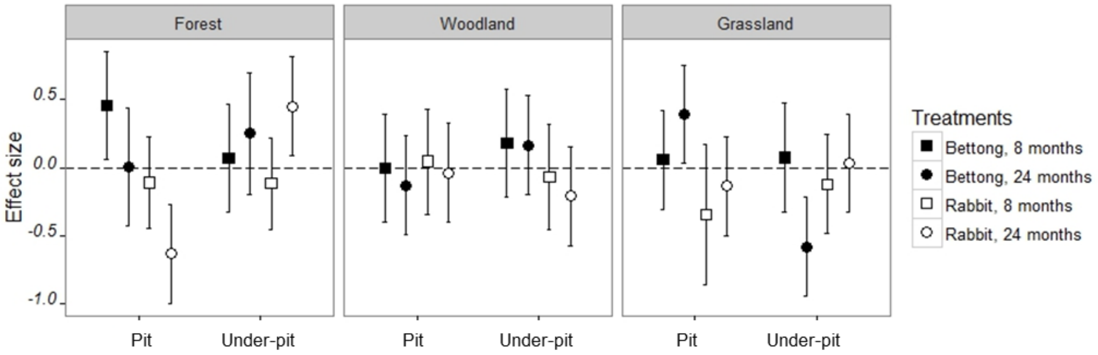
Pit
Under-pit
Treatments
■ Bettong, 8 months
● Bettong, 24 months
□ Rabbit, 8 months
○ Rabbit, 24 months

(h) EC


Forest
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Effect size
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Pit
Under-pit
Treatments
■ Bettong, 8 months
● Bettong, 24 months
□ Rabbit, 8 months
○ Rabbit, 24 months

Table S1. *Summary of results of linear mixed models showing change in pit dimensions and volume over time.*

Response	Fixed effects	Estimate	Std. Error	df	t value	Pr(>|t|)
Depth/radius	(Intercept)	1.67	0.03	5.56	48.09	**<0.001**
	Age.months.8	-1.11	0.03	442.96	-31.80	**<0.001**
	Age.months.24	-1.45	0.04	443.07	-37.90	**<0.001**
	speciesrabbit	-1.07	0.03	442.96	-30.56	**<0.001**
	Age.months.8:speciesrabbit	0.79	0.05	442.97	15.97	**<0.001**
	Age.months.24:speciesrabbit	1.07	0.06	443.09	19.35	**<0.001**
Volume	(Intercept)	31.95	3.53	3.54	9.04	**<0.001**
	Age.months.8	-9.34	2.81	442.97	-3.32	**<0.001**
	Age.months.24	-21.86	3.08	443.03	-7.09	**<0.001**
	speciesrabbit	27.34	2.80	442.97	9.75	**<0.001**
	Age.months.8:speciesrabbit	-23.78	3.98	442.97	-5.97	**<0.001**
	Age.months.24:speciesrabbit	-22.28	4.43	443.03	-5.03	**<0.001**

Table S2. *Summary of results of Tukey's post-hoc tests, based on predicted responses from the linear mixed models for pit dimensions and volume (see Table S1).*

Response	**Age (months)**	**species**	**lsmean**	**SE**	**df**	**lower.CL**	**upper.CL**	**group**
Depth/radius	24	bettong	0.22	0.04	8.32	0.09	0.35	a
	24	rabbit	0.22	0.04	9.40	0.09	0.35	a
	8	rabbit	0.29	0.03	5.82	0.15	0.42	a
	8	bettong	0.56	0.03	5.76	0.42	0.70	b
	0	rabbit	0.61	0.03	5.69	0.47	0.74	b
	0	bettong	1.67	0.03	5.69	1.53	1.81	c
Volume	24	bettong	10.09	3.76	4.62	-6.42	26.60	a
	24	rabbit	15.15	3.84	5.01	-0.94	31.24	ab
	8	bettong	22.62	3.54	3.63	4.24	40.99	bc
	8	rabbit	26.17	3.55	3.66	7.87	44.48	cd
	0	bettong	31.95	3.53	3.60	13.50	50.41	d
	0	rabbit	59.29	3.53	3.60	40.84	77.74	e

Artist Interlude no. 3

Paint your thesis

Rachael Robb

Rachael Robb completed her honours project at Mulligans Flat in 2018-19, and I had the privilege to be her co-supervisor. This was my first experience of supervising a student, so it was a great learning experience for me (and I hope for her as well!). Rachael's project continued on from my work on bettong diggings as germination niches, and explored the mechanisms driving this effect. Rachael also happens to be a fantastic artist, and I admired how she used her art to complement her own learning and communicate with others. She filled her journal with little sketches of plants and landscapes, along with notes and observations from the field. She also created characters based on the three seed species she used in her experiments, and used them in her final presentation to tell the story of her research in a highly engaging way. Rachael's thesis is illustrated with a painting at the start of each chapter, and she even painted some of her figures!

Rachael Robb 2019

Rachael Robb 2019

Chapter 4:

A reintroduced ecosystem engineer provides a germination niche for native plant species

Ross, C.E., McIntyre, S., Barton, P.S., Evans, M.J., Cunningham, S.A. & Manning, A.D., 2020. A reintroduced ecosystem engineer provides a germination niche for native plant species. *Biodiversity and Conservation*, 29, 817-837

4.1 *Abstract*

Grasslands and grassy woodlands worldwide have experienced declines in extent and condition, with substantial changes to their ground-layer biodiversity. In Australia, this decline has coincided with the extinction of many digging mammals that may have once created regeneration niches for native ground layer plants. These digging mammals are widely recognised as ‘ecosystem engineers’, due to their influence on biopedturbation and resultant soil functions. Yet there is uncertainty as to the benefits of digging in restoring grassland diversity with current levels of modification and the presence of exotic plants. We investigated the effect of digging by the reintroduced eastern bettong (*Bettongia gaimardi*) on seedling germination in a temperate grassy woodland in south-eastern Australia. We marked fresh bettong foraging pits and undisturbed control plots in dense and open grassland. We added seeds of seven native forb species and monitored germination and establishment over 2 years. We found significantly more seedlings in bettong pits than controls, particularly in dense grassland. This effect persisted beyond 1 year, suggesting that pits may have increased seedling survival in dry conditions. Surprisingly, native species displayed a stronger positive response to pits than exotic species, particularly in a wet year. There was an initial reduction in exotic species, but this was followed by their increase in 1-year-old pits, suggesting that the disturbance created by digging could eventually lead to an increase in weed abundance. Our results demonstrate that while bettong pits provide a germination niche for native forbs, reintroducing digging animals will not necessarily result in the desired restoration outcomes. Ongoing persistence of exotic species is to be expected, and seed addition may be required for species that are seed-limited.

Keywords: *Bettongia gaimardi*, eastern bettong, digging, disturbance, grassland, grassy woodland, restoration

4.2 *Introduction*

Digging or soil-disturbing animals occur in ecosystems all over the world, and play an important role as ecosystem engineers by increasing biodiversity and habitat heterogeneity (Gutiérrez and Jones 2006; Jones et al. 2006; Davidson et al. 2012; Coggan et al. 2018; Mallen-Cooper et al. 2019). In Australia, many digging mammals have experienced massive declines in population and range, largely due to predation by the introduced red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) (Woinarski et al. 2015). These species have therefore been targeted for conservation and reintroduction programs in areas where introduced predators are absent or have been removed, such as islands and fenced reserves (Legge et al. 2018). It has been suggested that the extinction of digging animals may have contributed to the loss of ecosystem function and diversity (Martin 2003; Davidson et al. 2012; Fleming et al. 2014), and that their reintroduction could be used as a tool for restoration (Byers et al. 2006; James and Eldridge 2007; Eldridge and James 2009; Manning et al. 2015).

Digging animals create soil disturbances through burrowing or foraging, which contributes to soil turnover, nutrient cycling, microclimatic effects and changes to microbial communities (Pike and Mitchell 2013; Eldridge et al. 2015; Platt et al. 2016; Mallen-Cooper et al. 2019). Several studies have shown that foraging pits and mounds provide sites for seed germination and increase growth rates of seedlings (Bragg et al. 2005; James et al. 2010; Travers et al. 2012; Gharajehdaghipour et al. 2016; Valentine et al. 2018; Lindtner et al. 2018), and in some cases plant species appear to rely on excavations for recruitment sites (Gutterman and Herr 1981). This is generally assumed to be due to the accumulation of nutrients and moisture in pits, creating patches of increased productivity (Davidson and Lightfoot 2008; James et al. 2009). However, most studies on the effects of soil disturbance by digging animals around the world have been conducted in arid biomes (Coggan et al. 2018), and it remains unclear whether the creation of germination niches by digging animals is beneficial to seedling establishment in temperate grasslands and grassy woodlands. Ecosystem engineering theory suggests that the magnitude of the engineering effect on the ecosystem should vary with environmental context, with a greater effect in more arid or resource-poor environments (Wright and Jones 2004; Wright et al. 2006). A recent global meta-analysis found that the effects of digging animals on soils tended to intensify with increasing aridity (Mallen-Cooper et al. 2019). On the other hand, Crain and Bertness (2006) proposed that in physically benign environments where competition is high, engineers may be important in reducing competition for certain plant species.

Grasslands and grassy woodlands are the most threatened biome worldwide, mostly due to clearing and degradation from agricultural use (Hoekstra et al. 2004; Habel et al. 2013). In south-eastern Australia, over 99% of temperate grasslands and grassy woodlands have been cleared, leaving only small, isolated and degraded remnants (Prober and Thiele 2005). Forbs are an important component of grassland diversity, accounting for a large proportion of ground-layer plant species richness (Pokorny et al. 2004). However, many of these species are particularly sensitive to changed grazing and fire regimes, competition from exotic species, and fragmentation, which has resulted in small isolated populations with low recruitment. This lack of recruitment is likely due to several factors, including low seed production and viability due to inbreeding depression (Morgan 1999), and a lack of suitable germination sites (Bosy and Reader 1995). The germination or regeneration niche is a limiting factor for many forb species (Grubb 1977; Morgan 1997; Moretto and Distel 1998; Clarke and Davison 2004). Trémont and McIntyre (1994) likened the structure of Australian temperate grasslands to the 'matrix-interstitium' model (Grubb 1977), in which the grass canopy forms a matrix interspersed with gaps of varying size. Disturbances such as grazing, fire an drought are important for maintaining this structure (Hobbs and Huenneke 1992) and conversely invasion by exotic species can infill the gaps and thereby transform the structure (Lindsay and Cunningham 2009). Many forb species are 'gap-dependent', and without regular disturbances, a dense grass sward develops that is relatively species poor (Bullock et al. 1995; Morgan 1997, 1998; Moretto and Distel 1998; Liu and Han 2007; Williams et al. 2007). Digging animals may play a role in creating a germination niche by opening the grass canopy and removing the soil crust, creating gaps and reducing competition (Reichman and Seabloom 2002; Dodd 2009).

Disturbance can also have negative effects on plants, particularly in degraded or highly modified ecosystems. Removing soil crusts, for example, can destabilise soils and increase erosion (Yair 1995; Neave and Abrahams 2001). Another result of grassland degradation is conversion from perennial species to annuals, and invasion by exotic species (McIntyre and Lavorel 1994; McIntyre et al. 1995). The disturbance created by animal digging could potentially promote ruderal species, which are often annual exotics (Hobbs 1991; Larson 2003). Torres-Díaz et al. (2012) found that soil disturbance by a native rodent facilitated invasion by an exotic plant. While several studies have found an increase in the total number of seedlings growing in foraging pits, they have failed to differentiate how native and exotic species respond.

The reintroduction of ecosystem engineers to areas where they have become locally extinct has been suggested as a tool for restoration (Byers et al. 2006; Manning et al. 2015). Current restoration techniques in grasslands and grassy woodlands have focussed mainly on restoring the tree and shrub layer, but have paid less attention to restoring the ground-layer vegetation (Wilkins et al. 2003; Nichols et al. 2010). Passive restoration through the removal of grazing pressure is the most commonly used method, and it is often assumed that this will be enough to result in an increase in forb diversity. However, there are many limiting factors that may prevent this, including elevated nutrient levels due to fertilisation, competition from exotic species, increased grass biomass due to the removal of grazing animals, inappropriate fire regimes, and seed limitation (Prober et al. 2002; McIntyre 2008; McIntyre et al. 2010). For plant species that are seed-limited or entirely missing from the ecosystem, seed addition is often required to reintroduce these species (Johnson et al. 2018). However, seed addition alone is often unsuccessful, because of a lack of suitable germination sites (Martin and Wilsey 2006; Smallbone et al. 2007). Therefore, a combination of techniques is needed to create the germination site and increase the availability of seed. Some methods have been developed to reduce biomass and/or disturb the soil surface to create a seed bed, including carbon addition, burning, spraying (with herbicides), dethatching, raking, mowing, scalping the topsoil to remove exotic seed banks and nutrients, and mechanical seed delivery machines (Fynn et al. 2004; Williams et al. 2007; Prober et al. 2009; Gibson-Roy et al. 2010; Valkó et al. 2012; Brown et al. 2017; Zamin et al. 2018). In some cases, these methods have been highly successful; for example, Zamin et al. (2018) found that raking improved the germination rate of hand broadcast seed by 50%. However, these methods are generally very destructive, making them inappropriate for high quality or structurally complex sites, especially those that contain threatened species or communities. These methods can also be expensive and are generally a one-off intervention, whereas fauna reintroduction provides an ongoing effect by reinstating a more natural disturbance regime.

The reintroduction of the eastern bettong (*Bettongia gaimardi*) to a fenced reserve in south-eastern Australia provided the opportunity to investigate the effects of bettong foraging pits on seed germination in a temperate grassy woodland. We asked the following questions:

1. *Do foraging pits provide a favourable habitat for the germination and survival of seedlings compared with undisturbed ground?* We predicted that there would be more seedlings germinating in bettong pits than in equivalent undisturbed control sites.
2. *Does the response of seedlings to digging depend on the following factors:*
    (a) *Grassland type*—we predicted that the seedling response to digging would be stronger in dense grassland where there is little bare ground and less opportunity for seedling germination and establishment, because foraging pits would create gaps in the grass canopy.
    (b) *Climatic conditions*—we predicted that the pits would provide a more favourable microclimate for seedlings (milder temperatures and higher moisture), resulting in a stronger response in dry conditions.
    (c) *Plant species*—We expected that seedlings of exotic species would be more likely to benefit from the disturbance created by digging compared with native species because exotic species tend to be early colonisers and adapted to disturbed environments.
3. *For plant species that are seed limited, could the reintroduction of digging animals improve the success of restoration using seed addition?* We predicted that adding seed of uncommon forbs would increase the total number of seedlings, and that the increase would be greater in bettong pits than controls.

We discuss our results within the broader context of reintroductions of ecosystem engineers to restore ecosystem function. We then discuss the implications of our results for the management of bettongs within our study area, for future reintroductions of digging animals, and how they inform future restoration projects of grassland and grassy woodland ecosystems.

4.3 *Methods*

4.3.1 Study site and species

Our study was conducted as part of the Mulligans Flat-Goorooyarroo Woodland Experiment, which is situated in two neighbouring nature reserves on the outskirts of Canberra in south-eastern Australia (Shorthouse et al. 2012). These reserves contain Yellow Box Blakely's Red Gum Grassy Woodland interspersed with Natural Temperate Grassland, both of which are listed as endangered ecological communities (ACT Government 2004, 2017 The experiment was designed to trial a range of restoration techniques, e.g., grazing management, addition of coarse woody debris, and burning (Manning et al. 2011; McIntyre et al. 2014). In 2009, a 485 ha predator-proof sanctuary was established in Mulligans Flat Nature Reserve (henceforth referred to as ‘the Sanctuary’), to exclude introduced predators and allow the reintroduction of several locally extinct species, including the eastern bettong (Batson et al. 2016).

The eastern bettong, *Bettongia gaimardi* (Desmarest, 1822), is a rabbit-sized marsupial in the family Potoroidea. The eastern bettong went extinct on mainland Australia in the early 1900s, mainly due to predation by introduced predators such as the red fox and the feral cat (Short 1998), and now survives only in Tasmania. It was successfully reintroduce to Mulligans Flat Woodland Sanctuary in 2012, and the population has since increased t between ~ 100 and 190 individuals (Manning et al. 2019). Its diet consists mainly of hypogeal fungi, roots, bulbs, seeds, fruits, and invertebrates (Taylor 1992). While foraging, it creates small pits with a distinctive ‘leaning cone’ shape, approximately 5 by 4 centimetres and 3.5 cm deep (Munro et al. 2019). Each individual bettong has been estimated to dig up to 200 pits per night, resulting in up to 3 tonnes of soil being turned over per year and accounting for 55% of all pits created by digging animals in the Sanctuary (Munro et al. 2019). These pits have been shown to last for more than 2 years in the environment, and to moderate daily extremes of temperature by up to 12°C (Ross et al. 2019).

4.3.2 Climate

The study area receives on average 695 mm of rainfall annually (Australian Government Bureau of Meteorology 2018). The first year of the experiment (2016) had a dry autumn, followed by one of the wettest winters on record in south-eastern Australia, while the second year (2017) experienced below average winter rainfall followed by a relatively wet spring. The monthly rainfall for Canberra over the experimental period compared with the long-term average is shown in Fig. S1 (see Supplementary Material).

4.3.3 Vegetation types

We selected sites within the two most common ground-layer vegetation types (identified by McIntyre et al. (2010), hereafter referred to as ‘Dense’ and ‘Open’ grassland), to compare the effects of bettong digging between these habitats. The ‘Dense’ grassland (referred to as Group 4 in McIntyre et al. 2010) occurs on higher fertility soils and is dominated by kangaroo grass (*Themeda australis*). In this grassland type, *Themeda* tussocks form a dense sward around 15–20 cm in height with little bare ground (< 10%). The ‘Open’ type (Group 6 in McIntyre et al. 2010) is found on poorer soils and is dominated by wallaby grass (*Rytidosperma* sp., previously named *Austrodanthonia),* which tends to form a shorter and more open grassland (5–10 cm tall and 30–40% bare ground). Bettongs have been observed digging frequently in both grassland types, typically targeting roots and tubers. We hypothesised that digging in the dense grassland would have a stronger positive effect on seedling germination due to the creation of gaps in the grass canopy.

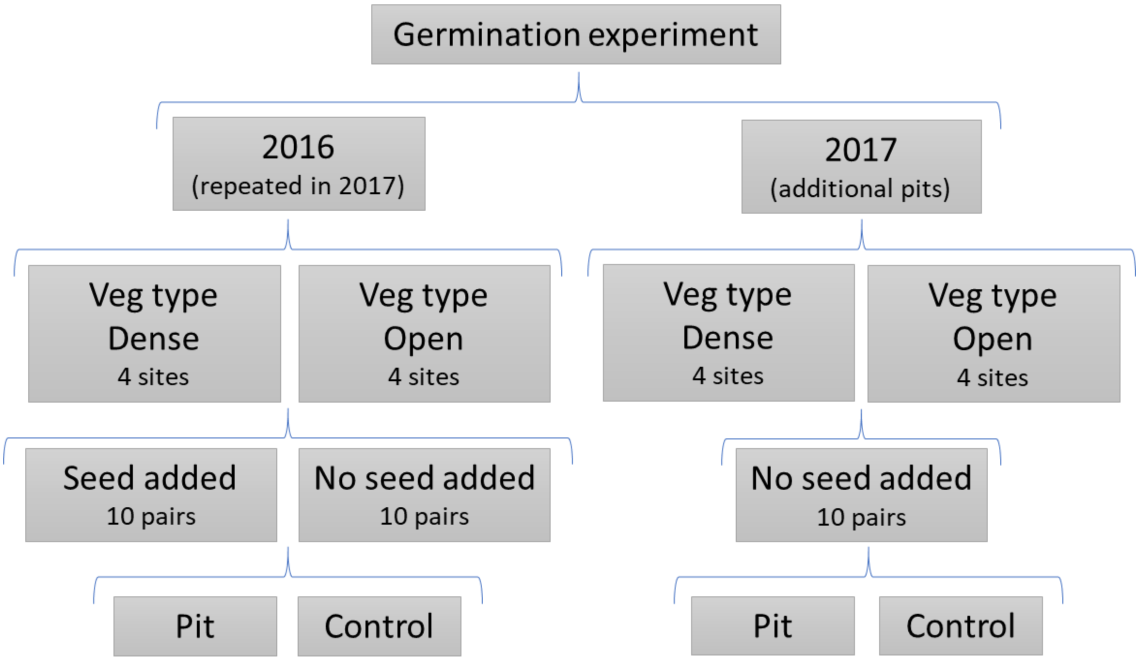


Figure 1. *Diagram of the experimental design, comparing digging pits to controls (i.e., undisturbed surface), with and without seed addition, in two different vegetation types over 2 years*

4.3.4 Experimental design

We chose eight sites, with four in each of the two grassland types (Fig. 1). At each site, we marked 20 bettong pits with a peg. Pits were selected randomly across the site, and were only chosen if they appeared to be relatively fresh (spoil heap still moist and loose, no infill or seedlings present). Next to each pit, approximately 30 cm away, we marked an equivalent control plot with similar properties to the area that had been dug, i.e., if the pit was next to a large grass tussock, the control was also placed in a similar position relative to a tussock (Fig. S2). Several studies have examined the influence of the mound or spoil heap created by digging or burrowing (Pyrke 1994; Eldridge and Simpson 2002; Eviner and Chapin 2003; Valentine et al. 2018). However, the soils at our site are highly dispersible and the spoil heap rapidly erodes, becoming difficult to monitor. For this reason we did not assess the spoil heap but chose to focus on the effects of the pit itself.

We predicted that seed limitation would result in low numbers of seeds of native species reaching the digs created by foraging bettongs. To control for differences in natura seed availability and ensure that the effect of digging would be measurable, we added see of seven native forb species to half (10) of the pit/control pairs within each site (Table 1). The species were chosen to represent a range of ecological preferences, and were all local native species of conservation interest. All seed was of local provenance (within 20 km), either collected within the reserves or sourced from a local native seed supplier (Greening Australia). Thirty seeds of each species were added to both the pit and the paired undisturbed control plot. To prevent the seeds from washing or blowing away, they were pressed lightly into the soil surface but left uncovered to replicate natural seed fall.

In the first year, we monitored 160 pits and their paired controls. The pits were marked and seeds added in May 2016, following a significant rain event. In November 2016, we measured the dimensions of the pits and counted all seedlings that had emerged, identifying all seedlings to species where possible. We used a metal ring of similar size to the digs (diameter 75 mm, area 44.2 cm^2) to define the control areas. The rings were aligned with the marker tags to ensure placement in a consistent location (Fig. S3). Occasionally, a plot could not be measured due to unplanned disturbance, such as trampling by kangaroos or further digging by bettongs, so these plots (and their pair) were excluded from analysis.

The first year of the study (2016) was conducted in unusually wet conditions, 240 mm (37%) above average for the year (Fig. S1). Many of the sites experienced waterlogging, and the results were likely to be atypical. For this reason, in May of the following year (2017) we marked an additional ten fresh pit/control pairs at each of the eight sites (n = 80). No seeds were added to these pits. In November 2017 we repeated the survey of seedlings in both the original (2016) and new (2017) pits (n = 240 total), counting and identifying all seedlings. In the case of the original pits, we counted all individuals that had germinated or established since the pits were created, because it was not always possible to distinguish between new seedlings and those that had germinated in the previous year.

Table 1: *Native forb species used for seed addition*

Family	**Species**	**Life form**
Asteraceae	*Stuartina muelleri*	Annual
	Vittadinia muelleri	Perennial
	Xerochrysum viscosum	Perennial
Campanulaceae	*Wahlenbergia multicaulis*	Perennial
Liliaceae	*Wurmbea dioica*	Perennial, geophyte
	Bulbine bulbosa	Perennial, geophyte
Plantaginaceae	*Plantago varia*	Perennial

4.3.5 Data analysis

Bettong foraging pits varied in size, and this meant they each had different potential to accommodate seedlings. We therefore standardised the number of seedlings by the area of their respective pits. We estimated the area of each dig assuming an ellipse shape (π × width/2 × length/2), and divided by the area of the control (44.2 cm2). This was then multiplied by the number of seedlings to calculate a standardised number of seedlings per plot. We then calculated seedling abundance for all species (including sown species), native species (not including sown), exotic species, and sown species only. Seedlings that could not be identified were included in the total seedling abundance, but not in any other groups.

We used Linear Mixed Models to quantify the effects of bettong foraging pits on seedling abundance. As the data had been standardised to account for differences in plot size, count data did not follow a Poisson distribution (which requires integer values). We checked model residuals and noted that they satisfied the assumption of normality. A summary of the data, response variables and formulae used for each model can be found in Table 2. We used Genstat (VSN International 2015) for all analyses and plotting.

Our overall question was whether bettong foraging pits provided a favourable habitat for the germination and survival of seedlings compared with undisturbed ground. To answer this question, we first examined only the original set of plots established in 2016 and monitored over 2 years (2016 and 2017). The response variable was total seedling abundance. The fixed effects were:

- *Treatment*—two-level factor (Pit or Control), tests for the effect of digging with respect to a paired control (surface);
- *Seed addition*—two-level factor (Seeded or Not), tests for the difference between plots with seed sown and those without;
- *Vegetation type*—two-level factor (Dense or Open), tests for the variation due to vegetation type;
- *Year*—two level factor (2016 or 2017), tests for the difference between years.

We used Block (paired pit and control) nested within Site as random effects to control for spatial correlation and repeat measures. We were interested in the overall effect of treatment, and any interactions with the other fixed effects. We ran a full interaction model, and reported all main effects and interactions for each response variable.

We then excluded the sown plots to look at natural germination only, and split the data into native and exotic species to examine their responses separately. The response variables were native seedling abundance, and exotic seedling abundance. We then looked at the responses for the planted species in the sown plots, both combined and for each species individually.

We then examined the data collected from the new plots marked in 2017. No seed was added to these pits, so the data represent natural germination only. The response variables were native seedling abundance, and exotic seedling abundance.

Table 2. *Summary of the data, response variables and formulae used for linear mixed models.*

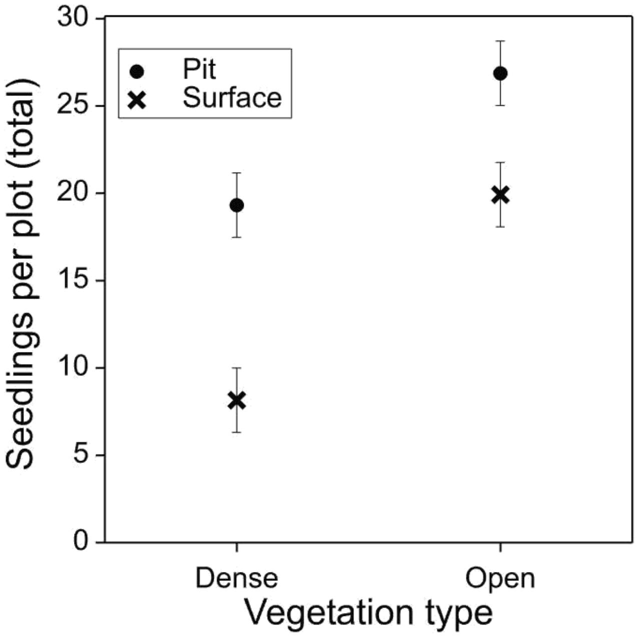
Data	Response	Full model
Original plots 2016/2017		
All plots **n = 160** **(pit + control)**	All species Abundance	Response ~ Treatment * Grassland type * Seed addition * Year (Site/Block)
Not-sown plots only **n = 80** **(pit + control)**	Native species Abundance	Response ~ Treatment * Grassland type * Year (Site/Block)
	Exotic species Abundance	Response ~ Treatment * Grassland type * Year (Site/Block)
Sown plots only **n = 80** **(pit + control)**	Planted species Abundance	Response ~ Treatment * Grassland type * Year (Site/Block)
	Bulbine bulbosa abundance	Response ~ Treatment * Grassland type * Year (Site/Block)
	Plantago varia abundance	Response ~ Treatment * Grassland type * Year (Site/Block)
New Plots 2017		
All plots **n = 80** **(pit + control)**	All species Abundance	Response ~ Treatment * Grassland type (Site/Block)
	Native species Abundance	Response ~ Treatment * Grassland type (Site/Block)
	Exotic species Abundance	Response ~ Treatment * Grassland type (Site/Block)

4.4 ***Results***

In total, 89 plant species were recorded across all sites and treatments (not including sown species) (Table S1, see supplementary materials). Of these, there were 49 native species and 40 exotics. Fourteen species were only recorded in bettong pits, of which 12 were native (2 exotic), and 8 were only found in the control plots (3 native, 5 exotic) (Table S2). The Dense (*Themeda*) grassland had 71 species, 19 of which were only found in that vegetation type (13 native, 6 exotic), while Open (*Rytidosperma*) had 70 species and 18 unique species (10 native, 8 exotic). Sixteen species were only recorded in 2016 (8 native, 8 exotic), and 2017 had 28 unique species (14 native, 14 exotic). The most common species were annual exotic grasses: *Aira elegantissima* and *Vulpia* spp., followed by *Juncus capitatus*, an annual exotic sedge.

Of the sown species, all seven were recorded at least once, but two species were more successful than the others: *Plantago varia* (recorded in 119 plots) and *Bulbine bulbosa* (97 plots). Only three of the planted species were recorded in non-seeded plots, and then only rarely (*Wahlenbergia* × 3 plots, *Wurmbea* × 3 and *Vittadinia* × 1).

__Figure 2.__ Total seedling abundance in bettong foraging pits with paired controls (surface) over 2 years (2016–2017), showing interaction between treatment (pit/surface) and vegetation type (Dense/Open). Predicted means shown with standard errors calculated using linear mixed models



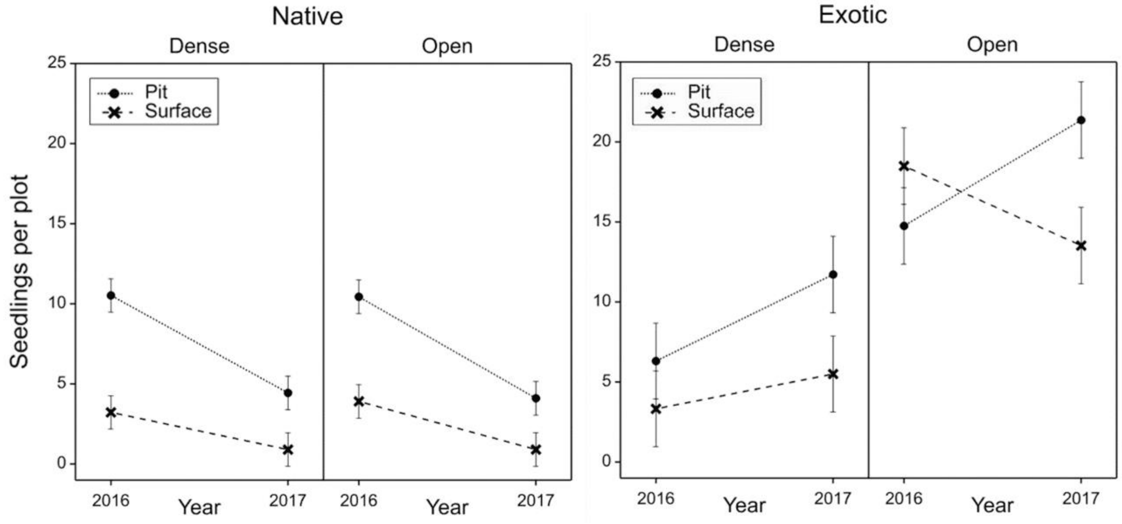


__Figure 3.__ Seedling abundance for native and exotic seedlings in bettong foraging pits with paired surface controls (non-seeded plots only), over 2 years (2016–2017). Pits were located in two grassland types, ‘Dense’ and ‘Open’. Predicted means shown with standard errors calculated using linear mixed models.

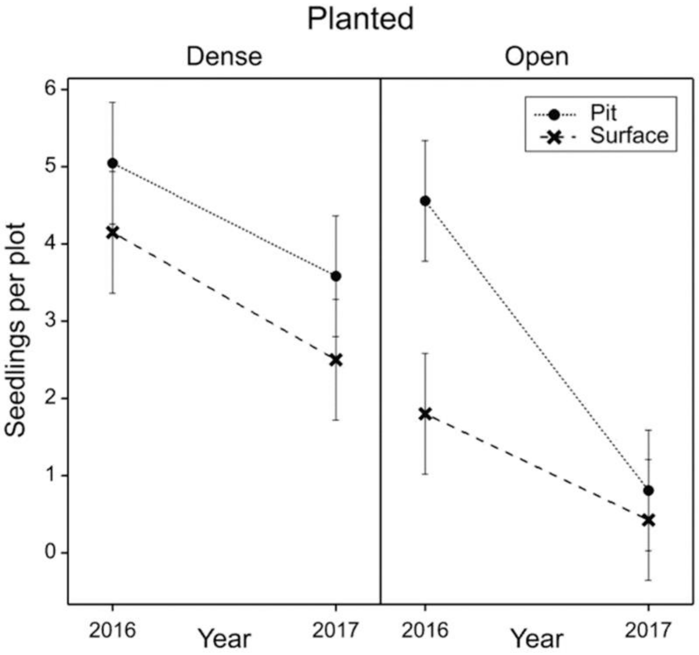
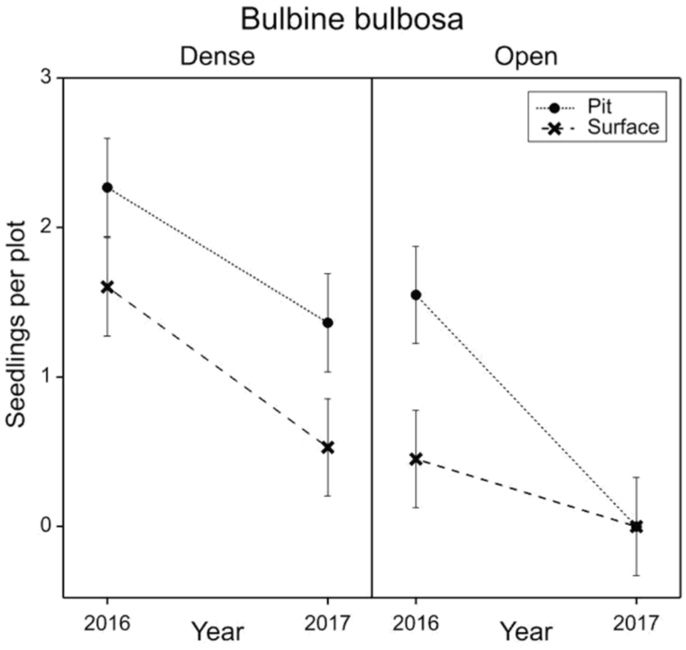


***Figure 4.** Seedling abundance for seven sown forb species (combined total) in bettong foraging pits with paired surface controls (sown plots only), over 2 years (2016–2017). Pits were located in two grassland types, 'Dense' and 'Open'. Predicted means shown with standard errors calculated using linear mixed models*

***Figure 5.** Seedling abundance of planted species Bulbine bulbosa in bettong foraging pits with paired surface controls (sown plots only), over two years (2016-2017). Pits were located in two grassland types, 'Dense' and 'Open'. Predicted means shown with standard errors calculated using linear mixed models.*



The results of the Linear Mixed Models are summarised in Table S3. When we compared the original set of pits over the 2 years of the study, we found that pits contained nearly twice the number of seedlings on average compared with the control plots (23 seedlings vs 14) ($p < 0.001$). There was a marginally significant interaction between treatment and grassland type ($p = 0.06$); while there were more seedlings overall in the open grassland ($p = 0.01$), the difference between pits and controls was greater in the dense grassland (see Fig. 2). Between the first and second year the total number of seedlings declined significantly ($p < 0.001$), regardless of whether they were in a pit or control plot. Seed addition also significantly increased the number of seedlings ($p = 0.03$).

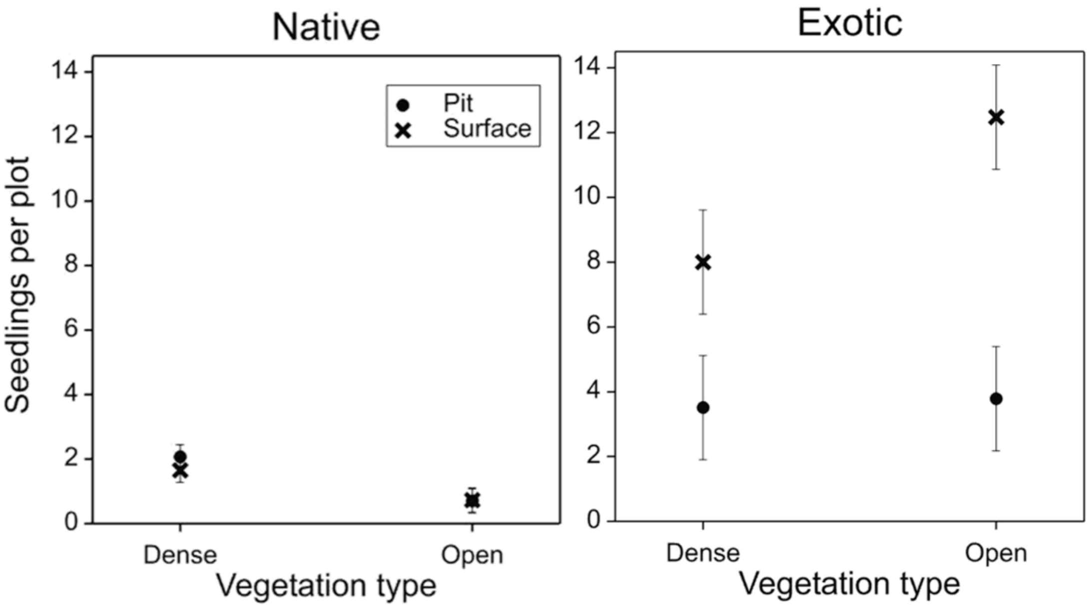


Figure 6. *Seedling abundance for native and exotic seedlings in bettong foraging pits with paired surface controls, for new pits established in 2017. Pits were located in two grassland types, 'Dense' and 'Open'. Predicted means shown with standard errors calculated using linear mixed models.*

Figure 3 shows the interaction between treatment, grassland type and year for native and exotic seedling abundance (natural germination in non-seeded plots only). For native species, digging increased the abundance of seedlings ($p < 0.001$), and there was a significant interaction between treatment and year ($p = 0.01$). There was no difference between the grassland types, but there were significantly fewer seedlings in the second year ($p < 0.001$). For the exotic species, the impact of digging on seedling abundance was moderated by year ($p = 0.01$), with a larger increase (compared to the control) in the second year. There were significantly more exotic seedlings in the open grassland ($p = 0.01$), but there was no interaction of grassland type with other variables. Interestingly, in 2016 the pits had slightly fewer exotic seedlings than the controls in the open grassland, however in 2017 this effect had reversed resulting in an increase in exotic seedlings in pits compared to controls.

For the planted species (sown plots only), there were significantly more seedlings in the pits ($p = 0.003$), and in the first year compared with the second year ($p < 0.001$), but there was no difference between grassland types (Fig. 4). Only two species had enough seedlings to be analysed separately: *Bulbine bulbosa* and *Plantago varia* (results in Table S3). Of these, only *B. bulbosa* had a significant (positive) response to bettong digging ($p = 0.002$), and grassland type ($p = 0.03$), with more seedlings in the dense grassland (Fig. 5). Both *B. bulbosa* and *P. varia* declined between the sampling years. We then looked at the new plots established in 2017, to compare the responses of seedlings in new pits under different climatic conditions (Fig. 6). Contrary to the results in the first year, pits had significantly fewer seedlings overall compared to the controls (p

< 0.001). However, this was largely driven by the exotic species as very few native seedlings germinated. For the native species, there was no difference due to treatment, but there were fewer seedlings in the open grassland (p = 0.03). For the exotics, there was a marginally significant interaction between treatment and grassland type, with a stronger negative effect of digging in the open grassland (p = 0.07).

4.5 ***Discussion***

We set out to test whether foraging pits of the eastern bettong provided a favourable site for germination and survival of seedlings in a temperate grassy woodland. We found that overall, bettong foraging pits had more seedlings than undisturbed areas. However, the effect was moderated by vegetation type, climatic conditions, plant species and seed limitation.

Our finding that pits increased seed germination was consistent with studies conducted on many different soil-foraging and burrowing animals around the world. In the Negev desert, porcupine (*Hystrix indica*) pits are important sites for seed germination, with pits containing up to 91% of all seedlings in a given area, and increasing survival (Gutterman and Herr 1981). Cape porcupine (*Hystrix africaeaustralis*) foraging pits also significantly in bluebell germination following rooting by wild boar. A recent global meta-analysis found that digging animals significantly increased plant recruitment, and attributed this to increased nutrient levels (Mallen-Cooper et al. 2019). However, most of these studies were conducted in arid areas, and very few have looked at temperate ecosystems or compared the responses of native and exotic species. Our study therefore provides some insights into the role of soil-foraging animals as ecosystem engineers and for restoration of temperate ecosystems.

4.5.1 Vegetation type

We predicted that the bettong foraging pits would increase the number of seedlings by creating gaps in the grass canopy, resulting in a greater benefit in the dense (*Themeda*) grassland. We found that while the dense grassland had fewer seedlings overall, the positive effect of digging was marginally stronger (Fig. 2). This suggests that the dense grass canopy normally suppressed germination, and the pits were able to open the canopy and provide those gaps. On the other hand, the open (*Rytidosperma*) grassland had significantly more exotic seedlings, perhaps because there was already a higher percentage of bare ground (Fig. 3). Surprisingly, the exotic species did not initially have the same positive response to the digging, resulting in a smaller effect in the open grassland overall (discussed further below).

Digging animals have been shown to be important for creating gaps and bare ground, which stimulates germination and establishment of many plant species. In North American alpine meadows, grizzly bears (*Ursus arctos horribilis*) digging for glacier lilies (*Erythronium grandiflorum*) create areas of bare soil, providing a germination niche for the glacier lily’s seeds (Tardiff and Stanford 1998). Martinsen et al. (1990) studied a shortgrass prairie community, and found that pocket gopher (*Thomomys bottae*) disturbances created gaps in the closed grass canopy that were colonised by herbaceous perennial dicots, which otherwise would be outcompeted by the dominant grass. In both these cases, animal disturbances were the primary source of bare ground, similar to the dense grassland type in our study.

4.5.2 Climatic conditions

Climatic conditions are also likely to be an important factor influencing seedling responses to disturbance (Hobbs and Mooney 1991). Depressions created by animals can capture runoff and increase infiltration, and provide protection from extremes of temperature (Laundre 1993; James et al. 2010; Ross et al. 2019). We therefore predicted that bettong pits would provide a more favourable microclimate and retain moisture, protecting seedlings from hot and dry conditions. Our study was conducted over 2 years, which experienced very different climatic conditions (Fig. S1). However, the first year of our study experienced one of the wettest winters on record, with some sites becoming inundated. While the pits did provide a significant benefit for seedling germination, we can conclude that this was not due to the amelioration of harsh conditions as we had predicted.

The following year, rainfall was well below average over the winter period. We resurveyed the original set of pits to look at survival and germination as the pits filled in over time, but also decided to add a new set of fresh pits, which allowed an interesting comparison between wet and dry years, and between 1-year-old and fresh pits experiencing the same dry conditions. Some of the variation in seedlings between years was probably not due to climatic differences, however, we can still make some valuable inferences from the comparison. Over the 2 years of the study, there was a clear decrease in the total number of seedlings between the first and second year (Fig. 3), and fewer seedlings germinated in the fresh pits established in 2017 compared to 2016 (Fig. 6). Unlike the first year, in the new pits (established in 2017), the effect of digging on total seedling abundance was negative overall. This was largely driven by exotic annuals, because very few natives germinated (see below). However, in the old pits that were established in the previous wet year, the effect of digging remained positive. This was mostly driven by a strong positive effect on exotic species, but also in part due to an increase in natives. This suggests that the pits may have increased survival of native species that germinated in the previous wet year, allowing them to persist into the dry year while new seedlings were unable to germinate.

As mentioned previously, we did not have separate counts for plants established in the first and second years because the age of the perennials could not always be determined. Seedling emergence is discontinuous throughout the year and cotyledons may not be evident at the time of counting if the plants germinated months before assessment. Native perennials can be very slow growing and second-year plants may be very small, with greater investment in roots than shoots. In addition, geophytes such as *Bulbine bulbosa* die back to underground storage organs during the summer, and when they emerge, only by excavating the roots can seedlings be reliably identified. For these reasons, our judgement is that self-thinning amongst perennials was not likely to be occurring, although there may have been some competition between annual species in both years.

In addition to inter-annual climatic variation, this study also provides some insight into the mechanisms driving responses to animal digging across environmental gradients. The positive effects of digging are usually attributed to the creation of resource ‘hotspots’ by collecting organic material and moisture, as well as providing a more mesic microclimate (James et al. 2009, 2010). However, several recent studies have found that these effects are less pronounced in higher rainfall areas, where the climatic conditions and availability of nutrients are not as limiting (Mallen-Cooper et al. 2019; Decker et al. 2019). Instead, competition and predation are likely to be the limiting factors in these environments (Menge and Sutherland 2002), so ecosystem engineers that are able to alleviate these pressures will be vital for maintaining heterogeneity and diversity (Crain and Bertness 2006).

In our temperate grassland system, we previously found that artificial bettong pits mediate daily extremes of temperature, but did not have a clear effect on nutrient levels (Ross et al. 2019). As mentioned above, in this study we have shown that digging had a stronger effect in dense grasslands, suggesting that competition was important for the establishment of native forbs. Similarly, Cushman et al. (2004) concluded that increased germination in pig disturbances was due to space clearing and reduced competition rather than changed soil conditions. The removal of litter has also been shown to increase recruitment of native forbs in a grassland within 20 km of our study site (Johnson et al. 2018). Our findings provide evidence to support the hypothesis that in benign or mesic environments, the role of ecosystem engineers is to reduce competition rather than ameliorate harsh conditions or provide resources (Crain and Bertness 2006). Nonetheless, climate variability in this biome is high and it is conceivable that foraging pits could provide a moister, more favourable microsite for seedling establishment in some seasons.

4.5.3 Species: native vs exotic

Plant species are likely to respond differently to disturbance, and many studies have found that animal digging can alter plant species diversity and relative abundance, leading to changes in the overall composition of the plant community (Hobbs and Mooney 1985; Gómez-Garcia et al. 1995; Sherrod et al. 2005; Gálvez-Bravo et al. 2011; Hagenah and Bennett 2012; Louw et al. 2017; Lindtner et al. 2018). For example, a study in the Chihuahuan desert found that Gunnison’s prairie dogs (*Cynomys gunnisoni*) and banner-tailed kangaroo rats (*Dipodomys spectabilis*) had distinct effects on plant species assemblages and vegetation structure, and increased landscape heterogeneity (Davidson and Lightfoot 2008). Several studies have suggested that animal digging may increase invasion by exotic species, because many of them are associated with recent disturbance (Milton et al. 1997; Larson 2003). Kurek et al. (2014) found that burrows created by the European badger (*Meles meles*) and the red fox (*Vulpes vulpes*) were dominated by short-lived ruderal species.

We predicted that the disturbance created by digging would have a greater positive effect on exotic species. We found that bettong pits supported a different suite of species than the undisturbed control plots. Of the 89 species we recorded, 14 were only found in pits, of which 12 were natives. Surprisingly, although there were fewer native seedlings overall, the positive effect of digging was stronger for native species, and in some cases the digging had a negative effect on the abundance of exotics (Figs. 3 and 6). However, while initially there was a neutral or negative effect on exotic seedling abundance in fresh pits in both years, there was an increase in exotic abundance in old pits (Fig. 3). The reason for this delayed response is unclear.

While disturbance can lead to weed invasion, this is not always the case. Rooting by feral pigs (*Sus scrofa*) benefitted both native and exotic species in meadows in northern California, and the early colonisers were largely native annuals (Kotanen 1995). Johnson et al. (2018) found that native forbs responded more strongly to the removal of litter compared with exotic species. Several studies have found that fertilisation may be more important for exotic species, particularly in nutrient-poor soils (Hobbs and Atkins 1988; Hobbs et al. 1988). Hobbs et al. (1988) found that fertilisation of a grassland community increased the biomass of annual grasses and led to the suppression of native forbs, but subsequent gopher (*Thomomys bottae*) disturbance removed the grass and allowed native forbs to re-establish. Several studies have found that foraging pits have increased levels of nutrients and organic matter, particularly in arid areas (Mallen-Cooper et al. 2019). However, a previous study in the same ecosystem as ours did not find any consistent effects on soil nutrients in artificial bettong pits (Ross et al. 2019). This may partly explain why the annual exotic species did not respond as we expected.

The positive response of native species, particularly in the wet year (2016), could in part be explained by the fact that the most abundant native species tended to be annuals, and those that prefer moist sites (e.g., *Isolepis hookeriana*, *Montia fontana*, *Schoenus apogon*, *Juncus bufonius)*. We observed that at particularly wet sites, some pits were filled with water for up to several weeks, and these species are likely to have benefitted from both the disturbance and the wet conditions. The same seasonal inundation may have disadvantaged the exotic species by disrupting their germination opportunities. It is also possible that native species have evolved specific adaptations to digging by native animals. For example, Larson (2003) found that 'natural' disturbances created by prairie dogs (*Cynomys ludovicianus*) increased the species richness of both exotic and native weedy species, while roadways were dominated by exotic species.

4.5.4 Seed addition

We found a significant positive effect of seed addition on the total number of seedlings across all treatments. However, in the sown plots, planted species only accounted for around 20% of all seedlings, and the rest germinated from naturally occurring seed. While seed addition increased the total number of seedlings per plot, there was no evidence for competition with natural germination, i.e., there was no difference in the number of natural seedlings between sown and unsown plots.

While many of the naturally occurring seedlings were native, the seven species we selected for seed addition were almost never found where they had not been sown, even though they have all been recorded within the sanctuary. It is possible that those particular species are seed limited, and may not be able to take advantage of the digging without the addition of seed. While the overall effect of digging was positive (Fig. 4), each species is likely to respond differently to the presence of digging; only *Bulbine bulbosa* showed a significant positive response (Fig. 5), while *Plantago varia* was equally successful in the control plots. Furthermore, some of the planted species did not do as well as others, suggesting that there may be other limiting factors for those species such as low seed viability. However, this should not influence the response of those species to the presence of digging, only our ability to detect those differences.

4.5.5 Limitations and further research

This study looked at seedling germination and survival over 2 years, and assessed early establishment rather than reproductive success or long-term survival. The 2 years encompassed strong differences in climatic conditions, resulting in strong seasonal differences in seedling abundance and species composition. Our results do suggest that in wet years, bettong digging may provide a site for native species to germinate, and that those seedlings were able to persist in the following dry year when very little was able to germinate. While it is clear from this study that bettong foraging pits provide a favourable site for seed germination, the mechanisms driving this effect are still unclear. We still do not know exactly what aspect of digging provides the benefit, and in what context, particularly for the native species. While we have some indication that the reduction of competition and creation of gaps is important for some species, other factors may include microclimatic effects (Eldridge and Mensinga 2007), protection from seed predators or herbivores (Radnan and Eldridge 2017), removal of the soil crust (Li et al. 2005; Deines et al. 2007), or dispersal of ectomycorrhizal fungi (Nuske et al. 2017).

Faunal reintroductions are expensive, difficult to manage, and may not be feasible in many cases—for example, where introduced predators cannot be controlled. In areas where digging animals are not present and reintroduction is not an option, it may be possible to replicate the effects by creating artificial disturbances. However, the mechanisms driving these effects are still unclear, and more research will be needed to test whether artificial disturbances can replicate natural pits, and how to implement this on a large scale.

4.5.6 Implications for restoration and management

Many of the soil-foraging or digging animals that play an important role as ecosystem engineers in Australian ecosystems are now lost from most of their original range, restricted to island refuges or entirely extinct (Legge et al. 2018). It is vital that we investigate their ecological roles and prioritise their conservation in areas where they continue to survive. While there have been many reintroductions of digging animals for conservation purposes, there is often little consideration of their effects on the recipient ecosystem, and their potential as tools for restoration is generally only an afterthought in management plans. In addition, managers need information on the potential for undesired or negative consequences so they can monitor and manage these effects.

Our results show that bettong foraging pits can have a positive effect on seedling germination and survival, particularly for native plant species. We suggest that this is largely due to a reduction in competition and the creation of gaps in the grass canopy providing a germination niche for gap-sensitive forb species. Bettong pits supported a different suite of species to the undisturbed soil surface, and over time this may lead to a significant change in the composition of the plant community (Kurek et al. 2014). This may be an effective way to increase heterogeneity and diversity in relatively high-quality grasslands and grassy woodlands, where invasive restoration techniques such as scalping are not appropriate.

While exotic plants did not colonise pits as quickly as we expected, under certain conditions the disturbance may lead to an increase in weed abundance. Management of exotic species, particularly annual grasses, may be required at sites where they are already present. Further, introducing a digging species on its own is unlikely to result in an immediate increase in native forb diversity because many species are seed-limited (either due to low seed production, viability, dispersal, or complete absence from the seed bank). Combining natural or artificial disturbances with seed addition could increase success for some plant species, as long as sufficient seed can be collected or grown in seed production areas.

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Author contributions

AM, SC and SM conceived the overall conceptual framework for the project. CR and SM conceived the ideas and designed methodology. CR and SM collected the data. CR, SM, PB and ME analysed the data. CR led the writing of the manuscript. SM, PB, ME, SC and AM provided advice and edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Chapter 4: Supplementary material

Figure S1. Monthly rainfall (in mm) totals for Canberra over the experimental period

Figure S2. Diagram of a bettong foraging pit with paired control, in cross section

Figure S3. A bettong foraging pit (left) and paired control plot (right) with germinating seedlings visible

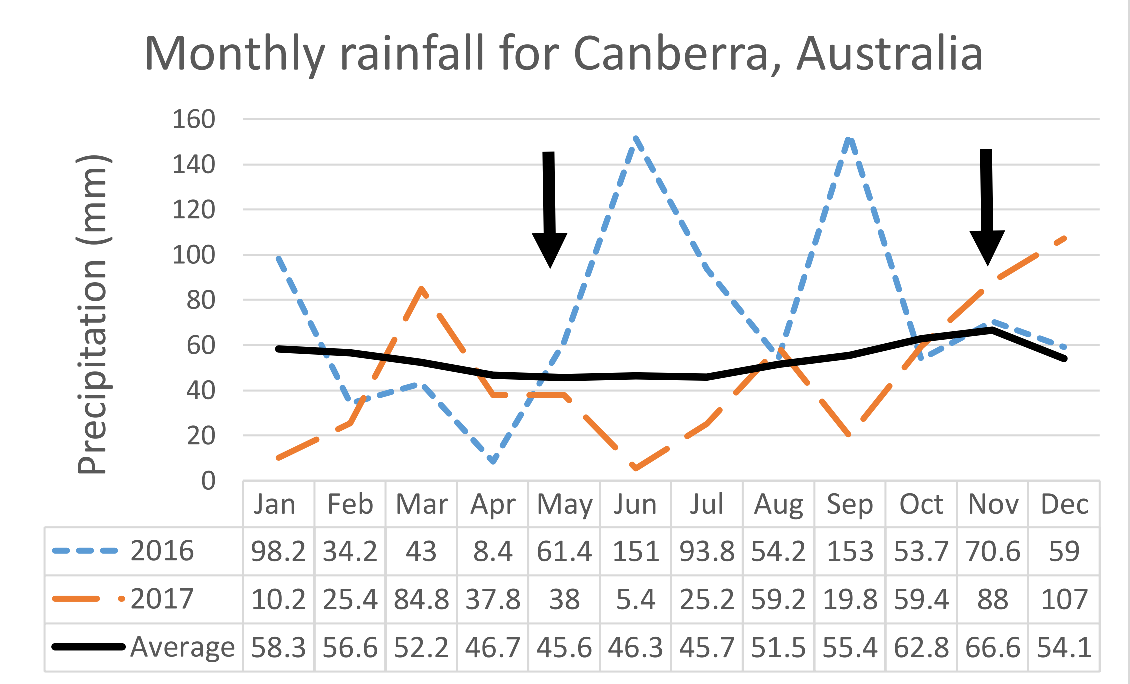
Table S1. Species list of all seedlings recorded in bettong pits and control plots

Table S2. Number of species (total, native, exotic) recorded by treatment, vegetation type and year

Table S3. Summary of results of linear mixed models. Significant results ($p<0.05$) are in bold.

Table S4. Summary of results of linear mixed models. Significant results ($p<0.05$) are in bold.

Figure S1. *Monthly rainfall (in mm) totals for Canberra over the experimental period (2016-2017) compared with the long-term average (1935-2017). Plots were marked in May, and sampling was conducted in November of each year (indicated with an arrow). Data sourced from the Australian Government Bureau of Meteorology (http://www.bom.gov.au/) 'Ainslie Tyson St' weather station no. 070000.*



	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2016	98.2	34.2	43	8.4	61.4	151	93.8	54.2	153	53.7	70.6	59
2017	10.2	25.4	84.8	37.8	38	5.4	25.2	59.2	19.8	59.4	88	107
Average	58.3	56.6	52.2	46.7	45.6	46.3	45.7	51.5	55.4	62.8	66.6	54.1

Figure S2. *Diagram of a bettong foraging pit with paired control, in cross section. Studied foraging pits were randomly selected from fresh bettong pits. Matching control sites were placed approximately 30cm away in an equivalent undisturbed site.*

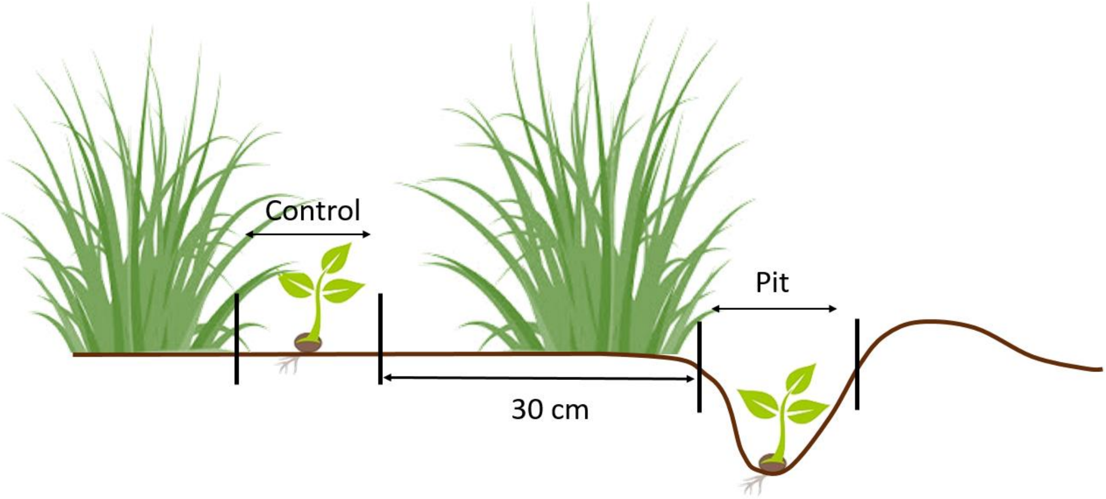


Figure S3. *A bettong foraging pit (left) and paired control plot (right) with germinating seedlings visible. A metal ring was used to define the area of the control plot.*

Table S1. *Species list of all seedlings recorded in bettong pits and control plots. Plots were located in two vegetation types (dense and open). For each species we have also recorded the origin (planted, native or exotic), life cycle (perennial or annual).*

Species name	***Origin***	***Life Cycle***	***Monocot/ Dicot***	***# Plots***	***# Individuals (standardised)***	***Veg Type (Dense/Open)***	***Year***	***Pit/Control***
Bulbine bulbosa	Planted	Perennial	Monocot	97	305.62	Both	Both	Both
Plantago varia	Planted	Perennial	Dicot	119	425.64	Both	Both	Both
Stuartina muelleri	Planted	Annual	Dicot	6	20.88	Both	Both	Both
Vittadinia muelleri	Planted	Perennial	Dicot	9	11.05	Both	Both	Both
Wahlenbergia multicaulis	Planted	Perennial	Dicot	24	59.44	Both	Both	Both
Wurmbea dioica	Planted	Perennial	Monocot	20	29.33	Both	2016	Both
Xerochrysum viscosum	Planted	Perennial	Dicot	29	62.65	Both	Both	Both
Achaena ovina	Native	Perennial	Dicot	6	6.97	Both	Both	Both
Aphanes australiana	Native	Annual	Dicot	5	4.95	Both	Both	Both
Asperula conferta	Native	Perennial	Dicot	20	31.63	Both	Both	Both
Bothriochloa macra	Native	Perennial	Monocot	2	4.69	Open	2017	Both
Carex inversa	Native	Perennial	Monocot	5	13.76	Both	2016	Both
Centipeda cunninghamii	Native	Perennial	Dicot	1	1.00	Dense	2017	Pit
Cheilanthes sieberi	Native	Perennial	Dicot	1	0.59	Dense	2016	Both
Chloris truncata	Native	Perennial	Monocot	1	1.00	Open	2017	Control
Coronidium scorpioides	Native	Perennial	Dicot	37	82.21	Dense	Both	Both
Crassula sieberiana	Native	Perennial	Dicot	7	18.32	Both	2016	Both
Cymbonotus lawsonianus	Native	Annual	Dicot	2	4.69	Open	2017	Pit
Cynoglossum australe	Native	Perennial	Dicot	2	1.74	Both	2017	Pit
Daucus glochidiatus	Native	Annual	Dicot	5	6.02	Dense	2017	Both
Desmodium varians	Native	Perennial	Dicot	4	6.76	Both	Both	Both
Dichelachne sp.	Native	Perennial	Monocot	1	0.64	Dense	2017	Pit
Drosera peltata	Native	Perennial	Dicot	30	44.37	Both	Both	Both
Elymus scaber	Native	Perennial	Monocot	3	2.68	Open	2017	Both
Eryngium ovinum	Native	Perennial	Dicot	1	2.01	Open	2017	Pit
Epilobium gunnianum	Native	Perennial	Dicot	1	1.34	Open	2017	Pit
Euchiton japonicus	Native	Perennial	Dicot	98	197.31	Both	Both	Both
Gonocarpus tetragynus	Native	Perennial	Dicot	16	26.33	Both	Both	Both
Goodenia pinnatifida	Native	Perennial	Dicot	5	6.17	Open	Both	Both
Haloragis heterophylla	Native	Perennial	Dicot	129	259.15	Both	Both	Both
Hydrocotyle laxiflora	Native	Perennial	Dicot	8	21.79	Dense	Both	Both
Hypericum gramineum	Native	Perennial	Dicot	154	692.68	Both	Both	Both
Isolepis hookeriana	Native	Annual	Monocot	85	556.62	Both	2016	Both
Isotoma fluviatalis	Native	Perennial	Dicot	2	3.98	Dense	2017	Pit
Juncus bufonius	Native	Annual	Monocot	36	81.35	Both	Both	Both
Juncus sp.	Native	?	Monocot	2	3.56	Both	2016	Both
Leptorhynchos squamatus	Native	Perennial	Dicot	31	55.31	Both	Both	Both
Lomandra multiflora	Native	Perennial	Monocot	1	1.00	Dense	2016	Control
Luzula densiflora	Native	Perennial	Monocot	27	45.13	Dense	Both	Both
Lythrum hyssopifolia	Native	Annual	Dicot	32	137.74	Both	Both	Both
Mentha diemenica	Native	Perennial	Dicot	1	4.82	Open	2017	Pit

Microtis unifolia	Native	Perennial	Monocot	1	1.34	Dense	2016	Pit
Montia fontana	Native	Annual	Dicot	84	364.26	Both	Both	Both
Oxalis perennans	Native	Perennial	Dicot	11	15.98	Both	Both	Both
Panicum effusum	Native	Perennial	Monocot	16	17.79	Open	Both	Both
Pentapogon quadrifidus	Native	Annual	Monocot	1	1.00	Dense	2017	Control
Ranunculus amphitrichus	Native	Perennial	Dicot	1	2.68	Dense	2016	Pit
Rytidosperma sp.	Native	Perennial	Monocot	18	30.21	Both	Both	Both
Schoenus apogon	Native	Annual	Monocot	102	283.46	Both	Both	Both
Sebaea ovata	Native	Annual	Dicot	4	7.54	Dense	Both	Pit
Solenogyne dominii	Native	Perennial	Dicot	10	15.13	Both	Both	Both
Themeda australis	Native	Perennial	Monocot	14	22.39	Both	Both	Both
Tricoryne elatior	Native	Perennial	Monocot	4	8.92	Both	Both	Both
Triptilodiscus pygmaeus	Native	Annual	Dicot	35	111.15	Both	Both	Both
Viola betonicifolia	Native	Perennial	Dicot	1	1.57	Open	2017	Pit
Wahlenbergia sp.	Native	Perennial	Dicot	12	22.88	Both	Both	Both
Aira elegantissima	Exotic	Annual	Monocot	370	2399.49	Both	Both	Both
Acetosella vulgaris	Exotic	Perennial	Dicot	2	3.34	Both	2017	Both
Briza major	Exotic	Annual	Monocot	14	53.13	Open	Both	Both
Briza minor	Exotic	Annual	Monocot	223	792.55	Both	Both	Both
Bromus hordeaceus	Exotic	Annual	Monocot	79	287.37	Both	Both	Both
Centaurium sp.	Exotic	Annual	Dicot	89	234.43	Both	Both	Both
Cicendia quadrangularis	Exotic	Annual	Dicot	18	26.67	Both	2016	Both
Cirsium vulgare	Exotic	Annual	Dicot	1	1.56	Dense	2016	Pit
Conyza sp.	Exotic	Annual	Dicot	2	2.00	Dense	2017	Control
Galium divaricatum	Exotic	Annual	Dicot	96	329.46	Both	Both	Both
Gamochaeta americana	Exotic	Perennial	Dicot	11	13.69	Both	Both	Both
Holcus lanatus	Exotic	Perennial	Monocot	2	1.80	Dense	2017	Both
Hypochaeris sp.	Exotic	?	Dicot	32	55.56	Both	Both	Both
H. glabra	Exotic	Annual	Dicot	28	41.89	Both	2017	Both
H. radicata	Exotic	Perennial	Dicot	40	94.34	Both	2017	Both
Juncus capitatus	Exotic	Annual	Monocot	160	846.41	Both	Both	Both
Lactuca serriola	Exotic	Annual	Dicot	1	1.00	Dense	2016	Control
Linaria pelisseriana	Exotic	Annual	Dicot	37	61.45	Both	Both	Both
Linum trigynum	Exotic	Annual	Dicot	2	2.41	Open	2017	Both
Logfia gallica	Exotic	Perennial	Dicot	4	8.00	Open	Both	Control
Moenchia erecta	Exotic	Annual	Dicot	30	71.98	Both	2016	Both
Myosotis discolor	Exotic	Annual	Dicot	10	61.03	Both	2016	Both
Parentucellia latifolia	Exotic	Annual	Dicot	1	2.00	Open	2016	Control
Petrorhagia nanteuilii	Exotic	Annual	Dicot	4	6.11	Both	2017	Both
Plantago lanceolata	Exotic	Annual	Dicot	18	28.77	Both	Both	Both
Psilurus incurvus	Exotic	Annual	Monocot	4	35.00	Open	2016	Both
Silene gallica	Exotic	Annual	Dicot	1	2.00	Open	2016	Control
Sisyrinchium micranthum	Exotic	Annual	Dicot	19	41.85	Dense	2017	Both
Tolpis barbata	Exotic	Annual	Dicot	25	41.26	Both	Both	Both
Trifolium sp.	Exotic	Annual	Dicot	14	25.36	Both	2017	Both
T. arvense	Exotic	Annual	Dicot	37	57.55	Both	Both	Both
T. angustifolium	Exotic	Annual	Dicot	5	5.95	Open	2017	Both

T. campestre	Exotic	Annual	Dicot	69	198.00	Both	Both	Both
T. cernuum	Exotic	Annual	Dicot	1	0.78	Open	2017	Pit
T. dubium	Exotic	Annual	Dicot	58	180.04	Both	Both	Both
T. glomerata	Exotic	Annual	Dicot	32	51.25	Both	Both	Both
T. striatum	Exotic	Annual	Dicot	47	180.80	Both	2017	Both
T. subterraneum	Exotic	Annual	Dicot	28	45.17	Both	2017	Both
Veronica anagallis-aquatica	Exotic	Perennial	Dicot	3	46.80	Dense	2017	Both
Vulpia sp.	Exotic	Annual	Monocot	254	2160.70	Both	Both	Both

Table S2. *Number of species (total, native, exotic) recorded by treatment, vegetation type and year.*

	Number of species		
	Total	**Native**	**Exotic**
All sites	89	49	40
Treatment			
Pit	81	46	35
Pit only	14	12	2
Control	75	37	38
Control only	8	3	5
Both	67	34	33
Vegetation type			
Open	70	36	34
Open only	18	10	8
Dense	71	39	32
Dense only	19	13	6
Both	52	26	26
Year			
2016	61	35	26
2016 only	16	8	8
2017	73	41	31
2017 only	28	14	14
Both	45	27	18

Table S3. *Summary of results of linear mixed models. Significant results (p<0.05) are in bold.*

RESPONSE	MODEL TERMS	ABUNDANCE		
		Wald statistic	**n.d.f.**	**F pr**
ALL SPECIES (ORIGINAL PLOTS 2016/2017)	Treatment	64.14	1	**<0.001**
	Grassland type	12.35	1	**0.01**
	Seed addition	6.11	1	**0.03**
	Year	15.03	1	**<0.001**
	Treatment * Grassland type	3.46	1	**0.06**
	Treatment * Seed addition	0	1	0.96
	Grassland type * Seed addition	0.01	1	0.93
	Treatment * Year	0.28	1	0.59
	Grassland type * Year	1.06	1	0.30
	Seed addition * Year	1.87	1	0.17
	Treatment * Grassland type * Seed addition	0.04	1	0.84
	Treatment * Grassland type * Year	2.73	1	0.10
	Treatment * Seed addition * Year	0.76	1	0.38
	Grassland type* Seed addition * Year	0.15	1	0.70
	Treatment * Grassland type * Seed addition * Year	0.16	1	0.69
NATIVE SPECIES (ORIGINAL PLOTS 2016/2017, NOT SEEDED SITES ONLY)	Treatment	58.74	1	**<0.001**
	Grassland type	0	1	0.97
	Year	43.22	1	**<0.001**
	Treatment * Grassland type	0.18	1	0.68
	Treatment * Year	6.93	1	**0.01**
	Grassland type * Year	0.12	1	0.73
	Treatment * Grassland type * Year	0.03	1	0.87
EXOTIC SPECIES (ORIGINAL PLOTS 2016/2017, NOT SEEDED SITES ONLY)	Treatment	6.23	1	**0.01**
	Grassland type	11.67	1	**0.01**
	Year	3.01	1	0.08
	Treatment * Grassland type	0.9	1	0.34
	Treatment * Year	7.63	1	**0.01**
	Grassland type * Year	1.25	1	0.26
	Treatment * Grassland type * Year	2.45	1	0.12
PLANTED SPECIES (ORIGINAL PLOTS 2016/2017, SEEDED SITES ONLY)	Treatment	8.72	1	**0.003**
	Grassland type	3.6	1	0.11
	Year	22.57	1	**<0.001**
	Treatment * Grassland type	0.44	1	0.51
	Treatment * Year	1.61	1	0.21
	Grassland type * Year	1.34	1	0.25
	Treatment * Grassland type * Year	2.18	1	0.14
ALL SPECIES (NEW PLOTS 2017)	Treatment	25.46	1	**<0.001**
	Grassland type	0.28	1	0.61
	Treatment * Grassland type	3.62	1	**0.06**
NATIVE SPECIES (NEW PLOTS 2017)	Treatment	0.32	1	0.57
	Grassland type	7.51	1	**0.03**
	Treatment * Grassland type	0.4	1	0.53
EXOTIC SPECIES (NEW PLOTS 2017)	Treatment	33.73	1	**<0.001**
	Grassland type	1.08	1	0.34
	Treatment * Grassland type	3.43	1	0.07

Table S4. *Summary of results of linear mixed models. Significant results (p<0.05) are in bold.*

RESPONSE	MODEL TERMS	*BULBINE BULBOSA*			*PLANTAGO VARIA*		
		Wald statistic	**n.d.f.**	**F pr**	**Wald statistic**	**n.d.f.**	**F pr**
ABUNDANCE BY SPECIES ORIGINAL PLOTS 2016/2017, SEEDED ONLY	Treatment	9.90	1	**0.002**	1.45	1	0.23
	Grassland type	7.51	1	**0.03**	1.33	1	0.29
	Year	22.86	1	**<0.001**	9.21	1	**0.003**
	Treatment*Grassland type	0.22	1	0.64	0.65	1	0.42
	Treatment*Year	1.26	1	0.26	0.00	1	1.00
	Grassland type*Year	0.00	1	0.98	0.96	1	0.33
	Treatment*Grassland type*Year	2.31	1	0.13	0.48	1	0.49

Artist Interlude no. 4

Mulligans Flat Artist in Residence

Ceilidh Dalton

The Woodlands and Wetlands Trust has a fantastic artist in residence program, which has so far engaged two artists for a year-long residency at Mulligans Flat and Jerrabomberra Wetlands. Ceilidh Dalton works with various metals to create jewellery and sculptural pieces inspired by nature. Ceilidh and I had several field trips to Mulligans Flat where we shared a passion for the tiny plants, mosses and fungi and the little creatures that often go unnoticed. For her final exhibition, Ceilidh produced some beautiful bettong pieces, and an amazing Eucalyptus ID guide with casts of the leaves, nuts and bark of each Eucalyptus species found in the reserve.

Silver bettong and eucalypt leaf pendant

Ceilidh Dalton 2019

Silver bettong brooch

Ceilidh Dalton 2019

Mulligans Flat Eucalypts

Ceilidh Dalton 2019

Cast bronze and silver on red stringybark base

Chapter 5:

Population demography of a native geophyte in response to a reintroduced ecosystem engineer

Ross, C.E., McIntyre, S., Barton, P.S., Evans, M.J., Cunningham, S.A. & Manning, A.D., in prep. Population demography of a native geophyte in response to a reintroduced ecosystem engineer. *Plant Ecology (in prep)*

5.1 *Abstract*

The reintroduction of ecosystem engineers to degraded ecosystems has the potential to restore important ecological processes. However, the impacts of these reintroductions on recipient ecosystems must be considered. A native digging marsupial, the eastern bettong (*Bettongia gaimardi*) was reintroduced to a predator-proof sanctuary in south-eastern Australia after an absence of over 100 years. Bettongs have been observed digging up and eating the bulbs or corms of several species of geophyte, including *Wurmbea dioica* (early nancy, Colchicaceae). We monitored populations of *Wurmbea* over five growing seasons to assess the impact of bettongs on *Wurmbea* survival, reproduction and recruitment. We also assessed life history traits for a subset of plants that we followed individually over three years. We observed a decline in the *Wurmbea* population where bettongs were present, which was exacerbated by several years of drought during the monitoring period. Bettongs consumed 13-24% of the *Wurmbea* population on average each year, but this varied widely between sites and years. Where bettongs were present, there was a shift in *Wurmbea* population demographics over time towards a greater proportion of young (1-leaf) plants and fewer flowering plants. Seeding rates were lower at sites with bettongs present, particularly in dry years. Amongst the surviving inflorescences there was a high rate of florivory across all sites (most likely by birds) (up to 93%). Interactions between digging animals and geophytes appear to be common in many ecosystems worldwide, but this is the first to be studied in Australia. When planning species reintroductions it is important to consider the potential trophic and engineering interactions, as well as the effects of population density of the introduced species on these processes.

Keywords: ecosystem engineer, trophic, restoration, reintroduction, temperate, woodland, grassland, conservation

5.2 *Introduction*

Species translocations are increasingly used as a conservation tool for threatened species. Research to date has largely focused on the success of these translocations in establishing self-sustaining populations, but recently there has been increasing attention on the impacts and responses of the recipient ecosystem (Seddon et al., 2014, 2007). For species that are ecosystem engineers this is even more important, due to their disproportionate effect on ecosystem structure and processes (Jones et al., 1994). When introducing ecosystem engineers, possible unintended or negative consequences need to be taken into account (Jones et al., 1997) such as the risk of overpopulation, and interactions with exotic species. Engineers also influence the ecosystem through trophic effects (i.e. herbivory, predation) and there can be positive or negative feedbacks to the engineer i.e. if the engineering has the effect of increasing resources or decreasing predation for the engineer (Sanders et al., 2014; Wilby et al., 2001). Negative trophic effects may outweigh the positive engineering effects (Verdon et al 2016), particularly in highly threatened and degraded ecosystems. The relative strength of these effects depends on engineer density (Jones et al., 1997). Integrating trophic and engineering effects and their interactions is vital to understand the overall impact of ecosystem engineers on the ecosystem (Sanders et al., 2014; Wilby et al., 2001).

Digging and soil-foraging animals often feed on the underground storage organs of plants (e.g. bulbs, tubers, corms) and are considered to be ecosystem engineers because they alter habitat structure and resource availability for other species (Berke, 2010; Jones et al., 1994). In the process of foraging for subterranean foods, digging animals create resource patchiness, alter soil properties, and provide habitat for other species (Mallen-Cooper et al., 2019; Martin, 2003; Whitford and Kay, 1999). They also have trophic effects through consumption, which depend on population densities and environmental context. These engineering and trophic effects are very closely linked because they stem from a single action of digging to access food (Wilby et al., 2001).

Geophytes are terrestrial plants with underground storage organs such as bulbs, tubers or corms which assist survival under unfavourable conditions. These structures contain high quantities of starch, water, and micronutrients, making them an important food source for many species (Anderson, 1997; Pate and Dixon, 1982). Several studies have suggested that there may be co-evolution between digging animals and geophytes, through a feedback mechanism whereby the animal digs up and consumes the plant's storage organ, but the plant benefits from dispersal or disturbance. For example, in the Negev desert of Israel, porcupines (*Hystrix indica*) have been observed to consume at least 18 different species of geophytes and hemicryptophytes, some of which benefit from the digging through enhanced seed germination and establishment (Gutterman, 1987, 1982). Tardiff and Stanford (1998) found that glacier lilies (*Erythronium grandiflorum*) had higher nitrogen levels in leaves and produced more seed after partial consumption by grizzly bears (*Ursus arctos horribilis*), and that seedlings established best on bare soil created by bear digging. Several species are known to harvest and store geophytes in their burrows, dispersing them in the process (Begall and Gallardo, 2000; Borghi and Giannoni, 1997; Galil, 1967; Hagenah and Bennett, 2012; Lovegrove and Jarvis, 1986).

Geophytes form part of the diet of many Australian mammals, including bettongs (*Bettongia spp.*)(Mcilwee and Johnson, 1998; Taylor, 1992a), long-nosed bandicoot (*Perameles nasuta*) (Thums et al., 2005), bilby (*Macrotis lagotis*) (Bice and Moseby, 2013), and southern hairy-nosed wombat (*Lasiorhinus latifrons*) (Allen, 2013). Despite this, there are no studies from Australia that have examined the ecological interactions between soil-foraging species and geophytes. Unfortunately, many of these species have experienced significant population declines due to introduced predators, habitat loss, and persecution, and many are now restricted to predator-free islands or fenced reserves (Legge et al., 2018; Woinarski et al., 2015). Digging animals are known to play an important role in many Australian ecosystems, and the reintroduction of these species has been suggested as a means of restoring ecosystem function and rehabilitating degraded landscapes (Fleming et al., 2014; Manning et al., 2015; Munro et al., 2019). However, given that in many cases digging animals have been absent for over a century and there has been significant degradation and loss of biodiversity, it is unclear how the recipient ecosystems will respond to these reintroductions. Many geophyte species have also declined due to clearing and inappropriate grazing and fire regimes, and are now restricted to isolated populations making them more vulnerable to disturbance. Addressing this knowledge gap is important to understand the trophic and engineering interactions that will occur when reintroductions take place, and predict and manage unintended consequences.

In this paper, we present the results of a five-year study of a native geophyte (early nancy, *Wurmbea dioica*), following the reintroduction of a locally extinct digging marsupial (eastern bettong, *Bettongia gaimardi*) to a predator-proof sanctuary in south-eastern Australia. Previous research at this site estimated that an individual bettong digs approximately 200 small pits each night, which equates to 8 kg of soil turnover (Munro et al., 2019). These pits have significant effects on soils and increase germination of certain plant species, particularly gap-dependent native forbs (Ross et al. 2019a; Ross et al. 2019b, Robb et al. unpublished data). However, apparently high rates of consumption have been observed for some species of native geophytes, particularly *W. dioica* (hereafter referred to as *Wurmbea*). This species seems to be an important food item in the bettong diet; the remains of *Wurmbea* corms are frequently observed in bettong pits (pers. obs.) and eDNA analysis of 64 bettong scats found that *Wurmbea* was present in ~90% of scats collected during winter and spring (C. Ross unpublished data). *Wurmbea* reproduces well from seed and prefers open sites so it was expected to benefit from the disturbance created by bettong digging (Kent et al., 2002). While *Wurmbea* is relatively common at the study site, it is possible that bettong consumption may have a negative impact on this species and other geophytes, some of which are of conservation concern.

The overall aim of this study was to examine the interaction between *Wurmbea* and the eastern bettong and determine whether *Wurmbea* populations are likely to persist in the presence of bettongs. To do this, we monitored populations of *Wurmbea* in areas with and without bettongs over five growing seasons, and monitored the total number of plants as well as flowering, seeding, recruitment, and mortality due to bettong consumption. For a smaller cohort of plants, we were able to identify individuals and follow them through time to identify life history attributes of *Wurmbea*, such as length of life stages (seedling, vegetative phase, adult phase), life span, dormancy etc. We asked the following questions:

1. What are the life history attributes of *Wurmbea*?
2. What is the trend in total population of *Wurmbea* over time in areas with and without bettongs?

3. What percentage of *Wurmbea* plants are consumed by bettongs each year?
4. Do bettongs influence population demography, i.e. recruitment, flowering and seeding success?

We hypothesized that bettongs would eat adult *Wurmbea* plants and therefore reduce flowering and seeding success, but their digging would also increase recruitment, resulting in a higher proportion of younger plants. The net effect on the *Wurmbea* population would depend on the relative rates of mortality and recruitment.

These findings will add to our understanding of the role of digging mammals as ecosystem engineers and as part of a food web. It will also inform management of the bettong population within the reserve as well as future reintroductions.

5.3 *Methods*

5.3.1 Study system and species

The Mulligans Flat-Goorooyarroo Woodland Experiment is located on the outskirts of Canberra in south-eastern Australia. It consists of two neighbouring nature reserves, Mulligans Flat Nature Reserve (683 ha established in 1994) and Goorooyarroo Nature Reserve (702 ha established in 2006). The reserves represent one of largest remaining patches of a critically endangered ecological community, Yellow Box-Blakely’s Red Gum Grassy Woodland. This ecosystem type has experienced a more than 95% reduction in range, and the remaining patches are small, isolated and often severely degraded, particularly in terms of ground-layer plant diversity. The experiment was set up to trial a range of restoration techniques for grassy woodlands, including the reintroduction of several locally extinct species within a predator-proof sanctuary. The 11km sanctuary fence was built in 2009 and encloses a 485 ha area within which introduced mammals have been removed i.e. foxes, cats, dogs, livestock, rabbits and hares. The climate of the region is classified as temperate, with an average annual rainfall of 636.2mm (see Figure S1), mean maximum temperature (January) of 28.5°C and mean minimum temperature (July) of 0.0°C (Bureau of Meteorology, 2020).

The eastern bettong (*Bettongia gaimardi*) is a rabbit-sized marsupial in the Potoroidae family, which was once widespread across south-eastern Australia and Tasmania but has been extinct on the mainland since the early 1900s. In Tasmania, their diet consists largely of hypogeal fungi (up to ~90%) as well as plant material (leaf, stem, seed, fruit, gum, roots, tubers) and invertebrates (Johnson, 1994a; Taylor, 1992a). Bettongs were introduced to the sanctuary in 2012, starting with a population of 32 individuals sourced from Tasmania (Batson et al., 2015). In 2015 the population was estimated to be approximately 150 individuals, but it has fluctuated seasonally (Manning et al. 2019, Figure S2).

Wurmbea dioica (early nancy) is a very small geophyte in the Colchicaceae family (Figure 1a). It has a wide distribution across southern Australia. Seedlings have a single filiform leaf, while adult plants produce up to three filiform-linear leaves, and 1-10 six-petalled white and purple flowers which may be dioecious, polygamo-dioecious or hermaphroditic (Macfarlane, 1980). All above-ground material dies back in late spring leaving the corm, a modified stem surrounded by layers of 'husk' consisting of the shriveled old corms (Figure 1b). The corm is replaced each year, with most of the stored reserves used in expanding the new shoot, roots and leaves (Pate and Dixon, 1982).

While *Wurmbea* has been the subject of much research on dioecious reproduction (Barrett and Case, 2006; Case and Barrett, 2001), very little is otherwise known about its life history. It is very difficult to determine the age of individuals because plants are not visible above ground for much of the year. Plants may take three years to flower when grown from seed (Kent et al., 2002). Other similar species have been estimated to live 10-20 years, with 4-5 years of vegetative phase (Pate and Dixon, 1982). Seasonal variation is likely to have a great effect on reproductive success, and in dry years many plants remain dormant (Pate and Dixon, 1982).

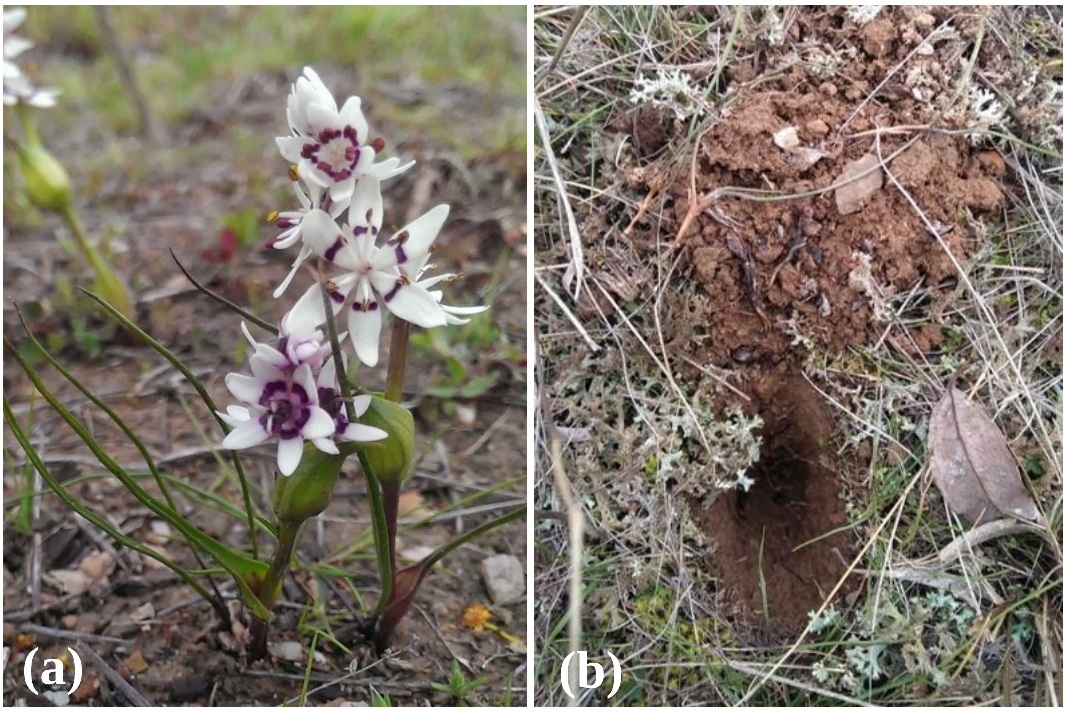


Figure 1. *(a) Early nancy, Wurmbea dioica. Adult plants produce up to three filiform-linear leaves, and 1-10 six-petalled white and purple flowers which may be dioecious, polygamo-dioecious or hermaphroditic. Photo shows both female (left) and male (right) plants. (b) Example of a bettong pit. The Wurmbea corm has been excavated and consumed, and the husk and discarded leaves are visible on the spoil heap. There is no evidence that bettongs harvest or store the corms. Credits: Catherine Ross*

5.3.2 Experimental design

To measure the impact of bettongs on the *Wurmbea* population, we monitored *Wurmbea* populations across nine sites between 2015 and 2019. We established five monitoring sites in 2015 and collected population data (emergence, mortality, flowering and seeding) in winter and spring of each year. Four additional sites were established in 2016 due to unexpected disturbance of control sites in 2015 (see below).

Table 1. *Description of Wurmbea monitoring sites. Each site had two adjacent plots representing two treatments: bettongs present and absent (control). Additional sites were set up in 2016 after bettongs gained access to the exclosure control plots established in 2015.*

Year set up	Number of sites	Treatment	Description	Bettong presence
2015	5	**Bettong**	The general sanctuary area	Yes - 2012
		Exclosure	1 ha fenced areas within the sanctuary, initially without bettongs	No - 2012-15 Yes – 2016/17
2016	4	**Bettong 2**	Additional sites within the sanctuary	Yes - 2012
		Outside	Outside the sanctuary	No

5.3.3 Sites and treatments

In 2015 we established five monitoring sites, with adjacent treatment and control plots. Treatment plots were within the sanctuary area where bettongs had had access since 2012. Control plots were in 1-hectare areas fenced to exclude bettongs (exclosures) which had been set up prior to the bettong reintroduction. We chose sites with relatively high numbers of *Wurmbea* plants both inside and outside the bettong exclosures to enable us to monitor a sufficient number of plants. On each side of the fence, the plots represented a cluster of permanently marked $0.5m^2$ quadrats delineating a total of at least 100 plants. In most cases only four quadrats were needed to reach 100 plants, and six quadrats were needed at one plot. This gave a total of 1372 individual plants in the initial survey.

After the data collection was completed in late 2015 (see below), bettong digging was observed inside several of the exclosures, meaning that they could no longer be used as control sites. For the 2016 monitoring season we set up an additional four sites with populations of *Wurmbea* occurring on either side of the outer sanctuary fence, to ensure that the controls would not be disturbed by bettongs. We also continued to monitor the original five sites, as they provided an opportunity to record the impact of the bettongs on previously undisturbed *Wurmbea* populations. This effectively created four treatments, described in Table 1.

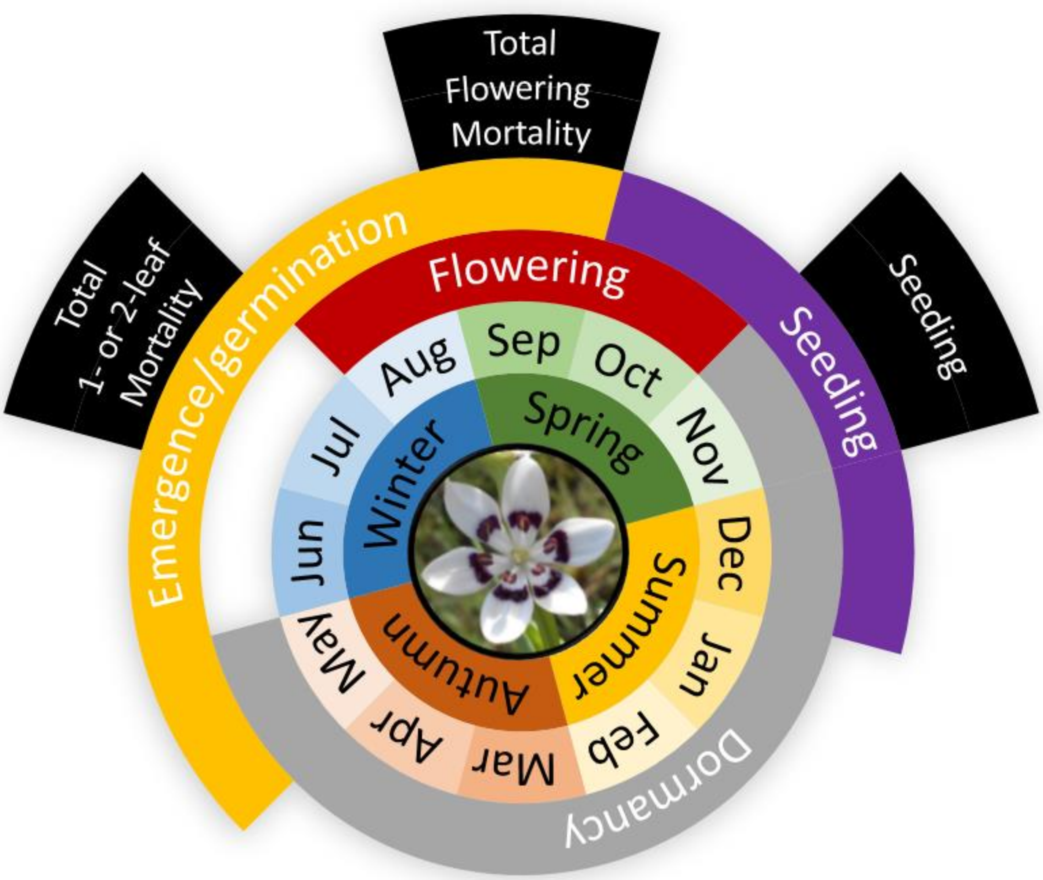


Figure 2. *Wurmbea dioica life stages and timing of data collection. Wurmbea dioica is a geophyte, and is only present as a corm from late spring to late autumn (dormancy). Emergence and germination occur from May to September, with flowering from late August to October and seeding from late October to December. We surveyed populations three times each year (black bars); in July we counted the total number of plants, the number of 1- and 2-leaf plants, and the number of plants consumed or buried by bettongs (mortality); in September we counted the total, the number of flowering and non-flowering plants, and mortality due to bettongs; in November we only counted the number of seeding plants.*

5.3.4 Monitoring

We set up the experiment in late July 2015, to capture the total number of *Wurmbea* plants at the time of emergence (Figure 2). We temporarily marked all plants within each quadrat and photographed the plot (Figure 3a). We recorded the total number of plants, whether they had 1 or 2 leaves, as well as the number of existing bettong pits. After the first year, we used different coloured markers for 1- and 2-leaf plants to identify them in the photos.

We surveyed the plots in late September 2015 to coincide with peak flowering (Figure 2). Using the photos from the previous session we were able to locate most of the plants that had been recorded in July (some plants had died off or been grazed by this time and could not be found, and sometimes new plants had emerged). We again temporarily marked each plant and photographed the plot, using different colours to indicate flowering or non-flowering plants, and mortality (due to bettongs) (Figure 3b). Mortality was recorded where there was a fresh pit with evidence that a *Wurmbea* plant had been there previously, either from the photos or from remains of the leaf, stem or corm left in the pit (Figure 1b). Only new pits were recorded; if a pit was visible in the previous photo it was not recorded again. We also observed during the study that many plants produced an inflorescence which was subsequently removed, most likely by birds. In this case, we still counted the plant as flowering, but we also recorded the number of flowers that had been removed for each quadrat. In November 2015 we recorded the number of plants that had successfully produced seed in each quadrat, but did not mark the plants or take photos. The same method was repeated for all sites in July, September and November each year from 2016 to 2019. In 2018 we did not survey in July, only September (in this case we used the photo from the previous September to help locate plants).

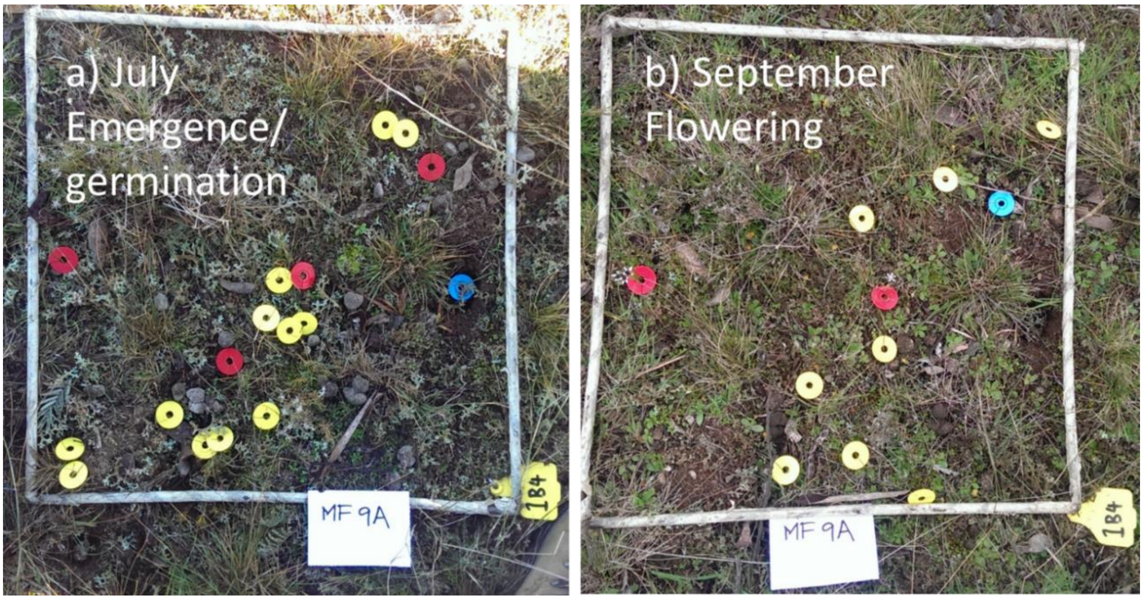


Figure 3. *Survey method. Full surveys were undertaken in a) July (emergence) and b) September (flowering) each year. All Wurmbea plants within each 0.5m*^{2} *were marked with coloured markers, and photos taken. At the July survey, yellow markers are 1-leaf plants and red markers are 2-leaf plants. In September, yellow markers are non-flowering plants and red markers are flowering plants. Blue markers are plants that have been consumed or buried by bettongs since the previous survey. Note that only plants in leaf could be counted, but an unknown percentage of the population remain dormant each year.*

5.3.5 Analysis

Question 1 – *Wurmbea dioica* life history

Where plants were well spaced, it was possible to use the photos to follow individuals over multiple surveys. We were able to follow 176 individuals from two sites over the first three years of the study. This information made it possible to address some important questions about *Wurmbea* life history, which would inform our analysis of population trends and demographics. Specifically, we asked the following questions:

- Lifespan – what is the longest time we observed the same plant?
- Seedlings - are 1-leaf plants always seedlings?
- Flowering - do 2-leaf plants always flower?
- Dormancy – do we observe plants disappearing and then reappearing after one or more years?
- Do bettongs prefer to eat older/flowering plants?

Question 2 – Total population over time

We calculated the total population at each plot, summed across quadrats. Note that only plants in leaf could be counted, but an unknown percentage of the population remain dormant each year. We summarized the data using boxplots for each treatment to examine trends in the population over time. We selected sites with a relatively high density of plants rather than sampling randomly, so we were interested in the change over time within sites, not comparing between sites at a single survey time. Some sites started with more plants than others, but this does not necessarily indicate a difference due to treatment.

Question 3 - Mortality rates

For each plot, we calculated annual mortality as the total number of dead plants at each plot in September, as a percentage of the total number of plants recorded the previous July. We then calculated the annual mortality rate as the average of all sites with bettong access. As no survey was conducted in July 2018, we could not calculate the mortality rate for that year.

Question 4 - Demography

At each survey, we recorded whether the plants had 1 or 2 leaves (in July) and whether they were flowering or not (in September). We summarized the data using boxplots for each treatment. Examining the relative proportions of these categories gives an indication of the demographic make-up of the population in each year. While we were unable to reliably identify seedlings, we used the number of 1-leaf plants as a measure of recruitment as 1-leaf plants are likely to be either seedlings or young plants that have not yet reached the flowering stage. We also looked at what proportion of the plants that flowered went on to successfully seed in November, or had the flowers removed (florivory).

5.4 *Results*

5.4.1 Question 1 - *Wurmbea dioica* life history

The results of the life-history analysis are summarized in Table 2. Of 176 individuals followed, 32 (18%) were seen in all three years, 73 (42%) were visible for two years, and 70 (40%) were only seen for one of the three years. One plant was observed flowering in all three years, suggesting that it must be at least four years old because *Wurmbea* can take several years to flower (Kent et al., 2002).

We found it impossible to determine with certainty which plants were seedlings. Four plants were observed to have one leaf for two years in a row, and two plants went from 2-leaf in one year to 1-leaf in the next year (including one that was flowering in the first year). It is also possible that the second leaf was missing due to grazing. This demonstrates that 1-leaf plants are not necessarily seedlings; they could be young plants in their vegetative phase, or adult (flowering) plants that only have produced one leaf in a particular season (perhaps due to poor conditions). Therefore, the number of 1-leaf plants includes all seedlings, but also an unknown proportion of older plants.

There was only one example where a plant was observed to have one leaf in July and then flowered in September. However, this could have been due to the second leaf being missing (due to grazing, damage or desiccation). We could therefore assume that all 2-leaf or flowering plants were at least two years old.

There were 112 observed cases of 2-leaf plants in July – of these, 46% went on to flower in September, 20% were consumed, 19% did not flower, and 15% were not observed in the September survey (grazed or desiccated).

Table 2. *Summary of life history attributes of Wurmbea dioica observed in a population of 176 individuals over three years.*

Question	Answer	Evidence
Lifespan – what is the longest time we observed the same plant?	3+ years	Flowering observed for 3 years in a row, plus at least one year non-flowering.
Seedlings - are 1-leaf plants always seedlings?	No	1-leaf plants may be seedlings or adult plants, but 1-leaf plants never flower in the same season.
Flowering - do 2-leaf plants always flower?	No	46% of 2-leaf plants flowered (averaged over all years)
Dormancy – do we observe plants disappearing and then reappearing after one or more years?	Yes	The maximum dormancy period observed was two years
Do bettongs prefer to eat older/flowering plants?	Yes	91% of plants consumed by bettongs were flowering or at least 2 years old

Two plants were observed in the first and third year but were completely missing in the second year. In addition, 17 (9.7%) and 2 (1.1%) 2-leaf plants were observed for the first time in year two and three respectively. Since these could not be seedlings, they must have been older plants that were dormant for the first one or two years of the survey.

Of the 176 plants, 56 (32%) were consumed by bettongs during the survey period. Of these, 51 (91%) were either flowering, had two leaves, or had been observed for at least two years.

5.4.2 Question 2 – Total population over time

Figure 4 summarizes the total number of *Wurmbea* plants recorded at each plot (summed across quadrats) (also see Table S1 in Supplementary material). To look at the effect of bettongs on the *Wurmbea* population we needed to compare the Outside treatment (no bettongs) with the three other treatments (in the first year, the exclosure plots did not have bettongs, but they gained access to three plots in 2016 and all plots in 2017). Over the 5 years of the survey the area also experienced a large variation in rainfall (Figure S1). The first year of the study was around average rainfall during the winter growing period, the second year was one of the wettest winters on record, and the final three years had well below average rainfall. We were therefore interested in how this climatic variation would affect the *Wurmbea* population and interact with the effect of bettong consumption. In September 2017, there was a sharp decline in the *Wurmbea* population across all plots, which was likely due to dry winter conditions (Figure 4). This decline continued across plots with bettongs in the last three years of the study, but there was no overall decline in the Outside plots. By the end of the five-year monitoring period, plots with bettong access had declined to 31% of their original population on average, while the control plots had only declined to 85%. However, there was a large amount of variation between plots.

5.4.3 Question 3 - Mortality rates

On average, bettongs consumed between 13-24% of *Wurmbea* plants between July and September each year. Table S2 shows the percentage mortality at each plot in each year (except 2018 when the mortality rate could not be calculated). 2017 had the highest average rate of mortality, with 24%. Interestingly, some plots had no recorded bettong digging despite bettongs having access to the area. For example, plot B_5 had very low rates of bettong digging throughout the whole study (Table S2). In the final year (2019), most of the Bettong and Bettong2 plots had very low mortality, while the exclosure plots remained high.

5.4.4 Question 4 – Demography

Over the study period, we observed an increase in the proportion of 1-leaf plants in all treatments, and a decrease in the proportion of plants that flowered and seeded successfully

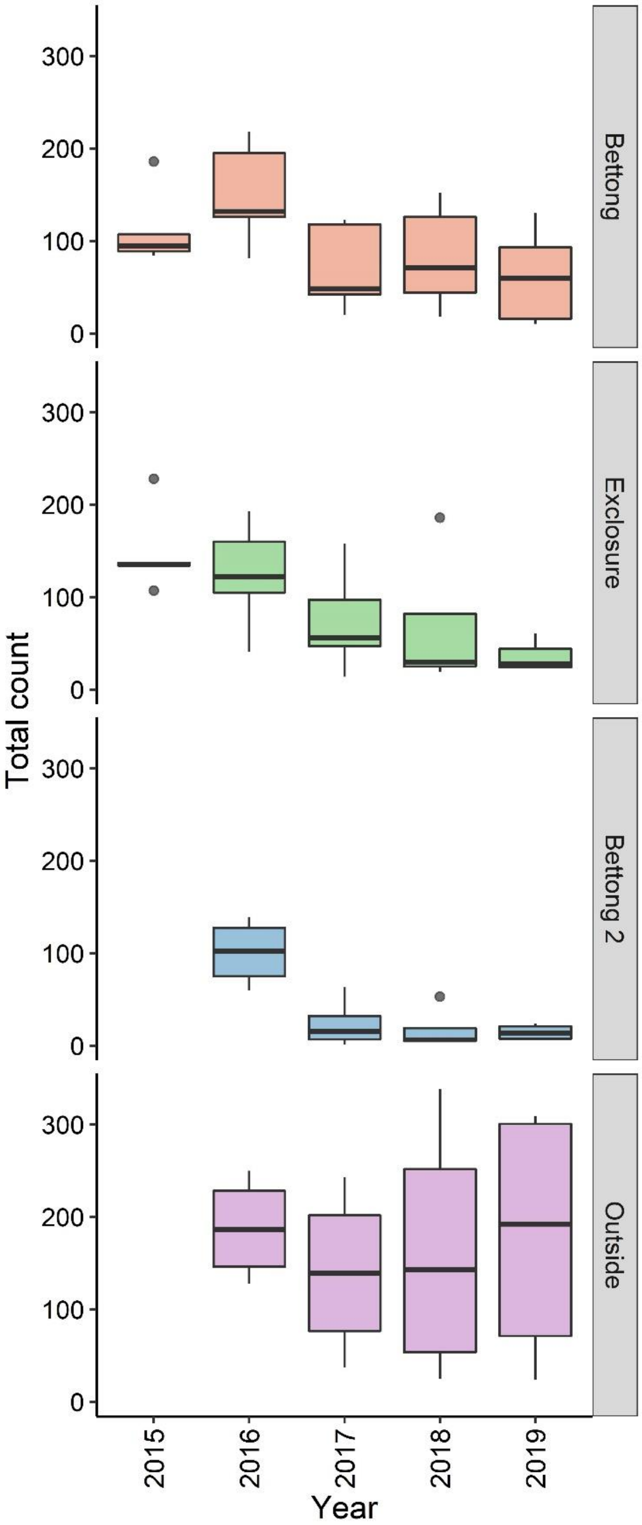


Figure 4. *Boxplots of Wurmbea dioica population by treatment (total counts in September). Values are means of 4-5 plots, treatments as described in Table 1. Note that only plants in leaf could be counted, but an unknown percentage of the population remain dormant each year. Boxplots represent the minimum, first quartile (bottom of box), median (middle line through box), third quartile (top of box), and maximum value, with outliers represented by dots above or below the box.*

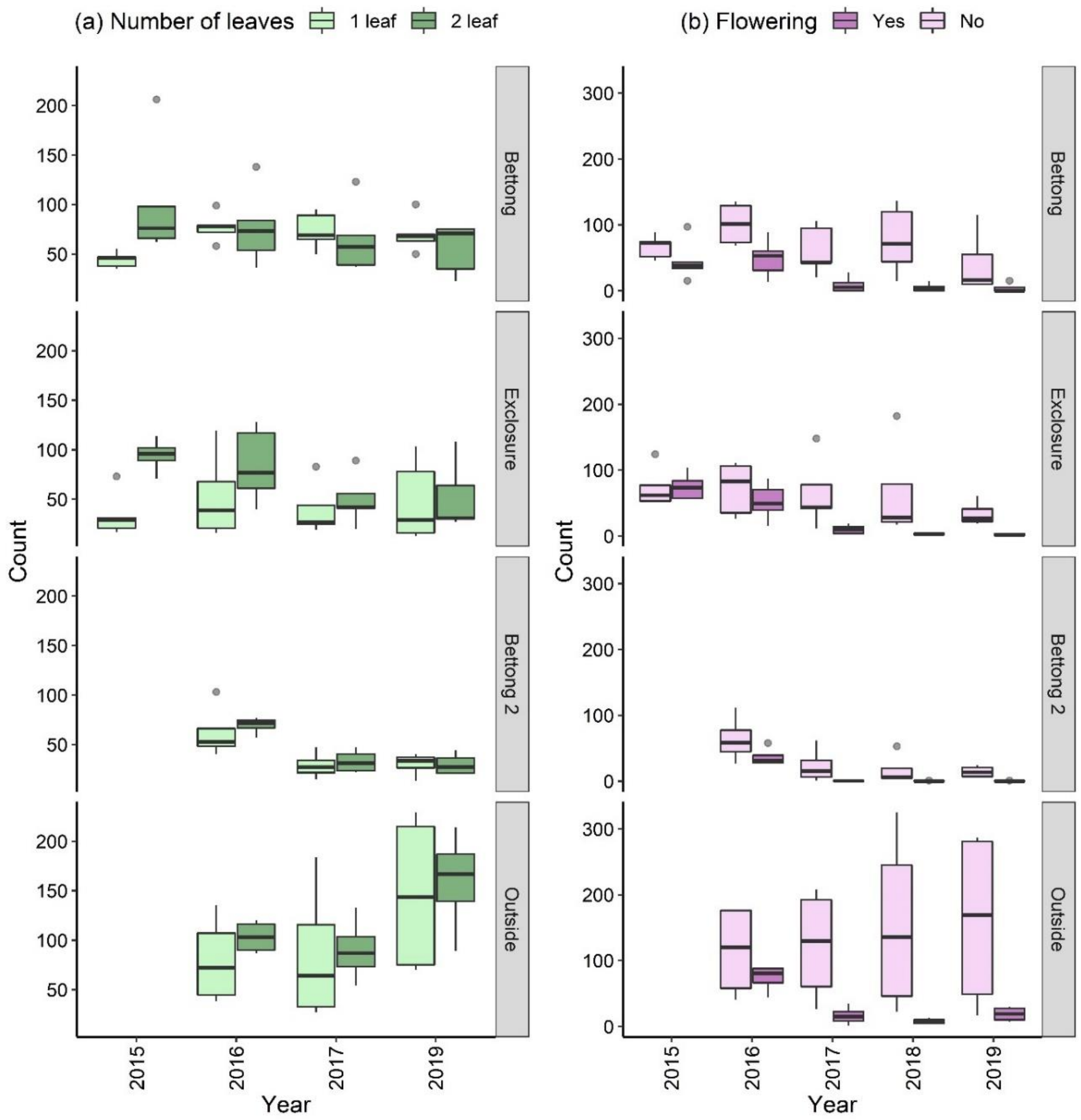


Figure 5*. Boxplots of Wurmbea dioica population demographics by treatment, plants with (a) 1 or 2 leaves in July and (b) flowering or not flowering in September. Values are means of 4-5 plots, treatments as described in Table 1. Boxplots represent the minimum, first quartile (bottom of box), median (middle line through box), third quartile (top of box), and maximum value, with outliers represented by dots above or below the box.*

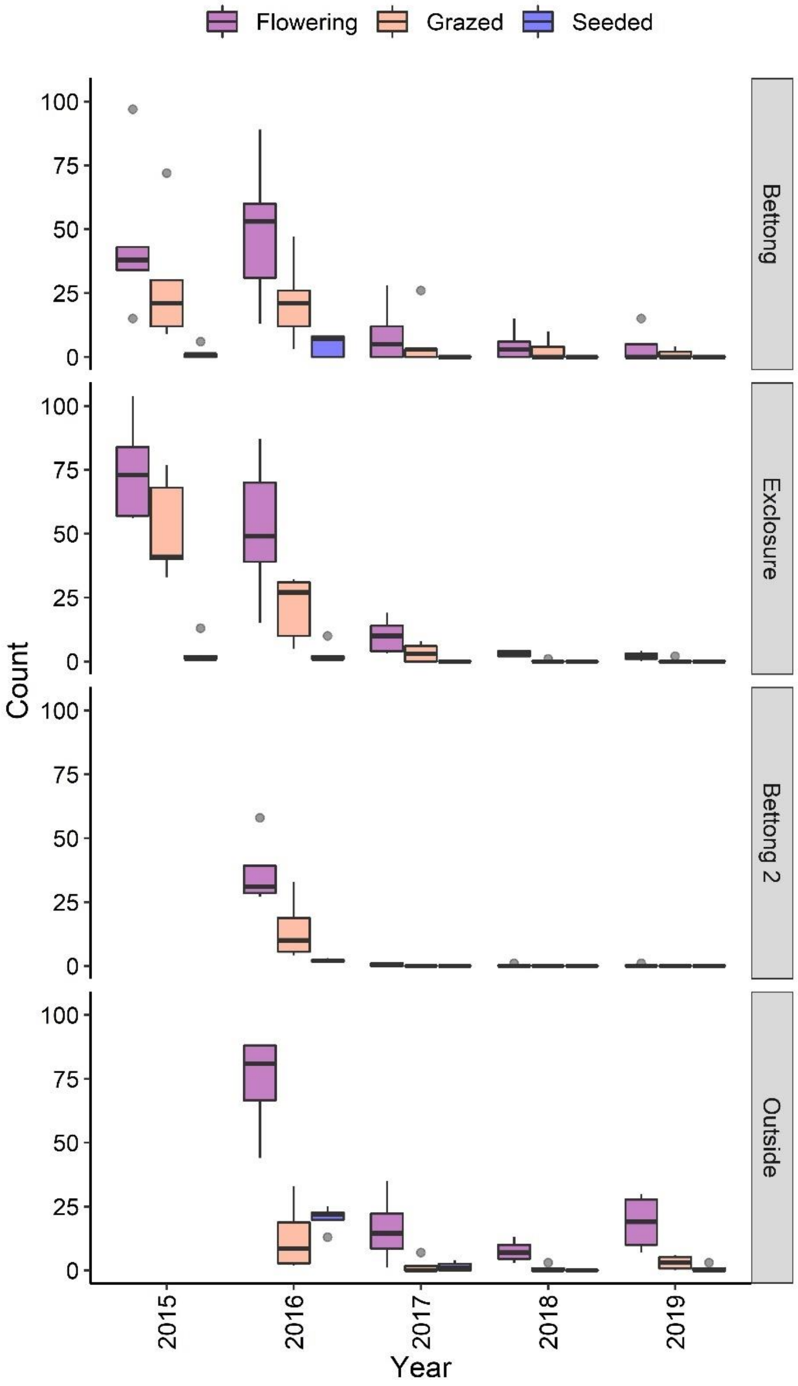


Figure 6. *Boxplots of Wurmbea dioica flowering, seeding and florivory by treatment. Values are means of 4-5 plots, treatments as described in Table 1. Boxplots represent the minimum, first quartile (bottom of box), median (middle line through box), third quartile (top of box), and maximum value, with outliers represented by dots above or below the box.*

(Figure 5). Rainfall appeared to have a strong effect on flowering and seeding rates, and both dropped dramatically across all plots in the last three years of the study. The presence of bettongs reduced seeding rates; Outside plots (without bettongs) consistently had a higher rate of seeding than all other treatments, particularly in the last three years, where seeding was only recorded in Outside plots (Figure 6). We also observed high rates of florivory, with up to 93% of flowers removed at some plots. This was not due to bettongs, but most likely the result of birds, lizards or insects.

5.5 *Discussion*

Our results indicate that the reintroduction of bettongs is having a negative impact (at least in the short term) on the *Wurmbea* population in the reserve in terms of population size and reproductive success, but that this effect was highly variable and also dependent on a range of other factors such as rainfall, macropod grazing and florivory. We observed that bettongs consumed on average between 13-24% of the *Wurmbea* plants that emerged each year. This resulted in a higher proportion of 1-leaf plants and fewer flowering and seeding plants. However, it is not yet clear whether there is a mutualistic relationship between bettongs and *Wurmbea* as has been suggested in other studies (i.e. a positive effect on *Wurmbea* germination and positive feedback to the bettong through increased food resources).

5.5.1 Life history

This study adds to knowledge of the life history of *Wurmbea dioica*. We observed that seedlings did not flower in their first year, and that plants can live for at least four years. Another source states that *W. dioica* ‘generally takes 3 years to flower’ when grown from seed in cultivation, but did not have any information on total life span (Kent et al., 2002). In a study on a similar cormous species (*Philydrella pygmaea*), plants did not flower for the first 4-5 years, took 8-10 years to reach adult size, and lived up to 20 years (established by counting the number of husk layers around the corm) (Pate & Dixon, 1982). In the time frame of this study (5 years) it was impossible to estimate the total life span, and more research will be needed to fully answer these questions. Without these data we cannot perform detailed population modelling to predict the future likelihood that *Wurmbea* will persist under current rates of bettong consumption.

We also observed that *Wurmbea* plants were able to remain dormant for 1-2 years (probably due to poor conditions) and then re-emerge the following year. This is important to note, because the total number of plants visible in any given year may not reflect the actual population, with an unknown proportion of plants remaining dormant underground. Bettongs appeared to target older plants, presumably because they have larger corms. However, it is unclear how bettongs detect or select plants.

5.5.2 Factors affecting *Wurmbea* population and demography

We aimed to fill important knowledge gaps in the life history of *Wurmbea*, as well as the potential impact of the eastern bettong on *Wurmbea* populations. However, it is important to consider the influence of several other factors that might interact with *Wurmbea* biology and the role of bettongs in the ecosystem. To assist with closing these gaps, we developed a conceptual diagram to represent the factors we have identified as being important for *Wurmbea* populations and how they interact (Figure 7).

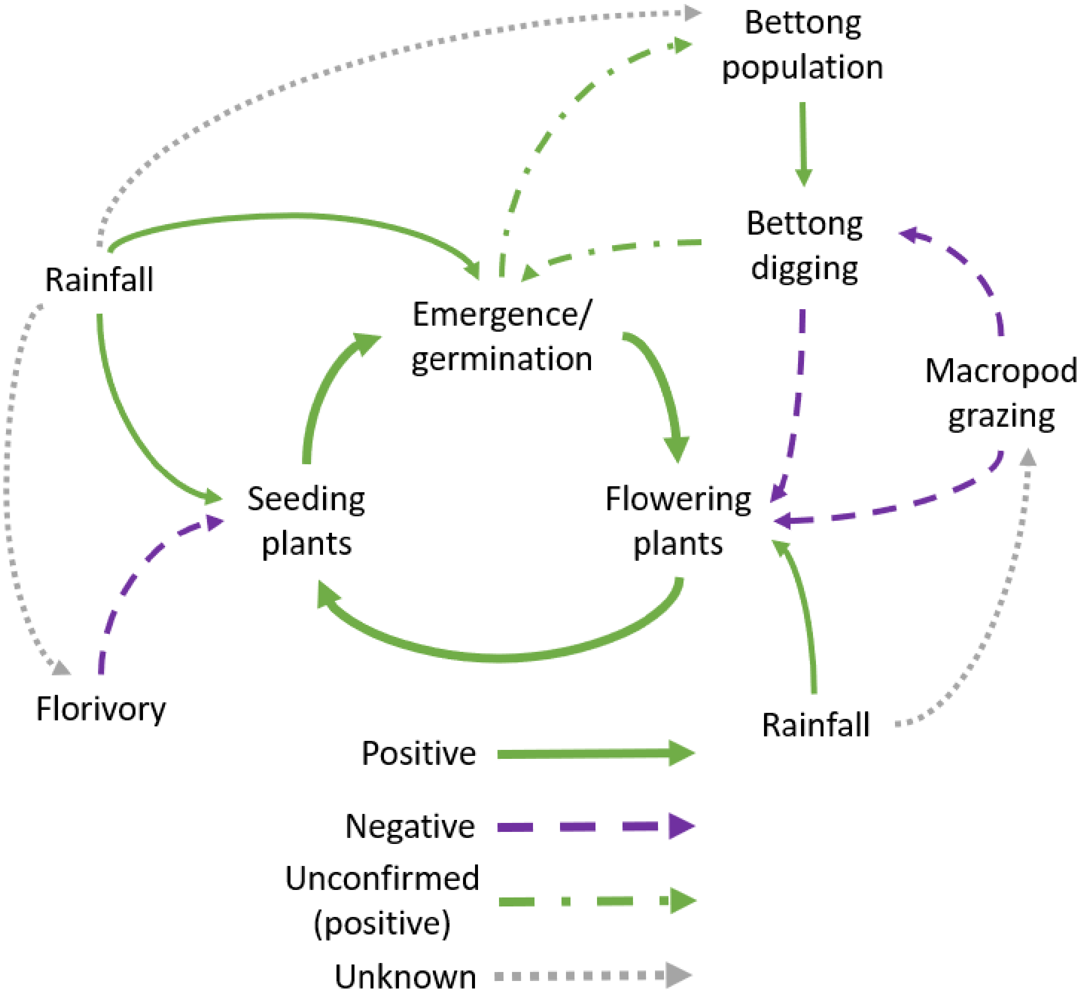


Figure 7. *Conceptual diagram of factors affecting Wurmbea dioica population in Mulligans Flat. Positive effects are shown in solid green arrows, negative effects in broken purple arrows, unconfirmed positive effects in broken green arrows, and unknown effects in dotted grey arrows. Bettong digging has a negative effect on the number of flowering plants through trophic effects (consumption). We were unable to confirm a hypothesized positive effect on recruitment through soil engineering, or a possible positive feedback effect to the bettong population as their food source is increased.*

Climate and weather

The results of this study were likely to be strongly influenced by climatic conditions. During the five years of the study we experienced average rainfall (2015), then one of the wettest winters on record (2016), followed by three years of very dry winter conditions (2017-19) (Figure S1). Over those dry years we recorded a decline in total *Wurmbea* population across most plots and very low rates of flowering and seeding, but this was more pronounced at plots with bettongs (Figure 5, 6). This suggests that there is a compounding effect of drought and bettong consumption. As well as directly limiting plant growth and survival, drought is likely to intensify predation and grazing pressure due to a reduction in overall food supply for bettongs, as well as macropods and other herbivores (Figure 7).

We note that the number of plants we observed each year might not reflect of the total population. As *Wurmbea* is a geophyte, a certain proportion of the population does not emerge in any given year and depends on climatic conditions. These individuals may remain dormant for several years before re-emerging. We would therefore expect to see at least some recovery of the population if there is sufficient rainfall. However, climate change is predicted to cause a decrease in average annual rainfall with more frequent and severe droughts, so *Wurmbea* and other geophytes may become more vulnerable (Dai, 2011). Continued monitoring will be required to observe how long-term fluctuations and trends in climate will impact the population.

Bettong population

The amount of digging and subsequent impact on *Wurmbea* populations will be dependent on the bettong population. The highest amount of bettong consumption was observed in 2017, which was the first dry year following a relatively wet period. Bettongs therefore can have a negative effect on *Wurmbea* (Figure 7). This could also have been related to the number of bettongs present - bettong population estimates suggest that there was a peak in the population in 2016, followed by a decline (Figure S2). Manning et al. (2019) suggest that the population switched to self-regulation due to resource limitation, and this may have put more pressure on their food sources in the first year of the drought. In 2018 and 2019, the bettong population had dropped and some plots experienced very little or no digging at all. Based on this study, it is difficult to determine the appropriate density for bettongs in Mulligans Flat because of the interactions and dynamics of the key factors. While the bettong population appears to be self-regulating, they may still be overexploiting particular species at current population levels.

Grazing and florivory

While bettongs appear to have a substantial impact on *Wurmbea* populations, it is important to put this effect into perspective compared with other herbivores such as macropods, birds, and insects. We observed high levels of grazing and florivory at some plots, which are likely to impact *Wurmbea* survival and reproductive success (Figure 7). Three species of macropods are present in Mulligans Flat: eastern grey kangaroo (*Macropus giganteus*), red-necked wallaby (*Macropus bennetti*), and swamp wallaby (*Wallabia bicolor*). These species are present in large numbers both inside and outside the reserve, resulting in high grazing pressure (McIntyre et al., 2010). However, the fenced exclosure plots had the unintended effect of deterring macropods, which resulted in our treatments being confounded by macropod grazing levels. While macropods tended to avoid directly grazing *Wurmbea*, macropod grazing and trampling is likely to damage plants. On the other hand, high levels of macropod grazing may also have an indirect positive effect on *Wurmbea* by reducing bettong activity and maintaining a short, open sward favourable to such a diminutive plant. A previous study by Munro et al. (2019) at the same site found that bettong digging rates were higher in areas where kangaroos were maintained at a lower population density. While the amount of bettong digging declined in most sites in 2018, it remained higher in the exclosure plots where bettongs had only recently gained access (Table S2). This could have been because these plots had not previously been exploited so there were more available resources. However, we also observed that the exclosures had lower levels of macropod grazing, which resulted in higher grass cover and biomass. This might have made the exclosures more attractive to bettongs due to increased soil moisture or protection from predators.

We found high levels of florivory, up to 93% at one site, but this was highly variable depending on site and year. We recorded much higher florivory rates in the first two years of the study, perhaps because there were more flowers available due to higher rainfall. A study by Faast and Facelli (2009) recorded florivory rates of up to 94% for two species of orchid, and identified white-winged choughs (*Corcorax melanorhamphos*) as the main florivores. Lizards (e.g. shingleback, *Tiliqua rugosa*), possums, and other birds (e.g. currawong, cockatoo) are also possible florivores which are common at Mulligans Flat.

Spatial and temporal distribution of disturbance

The amount of bettong digging varied widely between sites and years, leading to substantial heterogeneity among *Wurmbea* populations. Such heterogeneity through space and time is an important factor that allows for the persistence of populations, and we suggest this is likely to be a mechanism that allows for *Wurmbea* populations to survive. Heterogeneity in bettong diggings might be due to several different reasons. For example, digging animals may target areas of higher resource density (density dependent foraging), but once that resource has been exploited it is not returned to, allowing a period of regeneration (Wright et al., 2004). On the other hand, digging animals may forage in the same area repeatedly because the soil is easier to dig, even if there are other areas with greater resource availability (Holcroft and Herrero, 1984). Animals may also dig in certain areas or at different times of the year depending on resource availability (Sandom et al., 2013a; Welander, 2000). In this study, we deliberately selected sites with a relatively high density of *Wurmbea* plants, so we were unable to test the density dependence hypothesis across a wide range of plant densities. Further research should examine the spatial and temporal distribution of bettong foraging.

Foraging behaviour also can be influenced by social interactions or predation risk (Jarvis et al., 1998; Laundré et al., 2010). Seabloom and Reichman (2003) found that gopher foraging was limited by social interactions, as individuals are solitary and avoid neighbours. Bettongs also have individual territories and this may influence the spatial distribution of foraging. The reintroduction of a native predator, the eastern quoll, to Mulligans Flat in 2016 may also have had an effect on bettong foraging behavior by changing the ‘landscape of fear’ (Laundré et al., 2010). This effect has been observed in North America after the reintroduction of wolves, which resulted in deer avoiding areas with a high risk of predation and subsequent regeneration of vegetation (Ripple and Beschta, 2012). Density dependent foraging and behaviour attributes are therefore two ways for heterogeneity to occur in bettong digging, and this is likely to be important for allowing *Wurmbea* to persist.

Ecosystem engineering and trophic feedback

Many studies have suggested a mutualistic relationship between digging animals and geophytes, but few have demonstrated it. Contreras and Gutiérrez (1991) found that in areas dug by coruro (*Spalacopus cyanus*), there were higher numbers of geophyte bulbs but they were smaller on average. They also suggested that burrowing activities facilitated seed germination. Sims et al. (2014) noted that patches of bluebell that had been rooted by boar recovered quickly after boar were excluded, and suggested that a positive effect on germination may have contributed to the recovery. Wilby et al. (2001) attempted to integrate the engineering and trophic effects of porcupines in the Negev desert, and found that the engineering effects had a much larger impact on perennial plant communities than the trophic effects, because the consumed plants were replaced by increased recruitment from pits, resulting in a net positive effect.

In our study, we could not confirm whether there was a benefit for *Wurmbea* recruitment as a result of bettong disturbance. We did observe an increase in the proportion of 1-leaf plants, however this may have been driven by the loss of older plants due to consumption by bettongs, as well as the drought causing more adult plants to only produce one leaf. There is no evidence that bettongs harvest or store *Wurmbea* corms, as observed in other species (Galil, 1967). A previous study at the same site found that bettong diggings increased germination of native seedlings compared to the soil surface (Ross et al., 2020). In that study, not enough *Wurmbea* seed germinated to measure a response, but there was a significant positive response for *Bulbine bulbosa* (Asphodelaceae), a bulbous species with similar traits. Consumption rates are rarely calculated, but rates we observed were comparable to those recorded in a study of porcupines in the Negev desert (20-30%) (Gutterman, 1987). Since bettongs and *Wurmbea* have co-existed for millennia before the bettong’s extinction, it seems likely that they would have evolved mechanisms to enable this co-existence. However, as the ecosystem has been significantly altered in the intervening time, the return of the bettong may have unexpected results.

We should also be aware that our interpretation of these impacts as positive or negative is influenced by human values and perceptions. Disturbance is often perceived as negative, but it is also vital for ecosystem function and diversity (Hobbs and Huenneke, 1992). The phenomenon of ‘shifting baselines’ can also influence our perceptions, as the collective memory of what an ‘intact’ ecosystem should look like is forgotten (Pauly, 1995). A similar situation occurred in Britain, where reintroduced wild boar (*Sus scrofa*) have rooted large stands of bluebells (Sims et al., 2014). As bluebells are highly valued for their aesthetics, this disturbance is often viewed as negative. However, Sims et al. (2014) speculate that the monospecific stands of bluebells we see today may actually be the result of a lack of disturbance, which would have maintained greater species richness and diversity in the past. It is likely that the reintroduction of the eastern bettong to Mulligans Flat will have both positive and negative effects, but predicting how this will play out requires a greater understanding of the complex interactions of trophic and engineering effects.

5.5.3 Implications for management and conservation

This study is the first to examine the interaction between an Australian digging mammal and a native geophyte. However, similar interactions between digging animals and geophytes appear to be common around the world, so we would expect more examples to exist in Australia. For example, woylie (*Bettongia penicillata*) and southern brown bandicoot (*Isoodon obeselus*) have been observed eating *Wurmbea sp*, *Drosera bulbosa*, orchids and other monocots (Dr Per Christensen and J. Sampson, pers. comm. in Pate and Dixon 1982). They also observed possibly cormous or bulbous material in the scat of boodie (*Bettongia leseur*), bush rat (*Rattus fuscipes*), potoroo (*Potorous sp*.), and bilby (*Macrotis lagotis*).

Many geophytes also have cultural significance for Indigenous Australians, and were known to be an important food source (Cribb and Cribb, 1976; Gott, 1983; Pate and Dixon, 1982). *Wurmbea* corms were reportedly eaten by Indigenous people, and were known as ‘Blackman’s potatoes’ (Cribb and Cribb, 1976). Human cultivation and fire were important for maintaining populations of geophytes such as murnong (*Microseris walteri*) (Pascoe, 2014). There could therefore be interesting interactions between humans, digging animals and geophytes that need to be understood (Bird and Nimmo, 2018).

While *Wurmbea* is a relatively common species and is not listed as threatened, many other species of geophyte occur within Mulligans Flat (and grassy woodlands elsewhere), some of which are of conservation concern e.g. *Microseris walteri* (murnong), lily and orchid species. We occasionally observed remains of several other geophyte species in diggings, including *Bulbine bulbosa* (bulbine lily), *Arthropodium minus* (vanilla lily), and *Microtis unifolia* (common onion orchid). Several species were recorded in eDNA scat analysis, but in very low amounts compared to *Wurmbea* (unpublished data). While these species may not be as important in the bettong's diet, their rarity also means they are more vulnerable to disturbance and stochastic events. Further research will be required to identify which species are being eaten and may require management.

This study highlights the importance of considering the potential impacts of reintroducing digging animals on recipient ecosystems. Translocation and reintroduction programs are becoming increasingly important for the conservation of Australian digging animals, with the number of predator-free islands and fenced reserves increasing rapidly in recent decades (Legge et al., 2018; Ringma et al., 2018). While there is evidence that reintroducing ecosystem engineers can have widespread benefits, there are also significant risks, particularly if the recipient ecosystem is threatened or contains other threatened species (Harris et al., 2013). These risks are also likely to increase as droughts become more frequent and severe under future climate change. Managers should therefore consider the ecological roles and functions of reintroduced species, and be prepared to manage unexpected consequences. We recommend continued monitoring of *Wurmbea* and other vulnerable plant species to determine appropriate densities for bettongs in Box-Gum grassy woodlands, particularly during drought conditions. Management actions may include adjusting the bettong population or fencing off certain areas to protect threatened plant populations.

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Ethics approval - *This article does not contain any studies with human participants or animals performed by any of the authors.*

Authors' contributions

- AM, SC and SM conceived the overall conceptual framework for the project
- CR and SM conceived the ideas and designed methodology;
- CR and SM collected the data;
- CR, SM, PB and ME analysed the data;
- CR led the writing of the manuscript;
- SM, PB, ME, SC and AM provided advice and edited the manuscript.

All authors contributed critically to the drafts and gave final approval for publication.

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Chapter 5: Supplementary material

Figure S1. Monthly rainfall over the survey period

Figure S2. Bettong population estimates for 2014-2018

Table S1. Total number of surveyed *Wurmbea dioica* plants by plot

Table S2. *Wurmbea dioica* mortality rate

Figure S1. *Monthly rainfall over the survey period (2015-2019) and mean monthly rainfall (solid black line) at Canberra Airport (Bureau of Meterorology). The winter/spring survey period in 2015 was around average, 2016 was one of the wettest on record, while 2017, 2018 and 2019 experienced well below average rainfall.*

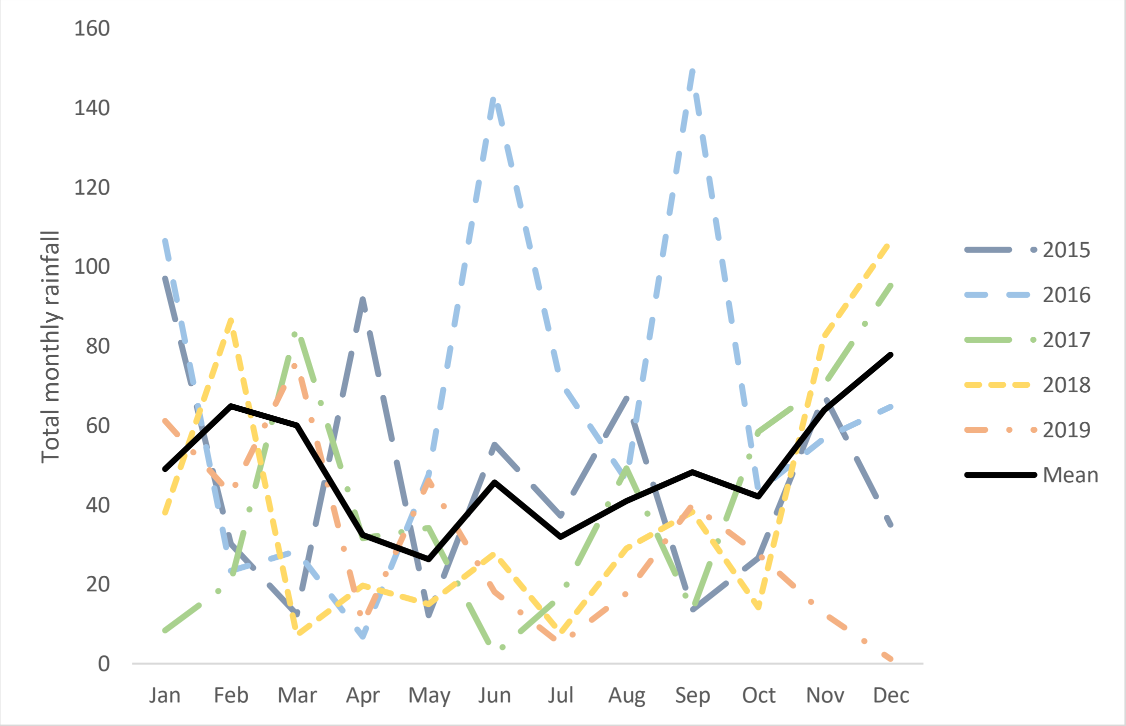

Figure S2. *Bettong population estimates for 2014-2018 (estimate with 95% confidence intervals), calculated from trapping data. For a full description of methods see Manning et al. (2019).*

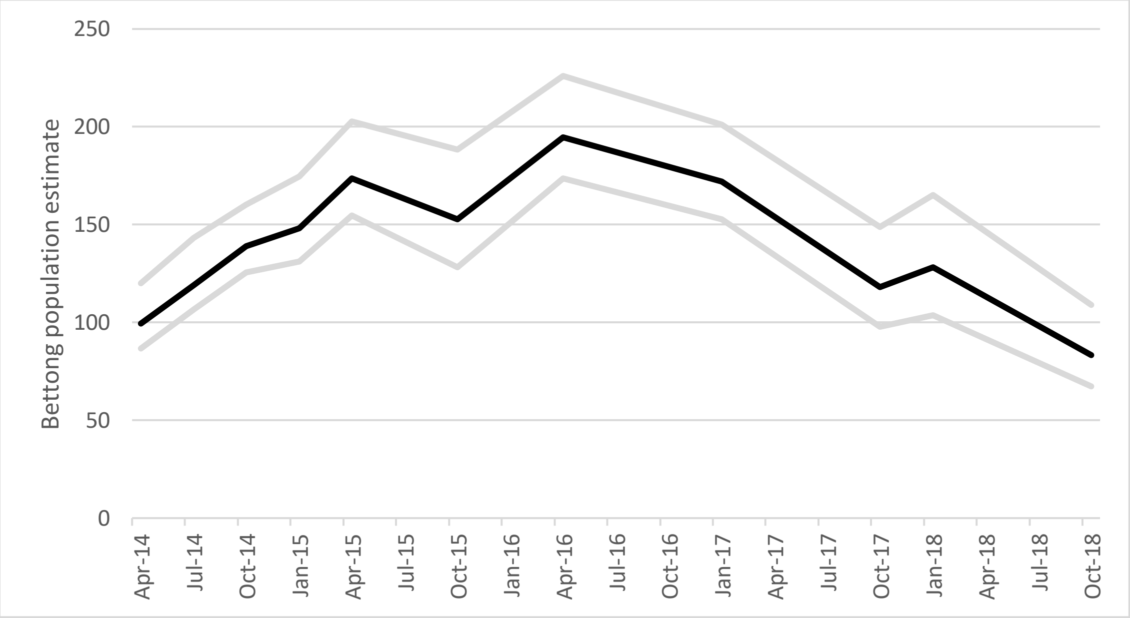

Table S1. *Total number of surveyed Wurmbea dioica plants by plot. Wurmbea plants were surveyed using permanently marked quadrats, treatments described in Table 1. At each survey, we recorded the total number of plants at each plot, summed across the quadrats. Note that only plants in leaf could be counted, but an unknown percentage of the population remain dormant each year. Shaded cells indicate sites where evidence of bettong digging was present. Bettongs gained access to three exclosure plots in the second year of monitoring (2016), and the remaining two plots in the third year (2017).*

SITE	JUL-15	SEP-15	JUL-16	SEP-16	JUL-17	SEP-17	SEP-18	JUL-19	SEP-19
BETTONG									
B_1	114	84	163	195	106	20	18	85	16
B_2	109	95	131	126	122	48	71	141	60
B_3	144	107	126	132	158	118	126	175	93
B_4	121	89	114	81	89	42	44	91	10
B_5	241	186	237	218	218	123	152	139	130
EXCLOSURE									
E_1	135	137	56	41	39	14	19	47	24
E_2	175	228	236	160	85	47	82	142	44
E_3	106	107	98	105	116	97	25	56	28
E_4	100	135	129	122	139	158	186	211	61
E_5	127	134	167	193	67	56	30	43	23
BETTONG 2									
$B2_1$	n/a	n/a	111	60	48	1	5	34	8
$B2_2$	n/a	n/a	180	139	94	63	53	74	24
$B2_3$	n/a	n/a	110	80	53	9	8	75	20
$B2_4$	n/a	n/a	125	124	52	22	5	57	7
OUTSIDE									
O_1	n/a	n/a	158	128	81	37	63	159	87
O_2	n/a	n/a	222	221	187	188	223	424	298
O_3	n/a	n/a	189	250	317	243	338	407	309
O_4	n/a	n/a	162	152	115	90	25	233	24

Table S2. *Wurmbea dioica mortality rate. Plants consumed by bettongs in September, as a percentage of total plants present at the previous July survey (no survey was done in July 2018, so the mortality rate could not be calculated). Mortality was recorded where there was a fresh pit with evidence that a Wurmbea plant had been there previously, either from the photos or from remains of the leaf, stem or corm left in the pit.*

TREATMENT	**SITE CODE**	**2015**	**2016**	**2017**	**2019**
BETTONG	B_1	23.68	4.29	29.25	28.24
	B_2	21.10	16.79	31.15	0
	B_3	15.97	3.17	7.59	0.57
	B_4	23.97	11.40	42.70	1.10
	B_5	0	0.84	0	2.88
	Mean (SD)	**16.94 (10.0)**	**7.3 (6.6)**	**22.1 (17.7)**	**6.6 (12.2)**
EXCLOSURE	E_1	no bettong	39.29	38.46	23.40
	E_2	no bettong	21.61	63.53	29.58
	E_3	no bettong	no bettong	23.28	42.86
	E_4	no bettong	17.83	1.44	9.48
	E_5	no bettong	no bettong	4.48	25.58
	Mean (SD)	**n/a**	**26.2 (11.5)**	**26.2 (25.7)**	**26.2 (12.0)**
BETTONG 2	$B2_1$	n/a	7.21	52.08	14.71
	$B2_2$	n/a	26.11	8.51	0
	$B2_3$	n/a	13.64	32.08	0
	$B2_4$	n/a	3.20	3.85	5.26
	Mean (SD)	**n/a**	**12.5 (10.0)**	**24.1 (22.4)**	**5.0 (6.9)**
OUTSIDE	O_1	n/a	no bettong	no bettong	no bettong
	O_2	n/a	no bettong	no bettong	no bettong
	O_3	n/a	no bettong	no bettong	no bettong
	O_4	n/a	no bettong	no bettong	no bettong
MEAN (SD) OF ALL SITES WITH BETTONG ACCESS		**16.94 (10.0)%**	**13.78 (11.4)%**	**24.17 (20.4)%**	**13.12 (14.3)%**
NO. OF SITES WITH BETTONG ACCESS		5/10	12/18	14/18	14/18

Artist Interlude no. 5

Mulligans Flat Artist in Residence

Emily Birks

Emily Birks was the first artist in residence at Mulligans Flat. Emily joined me in the field for a day to learn about my research on the bettong's relationship with the early nancy (*Wurmbea dioica*). Emily's final exhibition was a collection of highly detailed portraits of the wildlife at Mulligans Flat. Her portrait of the eastern bettong with early nancies, inspired by my research, is shown on the title page of this thesis. Below is a more recent painting by Emily as part of her residency at Tidbinbilla, a wildlife reserve in the south of Canberra which protects breeding populations of eastern bettongs, long-nosed potoroos, and southern brown bandicoots. The painting also includes some of the fungi, plants, and insects that these mammals eat and in turn may benefit from their ecosystem engineering, to illustrate the interconnectedness of the ecosystem. This story of connections and cascades is a strong theme in my thesis, and Emily's work beautifully tells this story and represents the beauty and complexity that draws me to this research.

> *'When we try to pick out anything by itself, we find it hitched to everything else in the Universe'* – John Muir

Hitched to Everything in the Universe

Emily Birks 2019

Ink on paper

Chapter 6:
Soil-disturbing animals as ecosystem engineers - clarifying goals for conservation and restoration in Australia

Ross, C.E., Barton, P.S., Cunningham, S.A., Decker, O., Eldridge, D.J., Fleming, P.A., Gibb, H., Johnson, C.N., Jones, C.G., Maisey, A., Manning, A.D., McIntyre, S., Munro, N.T., Valentine, L.E., in prep. Soil-disturbing animals as ecosystem engineers - clarifying goals for conservation and restoration in Australia. *Biological Conservation (in prep)*

6.1 *Abstract*

Digging or soil-disturbing animals are found in many ecosystems worldwide and play important roles as ecosystem engineers. In Australia, many digging animals have experienced widespread declines due to introduced predators and have therefore been targeted for conservation and reintroduction programs. Species translocations are increasingly being used as a conservation strategy, usually aiming to establish populations in fenced reserves or offshore islands (also known as ‘sanctuaries’ or ‘havens’). However, there are many gaps in our understanding of how soil-disturbing engineers impact ecosystem processes, and translocations often proceed without consideration of the potential ecological consequences. We explored research on soil-disturbing engineers and their contribution to restoration in Australian ecosystems, to identify knowledge gaps and factors that should be considered when reintroducing ecosystem engineers. We learned that while sanctuaries help to conserve populations of ecosystem engineers, they also provide an opportunity for research into their ecological roles. Sanctuaries also impose significant limitations and risks, however, which may be magnified when the species being reintroduced is an ecosystem engineer. We recommend that researchers and practitioners involved in species translocations first need to have clear and specific goals and an explicit framework to inform species and site selection. There is a need to incorporate experimental design in the early stages of planning and establish appropriate baselines, controls, and replication. Ongoing monitoring is vital to recognize and manage unexpected consequences. These actions will lead to improved management of sanctuaries and success of future translocations of ecosystem engineers.

Keywords: Biodiversity, conservation, haven, reintroduction, sanctuary, soil-disturbing, translocation

6.2 *Introduction*

Species translocations are increasingly being recognized as critical to the conservation of many vulnerable taxa worldwide (IUCN/SSC, 2013). The aim of translocations is usually to conserve particular species, but these species may also play important ecological roles. Species that are known as ‘ecosystem engineers’ are, by definition, expected to have widespread impacts on ecosystems because they modify habitat or resource availability for other species (Byers et al., 2006; Jones et al., 1994). For example, the reintroduction of beaver (*Castor* spp.) to parts of Europe has had significant impacts on waterways, increasing plant diversity and habitat heterogeneity (Law et al., 2017; Stringer and Gaywood, 2016; Wright et al., 2002). However, there are many gaps in our understanding of how ecosystem engineers affect ecosystem processes, and reintroductions are therefore likely to also have unexpected consequences (Nogués-Bravo et al., 2016). While the ecological effects of ecosystem engineers are widely recognized, they are still rarely considered in reintroduction programs leading to missed opportunities for research and a failure to consider potential negative effects (Ewen, Soorae and Canessa, 2014; Brichieri-Colombi and Moehrenschlager, 2016; Palmer *et al.*, in review). Managers must therefore have clearly defined goals when selecting species and sites for reintroduction and be prepared to monitor and manage potential outcomes.

Globally, soil-disturbing animals are regarded as important ecosystem engineers in many ecosystems (Berke, 2010; Davidson et al., 2012; Mallen-Cooper et al., 2019; Platt et al., 2016). These are species that either burrow or forage in the soil, and include mammals (e.g. prairie dogs, badgers, porcupines), birds (e.g. turkeys), reptiles (e.g. monitors) invertebrates and microbiota (e.g., worms and bacteria). Biopedturbation is an important ecosystem process, contributing to functions such as nutrient cycling and water infiltration (Hole, 1981; Whitford and Kay, 1999). The widespread decline and loss of soil-disturbing animals is thought to have contributed to the degradation of ecosystems and it has been suggested that their reintroduction could improve a range of ecosystem processes and assist with restoration (Eldridge and James, 2009; Fleming et al., 2014; Law et al., 2017; Manning et al., 2015; Munro et al., 2019; Smith et al., 2019).

Australia has a diverse vertebrate digging fauna, with species found across many ecosystems, and playing a variety of important ecological roles (Fleming et al., 2014). Many of these species have experienced severe population declines and have therefore been targeted for conservation and reintroduction programs. The reintroduction of soil-disturbing species has also created new opportunities for research into their role as ecosystem engineers and their potential for restoration (Manning et al., 2015). However, the establishment of reintroduction programs has, to date, often been *ad-hoc* and opportunistic, and limited by the availability of sites and funding. This has led to calls for more strategic planning in species and site selection to focus on underrepresented species or ecosystems (Ringma et al., 2017). Yet this approach still has a strong focus on species' conservation status, and there are many other factors that could be considered in such planning.

The goals of species translocations are often poorly defined, which makes it difficult to determine success (Ewen et al., 2014; Robert et al., 2015). While the potential for species reintroductions to contribute to restoration is increasingly recognized in theory, most translocations are still focused largely on the conservation of particular species, rather than restoring ecosystem function or communities (Palmer *et al.*, in review). Moreover, such introductions become the key focus of resourcing and public interest and can overshadow the more complex issues associated with the effects of reintroduced species on the whole ecosystem. Ecosystem engineers are likely to cause a range of effects through both engineering and trophic effects, which may be beneficial or detrimental to other species and may be perceived as positive or negative (Jones et al., 1997). In many cases, these animals have been absent for decades or centuries, and are being returned to ecosystems that have been fundamentally altered through soil degradation, clearing and introduced species. We therefore have varying capacity to predict the precise effects of reintroducing ecosystem engineers, due to a paucity of reference sites and the complexity of ecological cascades and feedbacks. It is important to fill these knowledge gaps to increase our understanding of the potential impacts of ecosystem engineers and inform management.

A major complicating factor is that many reintroductions have been in ‘sanctuaries’ or ‘havens’, usually taking the form of large fenced reserves or offshore islands where introduced predators have been eliminated (Legge et al., 2018). Sanctuaries are a vital component of species conservation strategies worldwide (Hayward and Kerley, 2009; Innes et al., 2012; Woodroffe et al., 2014), with the number of sanctuaries being established rising rapidly in recent decades (Burns et al., 2012; Ringma et al., 2018). Several features of sanctuaries provide unique opportunities for research on the ecological impact of ecosystem engineers, but they also present significant challenges for both managers and researchers (Dickman, 2012; Lindsey et al., 2012; Manning et al., 2011; Pickard, 2007).

Given the unclear goals and a focus on translocations into sanctuaries, we aimed to identify factors emerging from the literature to inform research and conservation of ecosystem engineers. We therefore asked the following questions:

1. Are reintroduced ecosystem engineers contributing to restoration in Australia? To address this question, we explored the literature examining ecological effects of soil-disturbing engineers in Australian ecosystems, and identified knowledge gaps and uncertainties around reintroductions.
2. What is the role of sanctuaries for the translocation of ecosystem engineers? To address this question, we discuss the benefits and limitations of sanctuaries for conservation and research on ecosystem engineers.
3. What factors need to be considered when reintroducing ecosystem engineers? To address this question, we constructed a new framework for identifying the goals of species reintroductions, incorporating the factors that should be considered in the planning and management of reintroductions. We also provide recommendations for future translocations and research on ecosystem engineers.

6.3 *Ecological effects of soil-disturbing engineers in Australian ecosystems*

Soil-disturbing vertebrates occur in most Australian ecosystems, and include species such as wallabies, bettongs, bilbies, bandicoots, echidnas, wombats, numbats, ground-foraging birds (e.g. lyrebirds, malleefowl) and reptiles (e.g. goannas). Many of these species have experienced significant declines in population and range, largely due to predation by introduced predators

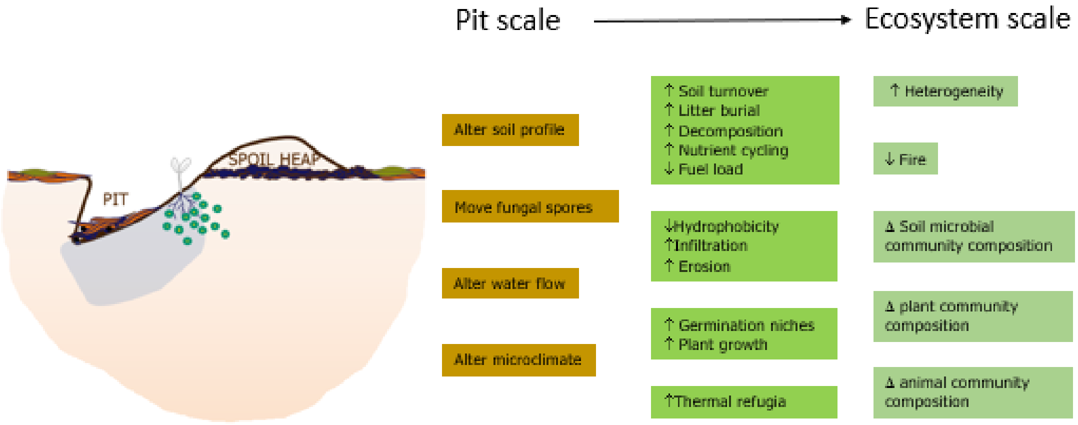

Figure 1. *Engineering effects of Australian digging animals across spatial scales***.** *Effects summarised from studies on Australian digging vertebrates. On the left is a diagram of the structure of a typical foraging pit with spoil heap of discarded soil. Effects can be observed at the scale of a single pit or burrow, or up to the ecosystem scale.*

such as cats (*Felis catus*) and red foxes (*Vulpes vulpes*) (McKenzie et al., 2007; Woinarski et al., 2015). Of 29 Australian digging mammal species, nearly 70% have an International Union for Conservation of Nature listing (Fleming et al., 2014). The threatened status of soil-disturbing animals has meant that digging animals have been disproportionately represented in recent translocations, and many species are restricted only to offshore islands or fenced sanctuaries (Legge et al., 2018).

Soil-disturbing animals can create a range of structures including deep burrow systems, foraging pits of varying depth, mounds, or they may simply disturb the top litter layer. Their diggings have a range of effects on ecosystem functioning (Figure 1) and provide resources for other species. For example, digging increases soil turnover, increasing water infiltration and creating patches of higher fertility (Davies et al., 2019; Eldridge et al., 2012, 2010; James et al., 2009). Burrows and pits create a more mesic microclimate, which may provide habitat for many species of vertebrates (Dawson et al., 2019; Hofstede and Dziminski, 2017) invertebrates (Grossman et al., 2019; Read et al., 2008), microbes (Eldridge et al., 2016, 2015; Valentine et al., 2018). Pits and mounds may also provide a germination niche for plants (Dodd, 2009; James et al., 2010; Pyrke, 1994; Ross et al., 2020; Valentine et al., 2018). Mycophagous species such as bettongs and bandicoots disperse the spores of ectomycorrhizal fungi in their faeces and alter soil fungal communities (Clarke et al., 2015; Lamont et al., 1985; Taylor, 1992b; Vernes et al., 2015). These fungi form symbiotic relationships with many plant species (Claridge et al., 1992; Johnson, 1996), and can therefore influence plant growth and resilience (Dundas et al., 2018; Moore et al., 2014; Reddell et al., 1997; Tay et al., 2018). The incorporation of litter into soil also accelerates decomposition (Decker et al., 2019; Valentine et al., 2017), reducing fuel loads and fire risk (Hayward et al., 2016; Nugent et al., 2014; Ryan et al., 2020; Smith et al., 2016).

While biopedturbation is widely accepted to be important for ecosystem function, soil-disturbing species also have effects that may be perceived as negative (Jones et al., 1997). For example, digging may increase erosion (Eriksson and Eldridge, 2014) or create sites for invasive plants to establish (Ross et al., 2020). The likelihood that negative effects will occur increases with engineer density. Therefore, in sanctuaries where predators are absent, overpopulation is a significant risk that could impact on other species or contribute to degradation (Linley et al., 2016; Moseby et al., 2018).

6.3.1 Engineering vs trophic effects

All ecosystem engineers also have trophic effects, for example as predators or herbivores, yet the engineering and trophic roles of engineers are very rarely considered together (Coggan et al., 2018; Sanders et al., 2014). In the case of soil-disturbing animals the trophic and engineering effects are closely linked because the engineering results from foraging, so introducing the species involves introducing both soil engineering and consumer functions (Coggan et al., 2018).

In some cases, trophic effects of introduced digging animals have led to unexpected and undesirable outcomes. While digging may have positive effects on seedling germination at the pit-scale (James et al., 2010; Ross et al., 2020), Verdon et al. (2016) found that seedling herbivory by reintroduced digging animals resulted in fewer seedlings overall. Reintroduced populations of the burrowing bettong (*Bettongia lesueur*) at Arid Recovery Reserve in South Australia increased rapidly in the absence of predators, leading to significant vegetation damage and declines in plant species richness (Linley et al., 2016; Moseby et al., 2018). At Mulligans Flat Woodland Sanctuary in Canberra, eastern bettongs (*Bettongia gaimardi*) have been observed digging up large numbers of geophytes, some of which are of conservation concern (Ross *et al.* in prep). Some digging animals may also act as seed predators (Mills et al., 2017) or prey on the eggs of ground-nesting birds (Fulton, 2017) and turtles (Bowler, 2018).

6.3.2 Trophic and ecological cascades and feedbacks

Both engineering and trophic interconnections can lead to ecological cascades. Silvey *et al.* (2015) found that sites with reintroduced digging animals had lower numbers of dune scorpions (*Urodacus yaschenkoi*), while wolf spiders (*Lycosa gibsoni* species group) increased. As scorpions are known to be predators of spiders, they hypothesised that the reintroduced vertebrates had an indirect effect on spider assemblages through predation on scorpions (Silvey et al., 2015). In another study, disturbance by reintroduced digging animals was shown to decrease the rate of decomposition by termites, and influence interactions between termites and ants (Coggan et al., 2016). Browsing by highly abundant burrowing bettongs has also led to declines of another reintroduced herbivore, the greater stick-nest rat (*Leporillus conditor*) (Moseby et al., 2018).

The structural, abiotic and biotic effects of ecosystem engineering may also have feedbacks to the engineer itself (Jones et al., 2010). Several studies from Australia and internationally have suggested that digging may assist dispersal of fungal spores or encourage seed germination, with the effect of increasing food availability for the engineer. However, it is difficult to demonstrate a direct mutualistic relationship (Gutterman, 1987; Johnson, 1996; Lovegrove and Jarvis, 1986; Murphy et al., 2005).

6.3.3 Native vs Exotic engineers

Ecological replacement or taxon substitution proposes that the ecological roles of extinct species could be replaced by non-indigenous species that are taxonomically or functionally similar (Griffiths et al., 2010; Seddon et al., 2014). Across much of Australia, the decline of native digging animals has coincided with the expansion of the introduced European rabbit (*Oryctolagus cuniculus*) (James et al., 2011). Rabbits act as ecosystem engineers in their native environment (Gálvez-Bravo et al., 2011, 2009), have a similar body size and create foraging pits and burrows like many native species. Studies comparing the pits and burrows of native digging species and rabbits in both arid and temperate ecosystems found that native species have substantially higher *per capita* digging rates than rabbits, and rabbit foraging pits are also shallower than those of native diggers (Eldridge and James, 2009; James and Eldridge, 2007; Munro et al., 2019). The morphology of pits can be very important, as steeper sided pits are more effective at trapping litter and seed, and may prevent removal of seed by ants (James et al., 2009; Radnan and Eldridge, 2017; Ross et al., 2019). Pits of native animals had higher labile carbon, and supported 80% more seedlings than rabbit pits (James et al., 2010; James and Eldridge, 2007). However, rabbit burrows were able to provide thermal refugia for some species such as echidnas (Read et al., 2008). The evidence from these studies suggests that rabbit diggings are not analogous to those of native digging animals, and cannot fully replace their ecological functions. In addition, rabbits have other negative impacts that may outweigh any positive effects (Eldridge and Koen, 2008; Radnan and Eldridge, 2017; Read et al., 2008). However, for some ecosystem processes (e.g. provision of thermal refugia), the activities of exotic diggers may be the only possible substitute for lost native fauna, and this should be considered where rabbits are controlled without replacement by native species (Read et al., 2008).

The negative regard we have for invasive species as disruptors of conservation goals has meant that their disturbances and foraging are generally also viewed in a negative light. Yet, it would also be a mistake to assume that the digging and foraging activities of native fauna will be beneficial for all native biota, or that their return will recreate a past or historical state. On the contrary, just as exotic species are viewed as disruptors, a native species that has been absent for over a century could also have the potential to disrupt species or processes that have adapted to their absence.

6.3.4 Spatial and temporal scale

There is still a large degree of uncertainty about the effects of soil bioturbation on ecosystems, particularly across different spatial and temporal scales (Hastings et al., 2007). Most research has been done at small scales, i.e. comparing a single pit or mound with a neighboring undisturbed area, and at a single point in time (Coggan et al., 2018). However, the effects of multiple pits are not necessarily additive, and digging rates can be highly variable depending on season, resource availability or substrate (Alkon, 1999; James et al., 2011; Johnson, 1994b). Studies performed at multiple scales show contrasting effects of digging (Decker et al., 2019; Grossman et al., 2019; Verdon et al., 2016). Grossman (2019) found that mammal pits were associated with an increase in the number and size of invertebrate burrows, but this effect was only visible at the pit scale and not at the landscape scale. Many studies only attempt to calculate pit density (number of pits per area) without considering spatial or temporal variability (Munro et al., 2019), and very few have measured decay rates i.e. how long it takes for the structure and effects of a disturbance to disappear after its creation (Raynaud et al., 2013). To understand the cumulative effects over the whole landscape, we need to understand these spatial and temporal patterns of disturbance. This is important for predicting appropriate population levels or distributions, and managing potential impacts. For example, a certain population might be sustainable if the impacts are spread over the whole area, but not if they are concentrated in parts of the landscape.

6.3.5 Environmental context

The effects of soil-disturbing engineers are likely to vary with environmental context at all spatial scales (Crain and Bertness, 2006). Worldwide, over 50% of studies on ecosystem engineering by digging animals have been in arid biomes, and in Australia there have been very few studies in temperate regions (Coggan et al., 2018). A global review by Mallen-Cooper et al. (2019) found that the effects of digging on soil properties were more pronounced as aridity increased. A study in a temperate grassland found that bettong diggings had little effect on soil nutrients, but were able to provide a germination niche for native plants by creating gaps in the dominant grass sward (Ross et al., 2020, 2019). The few large-scale studies addressing the impacts of ecosystem engineers in Australia have revealed surprising and contradictory results. For example, Decker et al. (2019) found that digging animals increased soil carbon, nitrogen and enzyme activity, but with greater effects at sites with lower rainfall (Decker et al., 2019). In contrast, The negative effects of digging mammals on termite assemblages and decomposition were greatest in more mesic areas (Coggan et al., 2016; Coggan and Gibb, 2019), and short-term microbial decomposition was only improved by digging mammals in wetter sites (Decker et al. in review). This context-dependency suggests that findings of studies based at a single site or time period have limited applicability to different sites or sampling periods.

6.3.6 Modified ecosystems and reference condition

Predicting the impact of ecosystem engineers is complicated by the fact that they are often being reintroduced into ecosystems that have been highly modified in the decades or centuries since these species disappeared (Hobbs and Cramer, 2008). Most Australian ecosystems have experienced degradation or modification to varying extents, due to clearing, overgrazing, soil erosion, invasive species, changed fire regimes, loss of biodiversity and climate change (The Department of Agriculture, Water and the Environment 2016). These factors may be significant barriers to restoration (Hardman et al., 2016; Hobbs and Cramer, 2008; Prober et al., 2002). In many cases there is no reference condition against which to assess the success of restoration; for example, appropriate population levels or digging densities. While it is hoped that the reintroduction of ecosystem engineers can assist with the restoration of key processes, there is a risk that they may also exacerbate or add to existing land management problems.

6.4 *Benefits and limitations of sanctuaries for ecosystem engineer conservation and research*

Sanctuaries are becoming an increasingly important part of conservation strategies, particularly in Australia and New Zealand (Hayward and Kerley, 2009). In Australia, there are currently seventeen fenced areas (with a further 7 under construction) and 101 island havens (22 have had reintroductions) containing 188 populations of 38 predator-susceptible threatened mammal taxa (Legge et al., 2018; Ringma et al., 2018). These sanctuaries are managed by both public and private organizations, including state and territory governments, and not-for-profit organisations (e.g. Bush Heritage, Australian Wildlife Conservancy). The benefits and limitations of conservation fencing have been widely discussed in the literature (e.g. Pickard, 2007; Scofield, Cullen and Wang, 2011; Burns, Innes and Day, 2012; Dickman, 2012; Malpas *et al.*, 2013; Woodroffe, Hedges and Durant, 2014; Bull *et al.*, 2018). Sanctuaries have been shown to greatly increase the success of species translocations and offer opportunities for research and informed management, but also risk disruption of the existing ecosystem if not managed appropriately. These risks may be magnified when the species being reintroduced is an ecosystem engineer that is expected to have widespread impacts on ecosystem processes and function.

Several features of sanctuaries make them ideal sites for research on the impacts of ecosystem engineers (Table 1). Sanctuaries can act as ‘outdoor laboratories’ and provide a level of control that enables the study of a known population within a defined area (Hayward and Kerley, 2009; Manning et al., 2011; Somers and Hayward, 2012). The ability to impose effective experimental treatments and controls is also an advantage, due to the potential to exclude or enclose selected species (Manning et al., 2011). Since most ecosystem engineering studies to date have been observational, this is a very useful feature (Coggan et al., 2018). Sanctuaries

Table 1: *Benefits and limitations of sanctuaries for ecosystem engineers*

Benefits	*Limitations*
Conservation	
Often only reliable method of predator control *Control over management* *Greater ability to monitor populations within limited area*	Expensive to build and maintain Limited size – not large enough for some species to have self-sustaining populations (including natural predators) Fence is a barrier to natural migration Risk of overpopulation and damage to ecosystem and other species Ongoing management required
Research	
Ability to apply experimental treatments and controls *Control over management* *Attracts resources and people* *Volunteering and citizen science*	Expensive to build and maintain Ongoing management required Lack of site level replication
Socio-economic	
Eco-tourism and education opportunities *Volunteering and citizen science*	Public access – overuse, vandalism Public perception

often act as research ‘hubs’ and as a focus for public engagement, attracting resources and people and providing opportunities for eco-tourism and citizen science.

Conversely, there are limitations to the sanctuary model in regard to the management of reintroduced ecosystem engineers (Table 1). While sanctuaries have been very successful in boosting populations of threatened species, they are limited in terms of their size, and there is a substantial cost of establishment and ongoing management. Their small size makes it difficult to maintain natural regulation of populations by native predators or natural abundances of species otherwise common in the landscape (e.g. kangaroos). This also limits our ability to capture landscape-level processes (e.g. watershed hydrological dynamics). The removal of exotic predators may also result in population increases of both reintroduced and pre-existing species, but also the loss of anti-predator behaviors (Jolly et al., 2018; Moseby et al., 2018; West et al., 2018). Most sanctuaries have several reintroduced species, leading to the potential for engineers to interact with one another in unexpected ways (though noting that this is often the aim). A further disadvantage is the difficulty of replicating research results, both within and between sanctuaries. Cross-sanctuary studies are rare and can generally only be done across different ecosystem types because of the limited site selection. This need for increasing levels of management can create dilemmas when it comes to scientific and socio-economic priorities.

6.5 *Recommendations for management and future research*

Reintroductions provide a unique opportunity to study the effects of ecosystem engineers, but unfortunately this is often overlooked in the planning process. Given the significant cost of sanctuaries and reintroductions, it is in the interests of managers, funding bodies and researchers to maximize the chances of success and return on investment. Yet, there is no clear way to achieve this, and guidelines are needed to show the links between goals and impacts. Here, we present a new framework (Figure 2) to guide the planning and monitoring of reintroduced ecosystem engineers and their effects, in order to improve outcomes for research, conservation and restoration, as well as mitigate the potential risks.

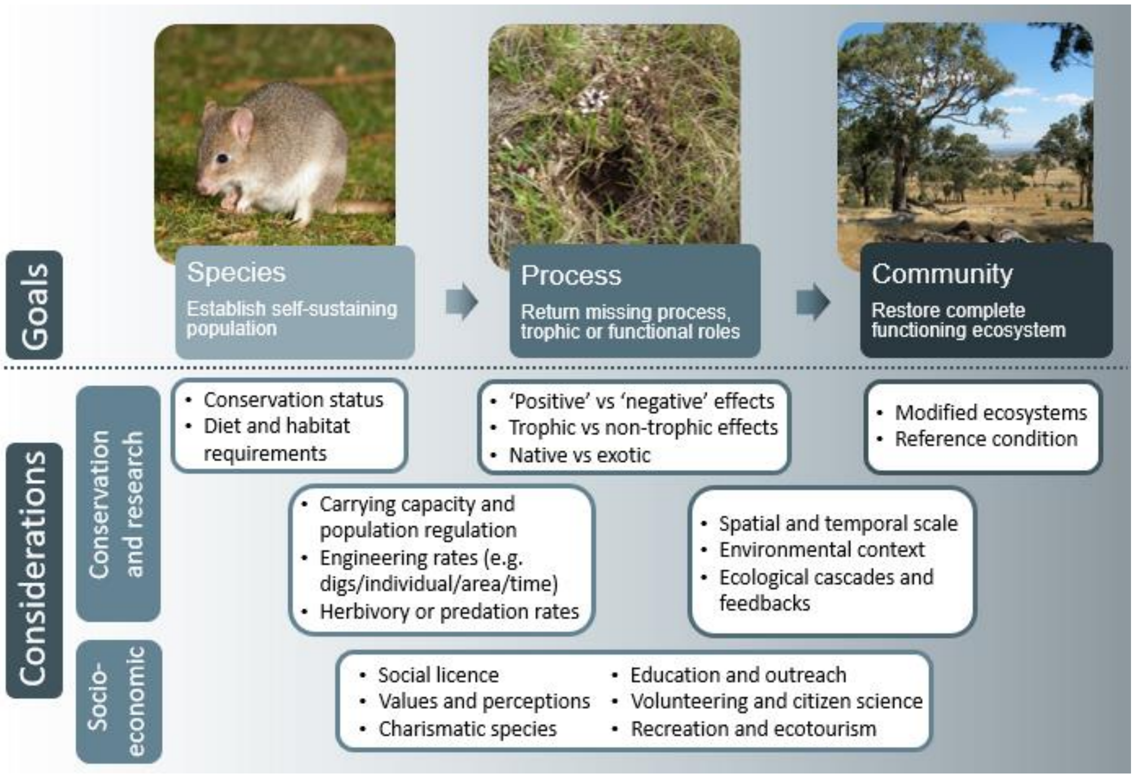

Figure 2. *Framework for linking translocation goals with considerations**.** The conservation goals of a translocation can be visualized along a spectrum from a focus on protecting individual species, to restoring ecosystem functions or processes (e.g. pollination, nutrient cycling), to a much broader aim of restoring or creating a fully functioning community. At each stage along this spectrum there are a range of factors that should be considered, to help guide site and species selection and what research and monitoring needs to be done. Photo credits (left to right): JJ Harrison (www.jjharrison.com.au), Catherine Ross, Philip Barton*

6.5.1 Goals and considerations for translocation and ecosystem engineers

The critical importance of clear goals that are measurable and informative has been highlighted in much recent conservation literature (Ewen et al., 2014; Lindenmayer et al., 2015; Lindenmayer and Likens, 2009; Westgate et al., 2013). However, the aims of translocations are often poorly defined in the planning stages, making it difficult to determine success (Palmer *et al.,* in review).We have therefore developed a framework to help managers clarify their goals and identify considerations for any translocation, particularly when ecosystem engineers are involved (Figure 2). These considerations can help to guide site and species selection, and determine what research and monitoring needs to be done. In this framework, the conservation goals of a translocation can be visualized along a spectrum from a focus on protecting individual species, to restoring ecosystem functions or processes (e.g. pollination, nutrient cycling), to a much broader aim of restoring or creating a fully functioning community. While it is important to consider the full range of this spectrum, one aspect will usually take priority over the others.

While it may not always be clearly stated, the implicit goal of most translocations is to protect a particular species, with the aim of establishing a self-sustaining population (Palmer *et al.*, in review). The field of reintroduction biology has largely focused on improving success for the introduced species, with species and site selection usually based on multiple priorities, such as the species' conservation status, diet and habitat requirements (Batson et al., 2015; Seddon et al., 2007). However, approaches to date have not necessarily considered the species' impact on ecosystem function or their role in the ecosystem as a whole. This may lead to unexpected outcomes and could threaten the long-term success of the project. We therefore need greater consideration of ecological roles of species prior to introduction, to avoid these risks and increase the chances of success.

If the main goal of the translocation is to restore ecosystem processes or functions, we start to consider the species' functional roles and the impact they may have on the recipient ecosystem. The identity of the species becomes less important, creating the option for taxon substitution with another native or exotic species that can perform the same function. As the impact of a species is dependent on the population density, issues such as the carrying capacity and individual engineering rates fall between Species and Process goals.

If the goal is to restore a fully functioning ecosystem, we need to define what this means and recognize that we are working in modified ecosystems. This can be complicated by a lack of reference sites and the effect of 'shifting baselines' (Manning et al., 2006). Many of the current knowledge gaps exist in the space between Process and Community goals; most of the ecosystem engineering research has been at small scales (i.e. individual foraging pits), so there is still a lot of uncertainty about how to scale up these effects across environmental gradients and over time (Coggan et al., 2018).

6.5.2 Public perceptions of ecosystem engineers

Public perception is an important consideration for any translocation, including how it shapes the conservation and research agendas of the organizations doing reintroductions, particularly those dependent on donor funding. The values that we as humans place on species and ecosystems may influence our perceptions of whether the outcomes are positive or negative. In some cases, education and tourism goals may be in conflict with conservation goals, and may sway the selection of species toward charismatic species. Ecosystem engineers may benefit from the fact that their role in the ecosystem makes it easier to communicate with the public about why we need to protect them. On the other hand, this can also make it more difficult to talk about perceived negative effects or the need for population control.

Sanctuaries have been criticized as being as expensive and demanding to manage as zoos, with little prospect of achieving long-term conservation of vulnerable species (Scofield et al., 2011). However, many species currently survive only in fenced reserves and on islands. The objective of free-living populations (i.e. outside predator-exclusion sanctuaries) is only likely to be achieved when predator control technologies are effective over entire landscapes. Until this is achieved, sanctuaries will play an important role as ‘stepping stones’ for managing populations and understanding their impacts on ecosystems before reintroduction into the wider landscape.

6.5.3 Site selection

Translocation sites and sanctuaries are often established opportunistically in response to funding availability and public support. However strategic planning that takes into account ecological circumstances is likely to be more effective at maximizing conservation outcomes (Ringma et al., 2017). If the goal is species conservation, the site must be suitable for the species that is to be introduced, with adequate resources and habitat to support a viable population. However, with a greater emphasis on restoring processes and ecosystems rather than just species, site selection should consider the impacts on the recipient ecosystem. This is particularly important where the site is a threatened ecosystem, and which may contain other threatened species (Harris et al., 2013). Where possible, we should also choose sites in locations that have been poorly researched (e.g. temperate or tropical regions), to facilitate more studies across different environmental conditions.

6.5.4 Directions for future research

Translocations of ecosystem engineers provide a unique opportunity for research, however this is rarely implemented in the planning phase (Palmer *et al.*, in review). Here we provide some recommendations for future research to address some of the knowledge gaps we have identified. Ideally, future translocations should be explicit about their goals, and put in place long-term monitoring to determine whether those goals have been met.

Once the site and species for translocation have been selected, it is vital to set up good experimental designs including collecting baseline data and appropriate control sites. Controls may be needed at multiple scales; studies of fenced reserves have often used ‘outside’ as a control, however this is likely to be confounded by the presence of predators and differences in management, and may not capture the small-scale differences created by digging pits. This also raises the issue of pseudoreplication (unless comparing across multiple reserves). Because many ecosystem engineers in Australia persist almost exclusively within sanctuaries, cross-sanctuary comparisons provide the best avenue through which to understand the context-dependence of their impacts on ecosystems (Coggan et al., 2018). However, this will require greater collaboration and use of methods that enable replication and comparison across sites.

Monitoring over time will prove relevant to identifying whether the reintroduction has met its goals in terms of species conservation, impacts on ecological processes, and community outcomes, for example:

Monitoring the translocated population regularly. Regular population surveys are vital to monitor the success of the reintroduction and provide accurate estimates for carrying capacity and *per-capita* digging rates. Assessing condition and reproductive success can also give an indication of resource availability and population stability (Manning et al., 2019). Population control could be necessary, and this option needs to be considered as part of initial planning, e.g. one-way gates, export to other areas, culling, fertility control, or introducing natural predators (which could also provide evolutionary advantages).

Identifying and monitoring at-risk species or potential problems (e.g. weed invasion, erosion). Since most of the detrimental effects that have been identified are due to trophic interactions, identifying diet of the monitored species (e.g. through analysis of scats) can be informative.

Estimating soil turnover, including spatial and temporal variation (e.g. between seasons or vegetation types). Estimating *per-capita* digging rates relies on quantifying the number of digs created by each individual in a given area, over a certain time period (Digging rate = Digs/Area/Time/Individual). Most studies have simply counted the number of digs in a certain area, but this method cannot give a *per-capita* rate and is therefore difficult to interpret under a fluctuating population (Munro et al., 2019).

Estimating longevity of diggings. Decay rates can be measured by monitoring pit dimensions and infill rates over time, taking into account variation due to vegetation type, substrate, weather conditions, season and resource availability (Ross et al., 2019).

Using experimental manipulation. For example, the use of artificial or simulated diggings can be a useful tool either before or after reintroduction, to predict possible effects of digging or to separate the physical effects of digging from other ecosystem effects such as herbivory or insectivory, or site effects such as different microsites. Observational or correlative studies may still be used, e.g. where baseline data was not collected.

6.6 *Conclusions*

Species translocations and sanctuaries are vital for the conservation of threatened species, and this is likely to continue into the future. The recent rapid increase in reintroductions in Australia has provided an opportunity to study the impacts of soil-disturbing ecosystem engineers and their potential to restore degraded ecosystems. However, many reintroductions proceed without full consideration of the ecological effects, which has led to missed opportunities for research and failure to manage adverse impacts.

Research to date has found that digging animals cause a range of impacts. While these species have the potential to assist with restoration of degraded ecosystems, there can also be unexpected consequences that may be perceived as negative. There are still many knowledge gaps that lead to uncertainty, such as engineering vs trophic effects, native vs exotic species, environmental context, and modified ecosystems. In addition, the fact that many reintroductions are happening within predator-free islands or fenced reserves increases the risk for overpopulation and adverse impacts on other species.

We recommend greater clarity is required regarding the goals of reintroductions in order to guide site and species selection and manage unexpected outcomes. We argue that planning for future reintroductions should consider the ecological role of the species and the effect that may have on the stated goals. Species that are recognized as ecosystem engineers may require extra consideration and caution. It may be prudent to avoid reintroductions into high quality sites where the risk to the existing ecosystem is greater. There is a need to establish baseline information and set up appropriate experimental design in order to monitor impacts after reintroduction. Finally, to increase our chances of success we should always expect the unexpected and be prepared to manage (or not) unintended consequences.

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Author contributions

Catherine Ross: Funding acquisition, Project administration, Writing – original draft preparation

Adrian Manning: Funding acquisition, Project administration, Supervision

All authors: Conceptualization, Writing – review and editing

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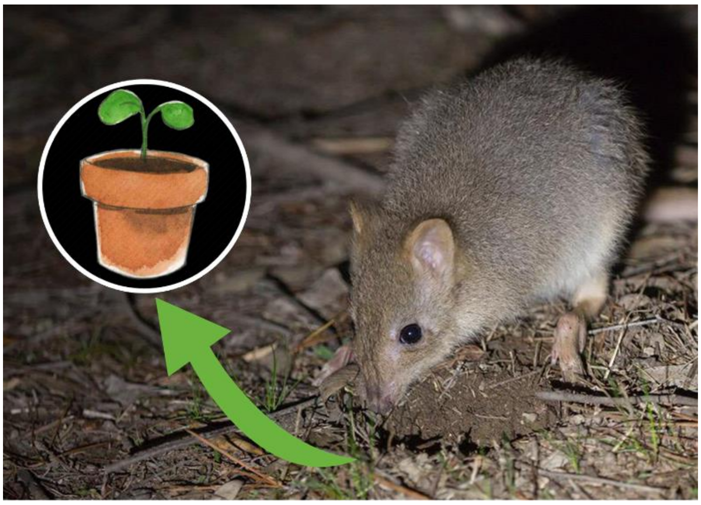
Appendix: ANU Three Minute Thesis

The Three Minute Thesis is an annual competition for PhD students, held at over 200 universities worldwide. Students have three minutes and a single slide to summarise their thesis, and make it interesting and understandable for a lay audience. I entered the competition in 2018, and was thrilled to win runner up and people's choice in the college round and be offered a chance to compete in the ANU finals. It was an amazing privilege to have this opportunity to talk about my research in front of a large audience and to improve my communication skills, and I found this experience to be one of the most valuable of my PhD. Below is a transcript of my talk and the slide that accompanied it.

After winning runner up and people's choice in the college round

Competing in the ANU 3MT Final at Lllewellyn Hall

Bringing Back the Bettong



If you took an evening walk in the bush around Canberra 100 years ago, what would you have seen? The woodlands would have been teeming with wildlife, small animals such as bandicoots, quolls and bettongs. But since European settlement, the woodlands have been cleared, overgrazed and overrun by weeds and feral animals, and many of our native species have disappeared. In fact, Australia has the highest mammal extinction rate in the world, and many of these species were lost before we really understood the roles they play in the ecosystem. So, what would happen if we could bring them back?

This is the eastern bettong, a rabbit-sized relative of the kangaroo. They were once so common in eastern Australia that they were considered a pest, but they disappeared from the mainland around 100 years ago. Luckily, the eastern bettong still survives in Tasmania, and six years ago we managed to bring a small population and release them into a fenced reserve called Mulligans Flat Woodland Sanctuary. The sanctuary acts like a giant outdoor laboratory, allowing us to study the impact of the bettongs on their environment.

Well, since the reintroduction, our bettongs have been getting busy, and not just in the way you might think. They have been digging away every night in search of truffles, roots and bulbs. I have estimated that each individual bettong can dig up to 200 pits every night. That adds up to over 3 tons of soil turned over every year. As a plant ecologist, I wanted to find out how this digging might affect the soils and vegetation. By measuring and monitoring soil nutrients, moisture and temperature in the diggings, and counting and identifying thousands of tiny seedlings, I have found that the diggings act like little flowerpots, providing the perfect conditions for seeds to germinate. But it's not quite that simple. Reintroducing a species after 100 years can have unexpected consequences, and the disturbance created by bettong digging could just increase weed invasion. But my research has shown that native plant species actually benefit more from the digging than the weeds.

Digging animals like the bettong alter the structure of the ecosystem and provide resources and habitat for other species, and for this reason they are known as ecosystem engineers. If we can bring back the bettong, then we could not only save one species, but also help to restore an entire ecosystem. So that maybe, 100 years from now, you'll be able to walk through a more diverse and resilient woodland that grew in soils turned over by the bettong.

Photo by Belinda Wilson