

Engineering the regeneration niche for the restoration of temperate grassy woodlands

by

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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.

Rachael Erin Robb

Date: 30th May 2019



Figure i. Rachael Robb counting seedling germination in Research Site A Plot 9, Mulligans Flat Woodland Sanctuary. Photo taken by Katherine Robb (2018)

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I acknowledge the Ngunnawal, Ngunawal, and Ngambri people who are the traditional custodians of this land, and pay respect to the Elders past, present and emerging. I recognise the continuing connection of Aboriginal and Torres Strait Islander peoples to their Country.

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*In grassy woodlands
Bettongs forage and forbs grow
Plant restoration*

Lastly, I take my hat off to all the native fauna and flora which make up the magnificent ecosystem of Mulligans Flat Woodland Sanctuary, and who kept me company during the hours of field work (Figure ii)



Figure ii. Rachael Robb greeting a bearded dragon encountered at Research Site A in Mulligans Flat Woodland Sanctuary. Photo taken by Katherine Robb (2018)

Rachael Erin Robb Engineering the regeneration niche for the restoration of temperate grassy woodlands

Abstract

Digging animals, considered ecosystem engineers in temperate grassy woodlands worldwide, play an important role in the creation of germination niches for ground-layer plant species. However, there is limited understanding of the influence that digging animals may have on temperate grassy woodlands, or on the role they may have for the restoration of these systems. This prompted a study into the dynamics of the native plant regeneration niche, and the small disturbances created by the foraging of digging animals such as the eastern bettong (*Bettongia gaimardi*).

My thesis included investigation of (1) the germination response in bettong-created pits and (2) artificial replication as a possible restoration technique. I selected four sites of *Themeda* grassland within Mulligans Flat Woodland Sanctuary. The study compared the germination of hand-seeded native forbs (small flowering herbaceous plants) in natural bettong pits, an artificially replicated pit, an artificial ‘scrape’ (removal of vegetation and soil surface disturbance to create a gap in the grass canopy), and a control. This design had the intention of addressing the following questions.

- 1) Do natural pits promote the germination and establishment of seedlings?
- 2) Can artificial pits create a similar environment for germination and establishment?
- 3) Is the possible facilitation effect of germination due to the removal of vegetation, or the structural effects of the pit?

This study found that all three disturbance treatments significantly increased germination of the native forbs yam daisy (*Microseris walteri*) and blue devil (*Eryngium ovinum*) compared to the control. There was also no significant difference in germination between artificial disturbances mimicking bettong foraging pits, and the scrape to create a gap in the grass canopy. Therefore, the results suggested there is potential to artificially replicate small scale disturbance events, like animal digging, to help restore diversity in temperate grassy woodland ecosystems. It also supported the hypothesis that the creation of gaps in the grass canopy is a major factor driving the plant response to bettong digging in grassy woodlands.

A future recommendation is to further investigate the effects of bettong-created pits on the longer-term growth and establishment of native forbs. Additionally, I suggest increasing the scope and scale of my study to include an additional site to MFWS. These avenues of study would further increase the available information on the influence of eastern bettong digging on the growth of native forbs, and in doing so allow more informed recommendations to management.

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List of acronyms and abbreviations

- ACT:** Australian Capital Territory
- AIC:** Akaike information criterion
- ANU:** The Australian National University
- CWR:** Critical Weight Range

GAM: Generalised Additive Model

GAMM: Generalised Additive Mixed Model

GLM: Generalised Linear Model

GLMM: Generalised Linear Mixed Model

IUCN: International Union Conservation of Nature

MFGO: Mulligans Flat-Goorooyarroo

MFGOWE: Mulligans Flat-Goorooyarroo Woodland Experiment

MFWS: Mulligans Flat Woodland Sanctuary

Glossary and Terms

Abiotic: physical or non-living components of the natural world, not derived from living organisms e.g. geology, soils, climate, atmosphere (Park and Allaby, 2013)

Anthropogenic: relating to, or originating from, the actions of humans, including the processes or substances made by humans (Park and Allaby, 2013)

Bettong: a native reintroduced marsupial, a member of the kangaroo family, sometimes known as a rat-kangaroo (Taylor, 1992; Johnson, 1994; Munro *et al.*, 2019).

Biotic: living, containing life (Park and Allaby, 2013)

Bioturbation/bioperturbation: the movement and manipulation of soil by living organisms (Whitford and Kay, 1999; Fleming *et al.*, 2014)

C₃: photosynthesis pathway with a three-carbon compound, using the Calvin cycle for initial steps that incorporate CO₂ into organic material, forming a sugar of three carbon molecules. Winter growing e.g. *Poa*, *Rytidosperma* (Barrett *et al.*, 2018)

C₄: photosynthesis with a four-carbon compound; the Calvin cycle is preceded by reactions that incorporate CO₂ into a four-carbon compound, the end product of which supplies CO₂ for the Calvin cycle. This provides an ecological advantage under arid conditions (Barrett *et al.*, 2018). C₄ Leaves tend to contain less protein than C₃ leaves, so are less attractive as a grazing source, and they have higher nitrogen use efficiencies (Cole *et al.*, 2017) e.g. *Themeda*

Canopy: the roof-like cover formed by vegetation, both tree and grass (Park and Allaby, 2013)

Dicotyledons: A flowering angiosperm plant, usually possessing a seed with two seed leaves (cotyledons)

Effect size: describes the slope of the relationship between the controls and treatment on the link scale, as determined by a linear or generalised linear model or mixed model (e.g. log, logit, probit or identity) (Nakagawa and Schielzeth, 2013; Harrison, 2014)

Ecosystem engineer: “organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In doing so they modify, maintain and create habitats” (p. 373) (Jones *et al.*, 1994)

Extant: still existing or living in the present time (Park and Allaby, 2013)

Extinct: taxa absent, locally or globally, from the landscape during the past 50 years and with no reasonable doubt that an individual has not been found in recent years (Park and Allaby, 2013)

Forb: small flowering herbaceous plant that is not a graminoid (grass) e.g. herbaceous dicotyledons, terrestrial orchids and members of Iridaceae and Liliaceae families (Trémont and McIntyre, 1994)

GAM: Generalised Additive Model is a generalized linear mixed model in which the linear predictor depends linearly on unknown smooth functions of some of the covariates (Wood *et al.*, 2017)

Heterogeneous: varied or not uniform (Park and Allaby, 2013)

Homogeneous: uniform (Sharp, 1994)

Keystone species: organisms whose influence to an ecosystem is disproportionately large relative to their abundance (Paine, 1969; Power *et al.*, 1996)

Matrix: The dominant perennial grasses that form the main structure of the grassland and exert competitive effects on the interstitial forbs and less competitive grasses (Grubb, 1986; Trémont and McIntyre, 1994)

Matrix Suppression: the reduction of the grass matrix e.g. through fire, trampling, mowing, grazing (Allcock and Hik, 2003; McIntyre *et al.*, 2017)

NUE: Nitrogen Use Efficiencies; the amount of plant material produced per unit of nitrogen (Cole *et al.*, 2017)

Pit: In this thesis, pit refers to the physical structure created by the foraging action of the eastern bettong digging in the soil (Martin, 2003; Munro *et al.*, 2019)

Regeneration niche: an expression of the requirements for a high chance of success in the replacement of one mature individual by a new mature individual of the next generation (Grubb, 1977).

Re-wilding: the recreation of ecosystems with minimal human intervention, where natural ecological processes dominate and occur within a natural range of variation (Marris, 2009; Sandom *et al.*, 2013)

Scalping: the removal of weed-containing topsoil to control annual weeds (Cole *et al.*, 2017)

Seed bank: the store of seed in the topsoil which is physiologically capable of germination (Park and Allaby, 2013)

‘Shifting baseline’ syndrome: or ‘environmental generational amnesia’, is the ongoing ‘ratcheting down’ of environmental knowledge and expectations in a continually degrading environment as generations of people consider the quality and environmental function of their childhood environment as a new standard (Kahn and Kellert, 2002; Miller, 2005)

State-and-Transition model: a conceptual framework which describes the many alternate states that an ecosystem can exist in, and the possible transitions between those states. The transitions are often prompted by a combination of factors including climatic circumstances and management action, and can be smooth, discontinuous or irreversible (Westoby *et al.*, 1989)

Sward: a dominating grass cover of near-continuous tussocks, usually of one species (Barrett *et al.*, 2018)

Vertebrate: an animal with a backbone (Park and Allaby, 2013).

Artist statement

During this thesis I supplemented learning of ecology and plant restoration with the practise of art. To assist in the learning and identification of native and exotic plant species common in the ACT, and specifically Mulligans Flat Woodland Sanctuary, I sketched and wrote descriptive notes of the different plant species in the field (Appendix II).

I think it is important to create a common ground between scientists and the community by clearly communicating the importance of ecological research. One of my ways of communicating the natural world, science and conservation is through art. In this way, I can engage a wider audience ensuring my scientific research is accessible. At the beginning of each chapter of my thesis, I have included heading banners I painted to represent each of the chapters they begin.

Similar to the push towards either animal or plant science, there has been a divide between science and art. However, they are connected; science can help inform art and art can be used to express and communicate science.

Chapter 1: Introduction



“Usually one person doesn't have the solution, but 100 people with 1% of the solution? That will get it done. I think that's beautiful, pieces solving a puzzle.” Whedon (2013)

Ecological management actions are increasingly focused on restoring both ecological communities and ecosystem function after European settlement of Australia and the interruption of ecosystem function by increased human activity (Prober *et al.*, 2005). Ecological restoration can involve tools or actions designed to improve ecosystem function or diversity, and consider both the target species and its habitat (Volis, 2019). Restoration of ecosystem function and diversity, in particular Australian temperate grassy woodlands, can be assisted through either natural or artificial disturbances (Wilson and Tilman, 2002). The natural disturbances of fire, flood, drought, and bioturbation can be used as a restoration tool (e.g. controlled burning) (Hayes and Holl, 2003), or to inform restoration actions (e.g. through mimicking the role of drought by removing biomass through mowing or dethatching) (Hodgkinson, 2014). Artificial approaches to restoration often use large-scale severe disturbances: scalping (complete removal of surface vegetation and top soil), ripping (loosening or elevating soil), herbicide use (chemicals used to kill unwanted plants), and cultivation (breaking the soil surface to improve air, water and nutrient access) (Bakker *et al.*, 2003; Cole *et al.*, 2004; Gibson-Roy *et al.*, 2010). These artificial approaches can be appropriate where changes in grassy woodlands are not easily reversible, whether through an established exotic ground layer or existing disturbance (e.g. prior removal of soil for agriculture or urban construction) (Cole *et al.*, 2004). For example, scalping combines the principles of matrix suppression (in this case complete, not partial, removal of the dominating grass structure) with that of nutrient removal to restore the competitiveness of the native species (Prober and Lunt, 2008; Gibson-Roy *et al.*, 2010). However, there are situations where the approaches of scalping and other large-scale restoration techniques are not appropriate, especially in relatively good quality grassy woodland ecosystems. To prevent further deterioration, this led to a need to overhaul the types of management techniques used in restoration (Lunt, 1991), and the pursuit of greater understanding of ecosystem function and processes with the aim of restoring native species (Hayes and Holl, 2003).

Ecosystem function involves the interaction between a variety of plants, animals, fungi, microorganisms, and other biotic and abiotic factors (Hobbs and Yates, 2000; Prober *et al.*,

2005). Therefore, the restoration of ecosystem processes and function may assist the re-establishment of the plant and animal species that are integral to the ecosystem (Hobbs and Huenneke, 1992; Martin, 2003; Prober *et al.*, 2005; Fleming *et al.*, 2014). This includes promoting populations of native plant species that are likely to have been lost under previous heavy grazing regimes or other disturbances (e.g. long-ceased cultivation or fertilization) (McIntyre, 2011). In grassy woodland ecosystems, past livestock densities are considered to have depleted populations of the small flowering herbaceous plants called forbs (McIntyre *et al.*, 2002). Decreasing diversity of forbs can be caused by the loss of seed production due to reduced population sizes (McIntyre, 2011), the lack of a regeneration niche, and in some situations due to the competitive effects of large perennial grasses (Trémont and McIntyre, 1994; Bakker *et al.*, 2003). The recovery of forb diversity is important because forbs account for a large proportion of ground-layer plant species richness (Pokorny *et al.*, 2004).

There are a number of studies that explore ecological restoration and regeneration niches, with the aim of restoring the threatened ‘natural temperate grassy’ and ‘box-gum grassy’ woodland ecosystems of south-eastern Australia (Threatened Species Scientific Committee, 2006; Maguire and Mulvaney, 2012). These ecosystems are home to unique communities and both plant and animal assemblages. The main tree species in the Australian Capital Territory (ACT) listing of ‘box-gum’ grassy woodlands are yellow box (*Eucalyptus melliodora*) and Blakely’s red gum (*E. blakelyi*) (Cole *et al.*, 2004). The ground cover comprises of tussock grasses such as kangaroo grass (*Themeda triandra*), and a range of forbs (Threatened Species Scientific Committee, 2006). The fauna include threatened species such as the striped legless lizard (*Delma impar*), grassland earless dragon (*Tympanocryptis pinguicolla*), and golden sun moth (*Synemon plana*) (ACT Government, 2017).

The restoration of ecosystem function can also include the restoration of the animals which contribute to essential processes such as soil engineering. Therefore, there is a focus on conserving the species that modify, maintain, and create habitats – often termed ecosystem engineers (Jones *et al.*, 1994; Fleming *et al.*, 2014). In Australia, digging or soil foraging animals such as bandicoots (*Parameles* spp. and *Isoodon* spp.), potoroos (*Potorus* spp.), greater bilby (*Macrotis lagotis*) and bettongs (*Bettongia* spp.) are considered to be important ecosystem engineers (Fleming *et al.*, 2014). Many of these species have suffered widespread declines, and are therefore the focus of conservation and reintroduction programs (Davies *et al.*, 2019). The role of ecosystem engineers has been studied in wild populations, or in the case of the eastern bettong (*Bettongia gaimardi*), through a reintroduction program in the Australian Capital Territory (Shorthouse *et al.*, 2012; Batson *et al.*, 2015a; Batson *et al.*, 2015b; Manning *et al.*, 2015). The eastern bettong was reintroduced to mainland Australia after becoming locally extinct (Batson *et al.*, 2015b). After reintroduction, natural soil engineering processes caused by bettong foraging were studied to inform restoration action for degraded landscapes and plant establishment (Munro *et al.*, 2019; Ross *et al.*, unpublished a). Within the field of restoration

ecology, the reintroduction of species with the ability to modify (or ‘engineer’) their environment can be an effective tool for integrating plant and animal factors into holistic ecological restoration (Jones *et al.*, 1994; Seddon *et al.*, 2007; Sandom *et al.*, 2013; Manning *et al.*, 2015). Reintroductions often occur in reserves, both for the conservation of the reintroduced species, but also to help restore ecosystem function (Legge *et al.*, 2018; Legge *et al.*, 2019; Ringma *et al.*, 2019). However, in some cases a reintroduction program is not feasible (Seddon *et al.*, 2007). By understanding the extent of lost plant diversity, management plans can better assess what can be artificially added to the system to increase species diversity, with the aim to restore, and not just reconstruct or statically conserve, the ecosystem (Volis, 2019).

Other digging animals associated with soil engineering have also been explored for their contribution to the function of ecosystems (Noble *et al.*, 2007; James *et al.*, 2009; Fleming *et al.*, 2014; Valentine *et al.*, 2017). Soil disturbance by digging animals can result in enhanced productivity and establishment of seedlings, improved soil moisture, and mycorrhizal distribution (Mallen-Cooper *et al.*, 2019). The pits or depressions caused by foraging animals also behave as ‘resource sinks’, accumulating organic matter such as leaf litter and seeds (James *et al.*, 2009). Digging can reduce root and shoot competition through the creation of gaps allowing for plant recruitment (Morgan, 1998b; Martin, 2003; Sandom *et al.*, 2013; Mallen-Cooper *et al.*, 2019; Munro *et al.*, 2019). Ross *et al.* (unpublished a) studied the effect of eastern bettong digging on seedling germination in two different grassland types, wallaby grass (*Rytidosperma*) and *Themeda*, and found that the digging caused a greater response in the denser grassland type of *Themeda*. This suggested that, in temperate grassy woodland ecosystems, the largest factor in increased germination may be the effect of competition from *Themeda* roots and/or shoots. The dynamics in these ecosystems appear to be different to arid ecosystems, where the chemical changes, resource sinks and microclimate effects which occur in foraging pits are crucial for ecosystem function (James *et al.*, 2009).

In some ecosystems where there is a lack of a closed grass canopy, especially arid zones, pits created by a digging ecosystem engineer primarily represent a resource sink, and not solely a gap in resource competition (James *et al.*, 2009). There is a lack of knowledge about whether the resource sink is the main driver in temperate grassy woodland ecosystems, or whether gap creation in the grass canopy is the primary influence created by animal pits. Additionally there could be an effect from the microclimate response to digging, such as milder temperatures, higher moisture retention, and increased humidity within foraging pits (James *et al.*, 2009; Valentine *et al.*, 2017). This study addresses this knowledge gap by providing information for the establishment of native forbs in temperate grassy woodlands, as well as investigating the role of the eastern bettong in bioturbation-driven restoration.

In this study, soil disturbance was used as a method of restoration of the small flowering herbaceous forbs, imitating the role of eastern bettong bioturbation. This addressed the challenge of how to restore forb diversity without disrupting the intact native perennial grass

matrix that occurs at the study site of Mulligans Flat Woodland Sanctuary (MFWS). Building on the existing literature, and the questions posed by the gaps in knowledge, my study explored the interactions of seed germination and the soil engineering of eastern bettongs when creating regeneration niches for native forbs (Munro *et al.*, 2019; Ross *et al.*, unpublished a) by artificially mimicking the natural process of regeneration in an ecosystem (Martin, 2003). I hypothesised that disturbances would create gaps in the grass canopy, providing a regeneration niche and promoting an increase in seed germination and therefore overall forb diversity. In my experiment, I used hand-addition of seeds into four treatments: A control; a natural bettong-created pit (to test grass canopy gap and pit dynamics); an artificially created pit based on eastern bettong foraging (artificial grass canopy disturbance and pit microclimate conditions); and an artificial 'scrape' (removal of vegetation and soil surface disturbance to create a gap in the grass canopy). This experimental field approach tested the influence of engineering regeneration niche and gap dynamics on seedling germination.

The primary research question guiding this thesis was:

Do artificially engineered regeneration niches, based on bettong-created pits, provide equal forb germination when compared to the natural bettong foraging pit?

I specifically addressed these aims with the research questions:

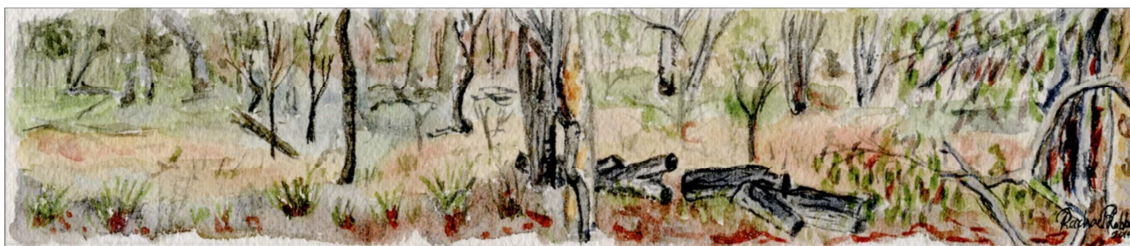
- 1) Do natural pits promote the germination and establishment of seedlings?
- 2) Can artificial pits create a similar environment for germination and establishment?
- 3) Is the possible facilitation effect of germination due to the removal of vegetation, or the structural effects of the pit?

I predicted that each treatment would have a positive effect on seed germination. Based on previous studies (Mallen-Cooper *et al.*, 2019), I hypothesised that the same type of disturbance, whether created naturally or artificially, would have similar disturbance effects. Additionally, I hypothesised that the artificial treatment, based on the natural bettong pit, would have better seed germination than the scrape treatment due to the additional benefits of the pit (e.g. microclimate, reduced seed predation, and resource accumulation).

The study's experimental design has the potential to be used for larger-scale restoration work (e.g. for rare forb reintroductions) and contribute to research into the recovery of native forb populations in temperate ecosystems (Manning *et al.*, 2011; Shorthouse *et al.*, 2012).

This thesis is structured into six chapters where I: (1) introduce my research, outline aims and research questions, (2) provide a review of relevant literature, (3) set out the background to my study site and methods, (4) present the key findings, (5) discuss the implications, limitations and significance of my findings and provide future recommendations, and (6) conclude with a reminder of my main argument, key findings, implications of the findings, and extension of my research into wider context.

Chapter 2: Literature Review



This literature review first describes the background regarding flora restoration, including faunal elements, before describing how restoration, ecosystem engineering, and digging animals combine in my thesis. I investigated this through the context of plant and animal research, biodiversity value of ecosystems, the decline of species diversity, the role of regeneration niches and small digging animals in the landscape. Additionally, I explored past and current restoration strategies before introducing animal reintroduction and gap dynamics as a restoration strategy for improving overall ecosystem function. This is designed to highlight the gap in the interaction of the two disciplines, using the case study of how bioturbation actions of the eastern bettong benefit forb diversity in the temperate grassy woodland ecosystem.

2.1 Grassy woodland biodiversity

Temperate grassy woodlands, once extending across south-eastern Australia, are of critical ecological and economic importance (McIntyre, 2011). Their value to agriculture has led to the ten types of grassy woodland communities being reduced to remnant fragments (Hobbs and Yates, 2000) and classified as endangered or critically endangered due to exploitation, e.g. through pastoralism, grazing and cultivation (Prober and Thiele, 1993; Threatened Species Scientific Committee, 2006; McIntyre, 2011; Threatened Species Scientific Committee, 2016). There have been severe negative effects on ecological functioning and floristic composition (McIntyre *et al.*, 2010): local losses of plant and animal species and populations through habitat loss, agricultural uses, human intervention, exotic competition, and the introduction of domestic and feral herbivores and carnivores (Trémont and McIntyre, 1994; McIntyre *et al.*, 2017). The addition of soil nutrients to increase agricultural and pastoral production (Trémont and McIntyre, 1994) triggered a transition into new states that were not favourable to the productivity of native forbs because native plants are accustomed to Australia's low-nutrient soils (McIntyre and Lavorel, 2007; Manning *et al.*, 2015).

Specifically, 'box-gum' grassy woodlands in eastern Australia have undergone a reduction in distribution and quality (Threatened Species Scientific Committee, 2006). For example, between 2004 and 2012, 192 hectares of woodland in the ACT was lost to urban development (Maguire and Mulvaney, 2012). In the ACT listing, the ecological community characteristically has a 30% tree canopy layer, dominated by a combination of yellow box (*E. melliodora*) and Blakely's red gum (*E. blakelyi*) (Cole *et al.*, 2004; Threatened Species Scientific Committee,

2006). Additionally, ‘box-gum’ grassy woodlands typically contain a patchy shrub layer and a ground layer dominated by tussock grasses such as kangaroo grass (*Themeda triandra*), and forbs, small flowering herbaceous plants that are not graminoids (e.g. herbaceous dicotyledons, terrestrial orchids and members of the *Iridaceae* and *Liliaceae*) (Trémont and McIntyre, 1994; Specht and Specht, 1999; Clarke, 2000; McIntyre and Tongway, 2005; Threatened Species Scientific Committee, 2006). Grassy woodlands can also include surface materials such as plant litter, bare ground, rocks, lichen, moss, fungi, and animal faecal matter (Trémont, 1994). The specific floristic composition of the grassy woodland changes with different dominant vegetation and species diversity (Trémont and McIntyre, 1994), and each have their own value as a unique ecosystem.

Forbs, as one of the components of grassy woodlands that have cultural, ecological and economic value, play a vital role in ecosystem functions (Tilman *et al.*, 2001; Pokorny *et al.*, 2004; Egan *et al.*, 2011; Walsh, 2016). Forbs provide food sources for fauna in the form of roots, flowers, tubers, and pollen (Pokorny *et al.*, 2004). Additionally, grasslands provide an aesthetic resource owing to the attraction of people to extensive displays of flowering plants (Priskin, 2003). Forbs also provide an important cultural resource and significance to Indigenous Australians as a food source, weaving materials, medicines e.g. the yam daisy (*Microseris lanceolata* and *M. walteri*) (Walsh, 2016; Silcock, 2018). There has been a history of land management, translocation and landscape manipulation within Indigenous Australian cultural practices (Pascoe, 2014; Silcock, 2016; Silcock, 2018).

2.1.1 Factors contributing to the loss of forb diversity

The recovery of forb diversity is important because forbs account for a large proportion of ground-layer plant species richness (Pokorny *et al.*, 2004). Historical accounts of the vegetation in grasslands report large numbers of flowering forbs (Gammage, 2011), which do not exist in the same qualities and distributions today (Cole *et al.*, 2004). Forbs are often sparse and vulnerable to decline because, once lost, forbs and native grasses are unable to re-establish due to the lack of a persistent seed bank, and a sensitivity to change of the grassland structure (Cole *et al.*, 2004; Threatened Species Scientific Committee, 2006). Restoration action and management therefore becomes necessary to re-establish these important assemblages of plants (Yates and Hobbs, 1997; Cole *et al.*, 2004).

Most of the native grasslands in Australian conservation reserves have a history of agricultural uses, and have consequently lost a significant component of their plant diversity (Lunt, 1991; Trémont, 1994; Trémont and McIntyre, 1994; McIntyre *et al.*, 2017). This is particularly relevant to those grazing-intolerant forbs more susceptible to disturbance such as the yam daisy (Threatened Species Scientific Committee, 2006; Walsh, 2016). Species richness and diversity of native forbs are often severely reduced, and do not spontaneously return with the removal of livestock (Martin, 2003). This is due to the change and the effect of competition

with the exotic plants that capitalise on the high nutrient level characteristic of grazing areas (Davies, 1997; Spooner *et al.*, 2002; Wilson and Tilman, 2002; Prober *et al.*, 2004). Therefore large-scale adaptive management is required to reintroduce the native plant species back into the landscape while controlling and managing exotic species (Manning *et al.*, 2015).

Some of the factors that may be preventing the spontaneous recovery of forb populations are related to the manipulation of the dominant grass matrix or structure (Martin and Wilsey, 2006). These include the ongoing effects of macropod grazing, the loss of seed production due to reduced population sizes (McIntyre *et al.*, 2010), the build-up of biomass, and the lack of a regeneration niche because of the competitive effects of large perennial grasses (Trémont and McIntyre, 1994; Lunt, 1995; Bakker *et al.*, 2003; Cole and Lunt, 2005; Cole *et al.*, 2017). Another threat to conservation includes inappropriately planned and managed fire regimes, which is more relevant under low grazing pressure, where the lack of fire is more likely to be a major factor limiting forb growth (Morgan, 1998a; Prober *et al.*, 2004; McIntyre, 2008; McIntyre *et al.*, 2010). Threats also include ploughing, mowing, trampling, herbicides and fertilizers (raising soil fertility for exotic species) (Prober and Thiele, 2005; Cole *et al.*, 2016), as well as competition from exotic annual plants (Lunt, 1991; Cole *et al.*, 2017). Additionally, there is the potential for ecosystem engineers to cause a negative effect on plant diversity, recruitment and survival rate when in high population densities (Howland *et al.*, 2014; Verdon *et al.*, 2016).

Another factor contributing to the absence of forbs is the limitations of the Australian seedbank (Buhler *et al.*, 1997; Lunt, 1997; Morgan, 1998b; Cole *et al.*, 2016). The seedbank is the store of seed in the topsoil which is physiologically capable of germination. It is important for restoration because species which are absent from the vegetation may still persist in the soil to later germinate and establish when conditions become favourable (Lunt, 1997). However, the viability of different seeds in the soil varies, some are able to germinate immediately and have a short life in the soil, while others can survive long periods of time in the soil and germinate intermittently (Lunt, 1995; Buhler *et al.*, 1997). This leads to a trade-off in dormancy response of native seeds, where quick germination with no dormancy mechanisms results in low persistence in the soil, and high dormancy causing prolonged absence in the vegetation (Lunt, 1997). Relatively few native grassland species form persistent seed banks due the low number and high dormancy of the seeds native species produce (Lunt, 1997). The issue of non-persistent seedbanks is exaggerated by competition with exotic plant species, the seeds of which often persist longer in the soil than native species (Willis and Groves, 1991; Lunt, 1995). This in turn leads to the seedbank being one of the main sources of weed infestation (Buhler *et al.*, 1997). Therefore, as a sole source, the soil seedbank is not reliable for regeneration. However, the success of germination and establishment of seedlings from the seedbank can be influenced, for example through understanding what effects seed removal by ants (Lipp *et al.*, 2005; Radnan and Eldridge, 2017). In some situations, the removal of seeds by ants negatively affects seedling

emergence (Clarke and Davison, 2001) and in others, some species (e.g. wattles/*Acacias*) benefit from ant seed theft because the seeds potentially germinate better in ant nests (Lengyel *et al.*, 2010; Radnan and Eldridge, 2017). In their study, Radnan and Eldridge (2017) found that soil architecture was relevant to the rate that ants removed seed, increasing seed retention by six-fold when the steep-walled and deeper foraging pits dug by bettongs hindered ant movement more than either shallower pits created by the European rabbit (*Oryctolagus cuniculus*), or the undug surface (Radnan and Eldridge, 2017). These results led Radnan and Eldridge (2017) to suggest native Australian mammal pits could provide potential safe sites for seed germination and establishment. This knowledge adds to the understanding of seed germination responses in foraging pits, and the beneficial influences created digging animals (Fleming *et al.*, 2014; Mallen-Cooper *et al.*, 2019; Munro *et al.*, 2019).

The absence of digging animals may be a factor which contributes to forb loss through the lack of the influence of soil, microclimate and vegetation manipulation that encourages increased forb reproduction (Munro *et al.*, 2019) (Section 2.2). Digging animals, in particular mammal species, have been increasingly absent from the Australian ecosystem over the last 200 years (McKenzie *et al.*, 2007; Fleming *et al.*, 2014; Verdon *et al.*, 2016). Even now, many extant digging mammal species have seen a reduction in their range, and approximately 50% are extinct or under conservation threat (Fleming *et al.*, 2014). Bettong-driven bioturbation has been around as a process for at least 100 years, so understanding the potential role is important. Munro *et al.* (2019) found that 55% of the digging in their site of MFWS was caused by the eastern bettong population, indicating the relative size of the process now lost. This loss of digging animals has a consequent effect on the function of ecosystem processes and the connected components, such as forb populations.

Macropod and livestock grazing has also been identified as a threat to regeneration of natural ecosystems (Sato *et al.*, 2016; Neilly and Schwarzkopf, 2018). This is due to the total grazing pressure from both native macropods and livestock. In the site of this study, MFWS, the main grazing pressure comes from kangaroos and wallabies. Selective grazing occurs by animals on different plants, based on palatability at different stages of the plant lifecycle (McIntyre and Martin, 2001; McIntyre *et al.*, 2003). This grazing leads to a reduction in recruitment, and therefore influences the overall species richness, because the younger generation of plants do not reach reproductive age.

2.1.2 Regeneration niche and gap-dependant species

The investigation into the influence digging animals have on temperate grassy woodlands has particular relevance to engineering gaps in the grass canopy and creation of a regeneration niche. The regeneration niche, and associated gap dynamics, have practical applications in conservation, ecological theories and restoration ecology (Yamamoto, 2000). The early work by Watt (1947) began to explore the dynamic relationships between and within plant communities, with increasingly more models and research put forward (Grubb, 1977; Chesson and Warner, 1981; Grubb, 1986) to develop into the concepts of the current regeneration niche (Yamamoto 2000). The current understanding of ‘regeneration niche’ (different from the niches realised, potential, habitat, life form, and phenological (Grubb, 1977; Grubb, 1986)) describes the biotic and abiotic conditions which coincide in space and time to allow certain species to germinate and reproduce (Grubb, 1986). In this way, the success of a regeneration niche is affected by a spatial measure of its size and surface features, but also incorporates the temporal lack or presence of native species in the seed bank, characteristics of seed dispersal (Grubb, 1986), limited recruitment and the stochasticity of rainfall and soil disturbance recruitment events (Clarke and Davison, 2004) as well as the interactions of pests and diseases (Grubb, 1986).

Some of the conditions necessary for a regeneration niche can be caused by disturbance; disturbance can create zones or ‘gaps’ of decreased competition (for light, nutrients, water, modified predation), which in turn can aid successful recruitment, establishment and growth of seedlings (Hitchmough *et al.*, 1996; Martin and Wilsey, 2006). Therefore, the regeneration niche, ‘gaps’ or ‘microsites’, which involve inter-tussock gaps in the grass matrix, can provide sites for the recruitment of forbs (Martin and Wilsey, 2006). However, there exists a trade-off because they also provide a foothold for exotic species (Clarke and Davison, 2004). Gaps can be caused by falling trees or branches, fire, and soil disturbance instigated by animals (Morgan, 1998a). A number of characteristics of a gap are important in the successful regeneration process e.g. time of gap formation, competition present, size and shape of resulting gap, microclimate, moisture, nutrients, and fungi, bacteria or viruses present (Grubb, 1977). The study of gap dynamics in herbaceous vegetation highlights the importance of the size of the emerging gap (Williams, 1992) in determining what species is more likely to have the advantage and become dominant e.g. a light-demanding tree species benefits from a large gap whereas a shade-tolerant tree would flourish in a smaller gap (Grubb, 1977). Gap-dependent species are those which rely on the lack of competition and regeneration conditions caused during the formation of a gap in the dominant grass matrix e.g. shrubs, graminoids, and forbs (Williams, 1992; Morgan, 1998a). The three forbs explored in this study are suspected to be dependent on gaps, and my study tests the potential benefit from the disturbance of the grass canopy created by the foraging behaviour of the eastern bettong.

2.1.3 Grass matrix

The grass matrix comprises the dominant perennial grasses that form the main structure of the grassland and exert competitive effects on the forbs and less competitive grasses that grow between or within gaps of the matrix species (Grubb, 1986; Trémont and McIntyre, 1994). The balance between the density and species richness of the matrix and interstitial components of an ecosystem is important for maintaining the function of the herbaceous community (Trémont and McIntyre, 1994). The loss of native species can be contributed to by large-scale disturbance to matrix dynamics (Lunt, 1991) and the competitive effects of the dominant grasses (Trémont and McIntyre, 1994).

Themeda triandra-dominated grasslands can require biomass reduction to control growth and limit the smothering of smaller plants (Lunt, 1991; Cole *et al.*, 2004; Cole and Lunt, 2005). Without grazing, burning or other disturbance, *Themeda* tends to grow densely to the exclusion of other native species (Lunt, 1995). This effect has been used in restoration to out-compete exotic plants, and is also the focus of grassland restoration to open up the *Themeda* community to increase native diversity (Lunt, 1990; Lunt, 1995; Cole and Lunt, 2005; Hodgkinson, 2014). The *Themeda* swards were more effective for suppressing exotic species than the other species tested (Cole and Lunt, 2005; Cole *et al.*, 2017).

The findings of Cole *et al.* (2017) favoured a mixed species selection being critical in suppressing exotic annuals, and therefore more likely to contribute to restoration of degraded ‘box-gum’ grassy woodland communities. However, management actions, for example burning, can also encourage the growth of exotic species, so careful monitoring is required to re-establish populations of native plants (Lunt, 1991). Matrix suppression creates gaps in the grass canopy and mitigate competition that can exist in dominant grass swards (Hitchmough *et al.*, 1996; Prober and Lunt, 2009). When fire or grazing cannot be used, alternative ways of matrix suppression to ensure gaps are present are required, which leads to my investigation into the influence animal bioturbation has on forb germination.

2.2 Ecosystem engineering and bioturbation

One of the key elements of ecosystem engineering that influences the possible regeneration of plants is the bioturbation, or disturbance, of soil and sediments by plants or animals (Whitford and Kay, 1999; Fleming *et al.*, 2014). Jones (1994) defines ecosystem engineers as ‘organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In doing so they modify, maintain and create habitats’ (p.373). Ecosystem engineers can have an important role to play in maintaining and restoring the health of the ecosystem because they influence their environment (Jones *et al.*, 1994). Examples include beavers (Castoridae), woodpeckers (Picidae), corals, trees (Jones *et al.*, 1994), porcupines (*Hystrix indica*) (Guttermann and Herr, 1981), wild boar (*Sus scrofa*) (Sandom *et al.*, 2013) and bettongs (Fleming *et al.*, 2014; Howland *et al.*, 2014).

While some ecosystem engineers change their environment by their physical structure (e.g. trees), others mechanically change their habitat between physical states by transforming both living and non-living materials (Jones *et al.*, 1994). One of the main examples of mechanical change is the process of bioturbation.

Bioturbation is a mechanical form of ecosystem engineering practised by digging animals. Therefore these animals, many of which are mammals, are associated with encouraging species diversity, and consequently being more recognised in restoration and conservation (Fleming *et al.*, 2014). Mammalian fauna have a significant role in plant survival and reproduction through both physical interactions of grazing, browsing, digging and trampling – which now is mostly absent with the decline of small digging mammals (Lunt, 1991; Jones *et al.*, 1994; Fleming *et al.*, 2014). They also had a role in the biological trophic interactions through the movement and ingestion of seeds and fungal spores during their foraging process (Lamont *et al.*, 1985; Tory *et al.*, 1997; Fleming *et al.*, 2014).

Disturbances like bioturbation are important for conservation management because they are integral to the function of numerous ecosystems (Wilson and Tilman, 1993; Wilson and Tilman, 2002), for example disturbance-dependant grassland communities (Hobbs and Huenneke, 1992; Hayes and Holl, 2003). The differences in the duration, frequency and severity of disturbance events can either alter the state of the system from its norm or, depending on what species are affected, disturbances can benefit some species (Wilson and Tilman, 2002; Cole *et al.*, 2004). Types of disturbance can include biotic (living) events such as grazing, fire (Allcock and Hik, 2003) and flood, but also abiotic (non-living) and anthropogenic (human-driven) system change through habitat loss and deforestation (Wilson and Tilman, 2002; Hayes and Holl, 2003). Soil disturbance can create zones or ‘gaps’ of decreased competition (for light, nutrients, water, modified predation), enhance soil nitrogen and phosphorus, which in turn enhances productivity, recruitment, establishment and growth of seedlings (Hitchmough *et al.*, 1996). The interactions between the causes of disturbance, gap characteristics, resource availability and competition are therefore important in the establishment and restoration of ecosystem processes and plant communities (Wilson and Tilman, 1993; Hitchmough *et al.*, 1996). On a smaller scale, biotic factors such as animals can create small and continual disturbances in ecosystems (Jones *et al.*, 1994). One of these biotic factors is bioturbation, or the manipulation and movement of soil by living organisms, including digging animals, foragers and grazers (Whitford and Kay, 1999; Fleming *et al.*, 2014). Additionally, if viable seeds persist in the soil, soil disturbance can enhance germination and recruitment (Spooner *et al.*, 2002). The five main ecosystem functions of Australian digging mammals reviewed by Fleming *et al.* (2014) from existing literature, are (i) soil turnover, (ii) increased organic matter capture, (iii) increased water infiltration, (iv) mycorrhizal fungal dispersal and recruitment, and (v) seed dispersal and plant recruitment.

Bioturbation is largely missing in the functional grassland structure because of the absence of digging animals (Fleming *et al.*, 2014). Some digging animals already in the landscape (e.g. short-beaked echidna (*Tachyglossus aculeatus*) and European rabbit) partially fill the role, but more than a quarter of Australian mammals are absent from the current system (McKenzie *et al.*, 2007). About 18% of Australian mammals and monotremes are considered diggers, nearly 70% of which have an International Union Conservation of Nature (IUCN) Listing (Fleming *et al.*, 2014). This is because the majority of these animals which contribute to bioturbation processes are in the critical weight range (CWR) and have suffered a decrease in abundance or range (Burbidge and McKenzie, 1989; Martin, 2003; Fleming *et al.*, 2014). The current loss of this group of mammals with this weight range of 35–5500g is due to their vulnerability to predation (e.g. by introduced foxes *Vulpes vulpes* and cats *Felis catus*), habitat loss and fragmentation (Burbidge and McKenzie, 1989; Short and Smith, 1994; Woinarski *et al.*, 2001; Martin, 2003; McKenzie *et al.*, 2007; Gibb, 2012). This led to the reintroduction of native digging animals (e.g. the eastern bettong in MFWS) with the aim of restoring some bioturbation processes and improving the condition of the ecosystem and habitat for other species (Munro *et al.*, 2019). However, ecological processes are full of trade-offs; when some species benefit, others are disadvantaged, and the overall process is rarely unambiguously ‘good’ for everything (McIntyre, 2008; James *et al.*, 2009; Mooney *et al.*, 2010; Massol *et al.*, 2011; Wilkerson *et al.*, 2014). Therefore, increasing the understanding of different disturbance effects is necessary for management and restoration of ecosystems, especially when techniques that mimic the natural disturbance regimes are used with the aim of conserving native species (Hayes and Holl, 2003). For example, using animal reintroductions for conservation goals is an increasingly popular idea (Seddon *et al.*, 2007), as seen in the reintroduction of the eastern bettong (Manning *et al.*, 2015).

2.2.1 Bettongs

The eastern bettong is a native reintroduced digging marsupial, a member of the Potoroidae family, sometimes known as a rat-kangaroo (Taylor, 1992; Johnson, 1994; Garkaklis *et al.*, 2003). In grassy woodland ecosystems, the eastern bettong acts as an ecosystem engineer (Fleming *et al.*, 2014; Neilly and Schwarzkopf, 2018; Davies *et al.*, 2019; Munro *et al.*, 2019) and can help restore soil-related functions which have been lost since local extinction on mainland Australia in 1906 (Short, 1998; Martin, 2003; Shorthouse *et al.*, 2012). Prior to this, eastern bettongs were common throughout eastern Australia, and had a significant impact on the landscape (Short, 1998; Manning *et al.*, 2015; Munro *et al.*, 2019). A wild population of eastern bettongs survived in Tasmania (Taylor, 1992; Munro *et al.*, 2019), allowing later establishment of an insurance population in ACT’s Tidbinbilla Nature Reserve (Batson *et al.*, 2015a) and the reintroduction within the fenced MFWS (Shorthouse *et al.*, 2012; Manning *et al.*, 2015). The MFWS eastern bettong population is treated as wild with no supplementary resources; it is being monitored to determine whether eastern bettongs, acting as ecosystem engineers, can help

restore some of the functioning ecosystem properties of temperate grassy woodlands to those before European settlement (Manning *et al.*, 2015).

Eastern bettongs – like bandicoots, potoroos, and the greater bilby– cause bioturbation in the soil while foraging for food (Johnson, 1994; Johnson *et al.*, 2017; Davies *et al.*, 2019; Munro *et al.*, 2019; Ross *et al.*, unpublished a). Their foraging behaviour creates numerous small scratchings, holes, and/or pits (Martin, 2003) (Figure 2.1). The average size of an eastern bettong pit is 50 by 40 millimetres and 35 millimetres deep in a ‘leaning cone’ shape, with a ‘spoil’ heap adjacent to the pit, where displaced soil accumulates during the digging activities of the bettong (Munro *et al.*, 2019).



Figure 2.1. Eastern bettong foraging pit in kangaroo grass (*Themeda triandra*) tussock.

Photo taken by Rachael Robb (2019), Mulligans Flat Woodland Sanctuary (MFWS).

An eastern bettong’s diet consists primarily of the fruiting bodies of mycorrhizal fungi, supplemented with seasonally available combinations of plant material (roots, tubers, leaves, fruits, seeds, and flowers) and invertebrates (Taylor, 1992; Johnson, 1994; Strahan, 1995; Martin, 2003; Manning *et al.*, 2015; Ross *et al.*, unpublished a). Having been shown to eat developed tubers of plants (Johnson, 1994), it follows the eastern bettongs may also eat the tuberous yam daisy (*Microseris walteri*), bulbine lily (*Bulbine bulbosa*), blue devil (*Eryngium ovinum*), and early nancy (*Wurmbea dioica*). Preliminary observations suggest that the above-

ground material of the early nancy is not eaten by the bettong (Ross *et al.*, unpublished a), and so the above-ground seedlings of my study species were also unlikely to be eaten.

It has been suggested that small digging mammals, such as the bettong, positively affect germination and the diversity of small grassland plants like forbs (Fleming *et al.*, 2014; Munro *et al.*, 2019; Ross *et al.*, unpublished a). The response to foraging behaviour by an ecosystem engineer can be chemical, physical and biological (Jones *et al.*, 1994; Davies *et al.*, 2019). This can include the physical creation gaps and changes in soil architecture, chemistry, and moisture. Animal-created pits are also important as resource sinks and sites for seedling establishment (Garkaklis *et al.*, 2003; James *et al.*, 2009). A few studies have investigated the changes in soil biology and physical soil and plant conditions caused by vertebrate bioturbation (Garkaklis *et al.*, 2003; Mallen-Cooper *et al.*, 2019; Munro *et al.*, 2019). However, most research has been in arid ecosystems, and there is a lack of research and understanding of how animal pits and digging processes function in temperate grasslands or woodlands (Munro *et al.*, 2019).

2.3 Past and current restoration techniques

2.3.1 Strategies overview

Strategies to return grasslands to a prior ‘natural’ state are widely mentioned in literature (Lunt, 1991; Martin, 2003; Fleming *et al.*, 2014). However, important factors are overlooked when the focus of management action is on static conservation or on the broad scale physical attributes of a landscape’s previous state rather than on restoring the full balance of an ecosystem (Lunt, 1991).

Techniques which are designed for large scale restoration include scalping to remove the exotic seed bank, controlling fire, and other methods which use machinery (Cole *et al.*, 2004). These methods can be effective on a large scale, and in the correct situation, but can also damage the existing vegetation and soil (Brown *et al.*, 2017). They also have limited application if access to a site is restricted, for example by listed woodlands and protected trees. Therefore the current techniques are not always appropriate when it comes to restoring and managing relatively good quality grassy woodland ecosystems. Lunt (1991) advocated that an overhaul of management is necessary to prevent further deterioration. Since then, it has become even more crucial to adopt adaptive management and set up effective monitoring programs to assess the success and failure of ecological restoration strategies (Manning *et al.*, 2011).

There has been a change in emphasis from conserving the current state of ecosystems, to restoration of ecosystem processes integrating both function and diversity (Lunt, 1991; Yates and Hobbs, 1997; Prober and Thiele, 2005). For example, conservation methods historically focused on preserving natural communities, thereby suppressing the physical disturbance important to its continued function (Hobbs and Huenneke, 1992). Now, there are studies exploring ecosystem restoration and integrating function and diversity, for example in the

restoration of grassy ecosystems (Prober and Thiele, 2005). The changing focus of conservation and restoration will help offset and improve the ongoing decline in landscape quality into the future, and over larger spatial scales (Manning *et al.*, 2006). Plant translocation has also been used to promote the conservation of specific species and ecosystems (Commander *et al.*, 2018). Plant translocations, with mixed successes, have included adding new seed, planting seedling tube stock, moving existing plants from one location to another, where density and competitive capacity influence the success of establishment of plants such as forbs (Hitchmough *et al.*, 1996; Silcock, 2016).

There has been recognition by ecologists and conservationists that a variety of forms of disturbance are actually beneficial and necessary for the function of natural systems (Wilson and Tilman, 1993; Hitchmough *et al.*, 1996; Hayes and Holl, 2003). Research has been expanding techniques which take advantage of the changes created by small and large scale disturbances, such as removing exotic seeds and allowing for regeneration in favourable conditions for native species (Smallbone *et al.*, 2007; Brown *et al.*, 2017).

To restore both the understorey and the tree layer of grassy woodlands, a variety of strategies have been previously employed to reduce the competition by exotic annuals and encourage depletion of the exotic seedbank: scalping, or spring burning or grazing (Prober *et al.*, 2004; Smallbone *et al.*, 2007; Brown *et al.*, 2017; Cole *et al.*, 2017). A combination of methods results in the best outcome because of the difficulty of complete exotic seed removal (Prober and Lunt, 2008; Gibson-Roy *et al.*, 2010). Even then, often the removal of exotic seed may not be sufficient for native plant regeneration if their seeds are no longer present (Morgan, 1998b; Cole *et al.*, 2004). Therefore, regeneration requires both the addition of native seed to complete the restoration process, and the creation of a viable regeneration niche to offer a germination environment (Smallbone *et al.*, 2007). However, difficulties arise because even after the mitigation of the disturbance or degrading process (Cole *et al.*, 2004; Brown *et al.*, 2017), native species rarely increase to their original levels while exotic species often persist in the seedbank (Spooner *et al.*, 2002; Wilkins *et al.*, 2003; Cole *et al.*, 2004; Briggs *et al.*, 2008; Spooner and Briggs, 2008; Cole *et al.*, 2017).

2.3.1.1 Scalping

Scalping is the process of completely removing the seedbank in the top 10-30cm of soil, thereby giving re-sown slow-growing native grasses the chance to germinate and establish in the absence of competitive fast-growing weeds (Brown *et al.*, 2017; Cole *et al.*, 2017). Scalping also removes much of the problematic soil fertility at sites which have high nutrient levels from previous fertiliser application (Gibson-Roy *et al.*, 2010; Brown *et al.*, 2017). Scalping is appropriate for eutrophied (high-nutrient and low-oxygen) soils that are dominated by exotic species (Prober and Lunt, 2008; Gibson-Roy *et al.*, 2010). It combines the principles of matrix suppression (in this case complete removal) with that of nutrient removal (e.g. through scalping

or carbon addition) to restore the competitiveness of the native species (Smallbone *et al.*, 2007). My experiment includes elements of these two principles and is an application of scalping method at a smaller spatial scale.

While there are benefits of scalping in the right situations (Prober and Lunt, 2008; Gibson-Roy *et al.*, 2010; Brown *et al.*, 2017), scalping has restrictions dependant on access to the intended site, can be impractical in broad areas (Cole *et al.*, 2004), can be expensive to implement, and uses heavy machinery which produces large amounts of ‘waste’ topsoil and intensifies the risk of soil erosion, especially on sloping sites (Brown *et al.*, 2017). As a result, scalping could be a problematic method to use in an established or protected grassland or grassy woodland ecosystem.

2.3.1.2 Role of Fire

Fire has also been used as a restoration technique for grass matrix suppression, minimising the build-up of thatch, controlling density, and ensuring heterogeneous mosaic patterns for a range of appropriate habitats and species diversity (Lunt, 1990; Bowman *et al.*, 2008; Hodgkinson, 2014; Morgan, 2015). In this way, fire is a process that fulfils one of the roles that bettongs once held; fire can create space for forb establishment by opening the canopy (Hodgkinson, 2014; Morgan, 2015), reducing competition from grasses, and controlling exotic annual seed banks (Prober *et al.*, 2004; Cole *et al.*, 2017).

In the past, fire would have been used by indigenous land managers to promote the growth of various interstitial species (species not included in the matrix) (Pascoe, 2014). Grazing was also present, but not to the extent that fire was not required, and fire was used to promote the presence and effects of grazers for hunting (Short and Smith, 1994). Post-European settlement, the role that fire had in matrix suppression in south-eastern Australia has been largely replaced by fertilization and heavy livestock grazing (Dorrough and Scroggie, 2008; Dorrough *et al.*, 2011). In the tropics, fire is still an important management tool for graziers (Trémont and McIntyre, 1994; McIntyre *et al.*, 2002). In MFWS, high macropod numbers has meant that fire is largely irrelevant because there is not enough biomass to need to burn. Drought is also a natural way of limiting biomass, and some methods of managing biomass other than fire include grazing, mowing, and raking (Wilson and Tilman, 2002; Hodgkinson, 2014). Both fire and grazing are strategies used to prevent sparse plant species from disappearing (Grubb, 1986).

2.3.1.3 Grazing

Limiting biomass in restoration techniques can also be achieved by strategic livestock grazing or managing native grazers: it opens up grass swards, allows native plant establishment, improving native grass sward health and competitiveness (Cole *et al.*, 2017). Like most ecological processes, there are trade-offs. Grazing can be compatible with high levels of diversity in the absence of fertiliser and planting weeds, but unsustainable livestock grazing can

have a negative effect on the landscape biodiversity (Neilly and Schwarzkopf, 2018), for example grassland reptiles (Howland *et al.*, 2014). This is because in some situations small-scale disturbances (e.g. hoof prints of grazing animals) prompt the persistence of shorter-lived species like annual plants, including weeds (Grubb, 1986). Grazing has been selectively employed as a tool to promote or reduce native species depending on intensity and timing (McIntyre *et al.*, 2003; Martin and Wilsey, 2006; McIntyre *et al.*, 2015).

2.3.2 Reintroduction as a restoration tool

Animal reintroductions began as management exercises, with ‘wildlife releases to establish new food resources, for biological pest control, and for aesthetic reasons’ (Fischer and Lindenmayer, 2000; Seddon *et al.*, 2007). This developed to include research, monitoring, and application of experimental approaches (Seddon *et al.*, 2007). However, a relatively recent secondary motivation involves biodiversity preservation through the recognition that there are missing ecological roles in an ecosystem which, if restored, can assist in improving ecosystem diversity and health (Seddon *et al.*, 2007; Sandom *et al.*, 2013). This has occurred as a response to increasing global awareness of the need to conserve biological diversity in the face of species extinctions (Seddon *et al.*, 2007).

While flora and fauna species reintroductions have become more prevalent in restoration ecology (Lunt, 1991; Morgan, 1999; Soulé *et al.*, 2003; Seddon *et al.*, 2007; McIntyre *et al.*, 2018), animal reintroduction is something that is missing from broader grassland restoration literature. Restoration ecology has not prioritised the quantification of interactions between reintroduced animals and their environment (Martin, 2003; Seddon *et al.*, 2007; Sandom *et al.*, 2013). While there is an area of animal research which explores the influence of ecosystem engineers and digging animals on the environment, digging animals are not widely explored with regards to grassy woodland restoration or management techniques (Fleming *et al.*, 2014; Chapman, 2016; Valentine *et al.*, 2017; Valentine *et al.*, 2018; Mallen-Cooper *et al.*, 2019). Therefore, there needs to be communication between plant and animal research communities, and recognition of the need for animal interactions within plant research circles.

The reintroduction of digging animals which provide a missing soil engineering role in the ecosystem (e.g. the eastern bettong) presents an opportunity to study both the digging animal’s effect on the ecosystem, and their potential for restoring degraded grasslands (Shorthouse *et al.*, 2012; Fleming *et al.*, 2014). Preliminary studies have suggested bettong digging has a beneficial influence on forb germination and establishment (Munro *et al.*, 2019; Ross *et al.*, unpublished a; Ross *et al.*, unpublished b). However, the exact influence that bettongs have on forb germination has yet to be determined (Mallen-Cooper *et al.*, 2019; Ross *et al.*, unpublished b). It is thought that through creating a regeneration niche for native forbs more functional than undisturbed areas, foraging bettongs have the potential to contribute to the increase of forb diversity (Chapman, 2016; Ross *et al.*, unpublished a). The different influences explored include

chemical change, function as a resource sink, modification of gap dynamics, and change in soil architecture and microclimate (Eldridge and Mensinga, 2007; James *et al.*, 2009; Valentine *et al.*, 2017; Munro *et al.*, 2019). The effect of the bettong pit on forb germination involves changes in physical conditions: the opening of the vegetation grass canopy, changes in temperature, moisture, resource collection, and pit topography (Garkaklis *et al.*, 2003; Sandom *et al.*, 2013).

When assessing seedling germination in natural bettong pits at my research site of MFWS, Ross *et al.* (unpublished a) found that a positive effect of bettong digging was greater in the denser *Themeda* grasslands compared to more open *Rytidosperma* dominated grassland. This suggests a connection to the creation of gaps in the grass canopy, but was not definitive. Therefore, guided by previous research and time constraints, I chose to focus on one patch or ecosystem type, the *Themeda* dominated grassland. I introduced the element of artificial engineering by directly comparing the germination of forbs in naturally and artificially created pits. While Ross' study suggested that the creation of gaps in the grass canopy is important, the reason behind this was not clear. Therefore, I took the question a step further, and my study aimed to clarify the influence that bettongs were having on seedling emergence.

A range of digging animals have been more thoroughly researched, especially in arid ecosystems: examples include the burrowing bettong (*Bettongia lesueur*), bandicoot (*Perameles*), and bilby (Fleming *et al.*, 2014; Chapman, 2016). It is difficult to transfer assumptions between different ecosystem types. Some of the assumptions about the flow of nutrients, runoff, and resource accumulation in ground hollows cannot be directly applied to the grassland ecosystem. Therefore, other bettong studies (James *et al.*, 2009; Fleming *et al.*, 2014; Valentine *et al.*, 2018) cannot be directly compared to a study on eastern bettongs in temperate grassy woodland ecosystems. However, some of the background can be used to support findings and general observations on the function of bettongs as ecosystem engineers (Manning *et al.*, 2015; Ross *et al.*, unpublished a).

My study explored grassland restoration strategies which involve small-scale disturbances and dynamics of gaps in the grass canopy. These strategies are therefore less disruptive to the existing ecosystem function than large-scale techniques such as scalping, and provide an option for restoration which is not yet widely available. By mimicking the natural process of regeneration in a temperate grassy woodland ecosystem, I artificially engineered the beneficial effect driving the increased germination in bettong foraging pits. Using artificially-created disturbances, I explored how restoration of rare or threatened species richness can proceed in temperate grassy woodlands that are already of relatively good quality. In doing so, I explored the knowledge gap in studies on soil disturbance of digging animals in temperate grassy woodland ecosystems (Fleming *et al.*, 2014; Mallen-Cooper *et al.*, 2019; Munro *et al.*, 2019; Ross *et al.*, unpublished a).

Chapter 3: Study site and Methods



3.1 Study location

This study was conducted in Mulligans Flat Woodland Sanctuary (MFWS), a 485-hectare area within the Mulligans Flat Nature Reserve that is an important ecological site in the city of Canberra, ACT (Manning *et al.*, 2011; Shorthouse *et al.*, 2012; Manning *et al.*, 2015). The climate is temperate, with a mean temperature range in winter of -1.5°C to 14.1°C , a mean temperature range in summer of 17.3°C to 31.3°C (2008 to 2018), and a mean annual rainfall of 695mm (1962 to 2018) (Australian Government Bureau of Meteorology 2018).

MFWS is a key point of engagement between science and the local community, due to its adjacent border with the residential northern suburbs of Canberra (Batson *et al.*, 2015a). Established in 1994, MFWS is home to the Mulligans Flat-Goorooyarroo Woodland Experiment (MFGOWE) that aims to research the restoration and protection of the critically endangered ‘box-gum’ grassy woodland ecosystem (McIntyre *et al.*, 2010; Manning *et al.*, 2011; Shorthouse *et al.*, 2012). The MFGOWE includes the restoration treatments of coarse woody debris addition, the reintroduction of locally extinct mammal species, and the manipulation of kangaroo grazing levels and fire (Manning *et al.*, 2011). One of the noteworthy features of MFWS is the feral animal-proof fence designed to exclude introduced cats, foxes and rabbits (Shorthouse *et al.*, 2012). The fence allows the safe reintroduction of animals which otherwise would be preyed upon by foxes and feral cats. To date, four fauna species have been reintroduced within the sanctuary, with the intention of restoring a missing functional role back into the landscape (Shorthouse *et al.*, 2012): the New Holland mouse (*Pseudomys novaehollandiae*), eastern quoll (*Dasyurus viverrinus*), bush-stone curlew (*Burhinus grallarius*) and the eastern bettong (*Bettongia gaimardi*).

Further information about the experiment can be found in Manning *et al.* (2011), Shorthouse *et al.* (2012), Batson *et al.* (2015a), and McIntyre *et al.* (2017). A comprehensive plant species list can be found in the supplementary material of McIntyre *et al.* (2010), and soils information can be found in McIntyre *et al.* (2010) and McDonald *et al.* (1998).

3.2 Experimental design

As stated in my introduction, the primary question guiding this thesis was:

Do artificially engineered regeneration niches, based on bettong-created pits, provide equal forb germination when compared to the natural bettong foraging pit?

To address my research questions and examine the effects of bettong digging on seed germination, I conducted a seed addition experiment comparing the control with natural and artificial bettong foraging pits, and a scrape treatment. These treatments were designed to test the effects of small-scale soil and grass canopy disturbances on the germination of three native grassland forbs.

The experimental design, statistical analysis and focus research questions are inherently linked, based on the motivation to investigate the exact influence bettong foraging has on the germination of seedlings. Within the main research question, I asked three specific questions relating to the relationships between different treatments:

1) Do natural pits promote the germination and establishment of seedlings?

I hypothesised that bettong pits would significantly increase the number of seedlings compared to the control, as shown by previous studies (e.g. Ross *et al.* (unpublished a)).

2) Can artificial pits create a similar environment for germination and establishment?

I predicted that both treatments would have a significant positive effect on germination, and that there would be no difference between the two treatments. This would indicate that the effects of a bettong pit can be replicated artificially. However, if the natural pit is significantly better than the artificial pit, this would indicate that bettongs provide an unknown additional benefit to seed germination (e.g. dispersal of mycorrhizae).

3) Is the possible facilitation effect of germination due to the removal of vegetation, or the structural effects of the pit?

Comparing the artificial pit and scrape treatments allowed me to separate the structural effects of the pit (microclimate, chemical effects) from the effect of disturbance of the grass canopy and soil surface. I predicted that both the artificial pit and scrape would improve germination compared to the control, but that the artificial pit would have a greater effect than the scrape due to the additional benefit of the pit itself. However, if there is no difference between the treatments, this would indicate that the pit does not provide any additional benefit over the disturbance effect.

I conducted the germination experiment using a blocked design with four sites in temperate grassy woodlands. I implemented ten replication plots in each site: each with four different disturbance treatments, and three plant species (Figure 3.1).

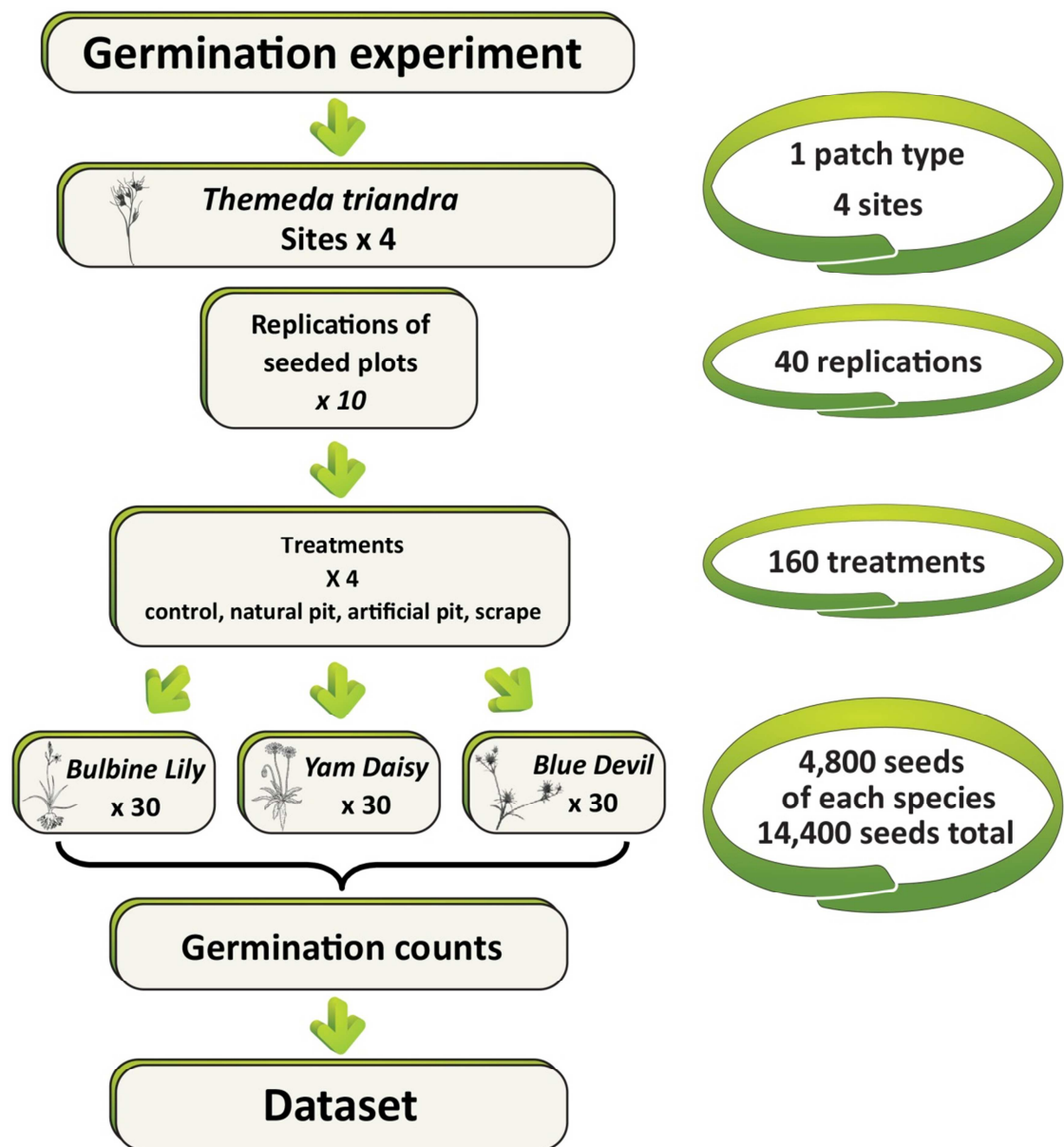


Figure 3.1. Flow diagram of germination experiment methodology

3.2.1 Study sites

The research sites fall within the dominant grassy woodland ecological community of MFWS (Clarke and Davison, 2001; Clarke and Davison, 2004; McIntyre *et al.*, 2010). The ecologically community is discussed in more detail in the study by McIntyre *et al.* (2010). I chose specific study sites in MFWS that adhered to the criteria of eastern bettongs being active, and were dominated by *Themeda triandra* as identified by McIntyre *et al.* (2010) (Figure 3.2 and Figure 3.3).

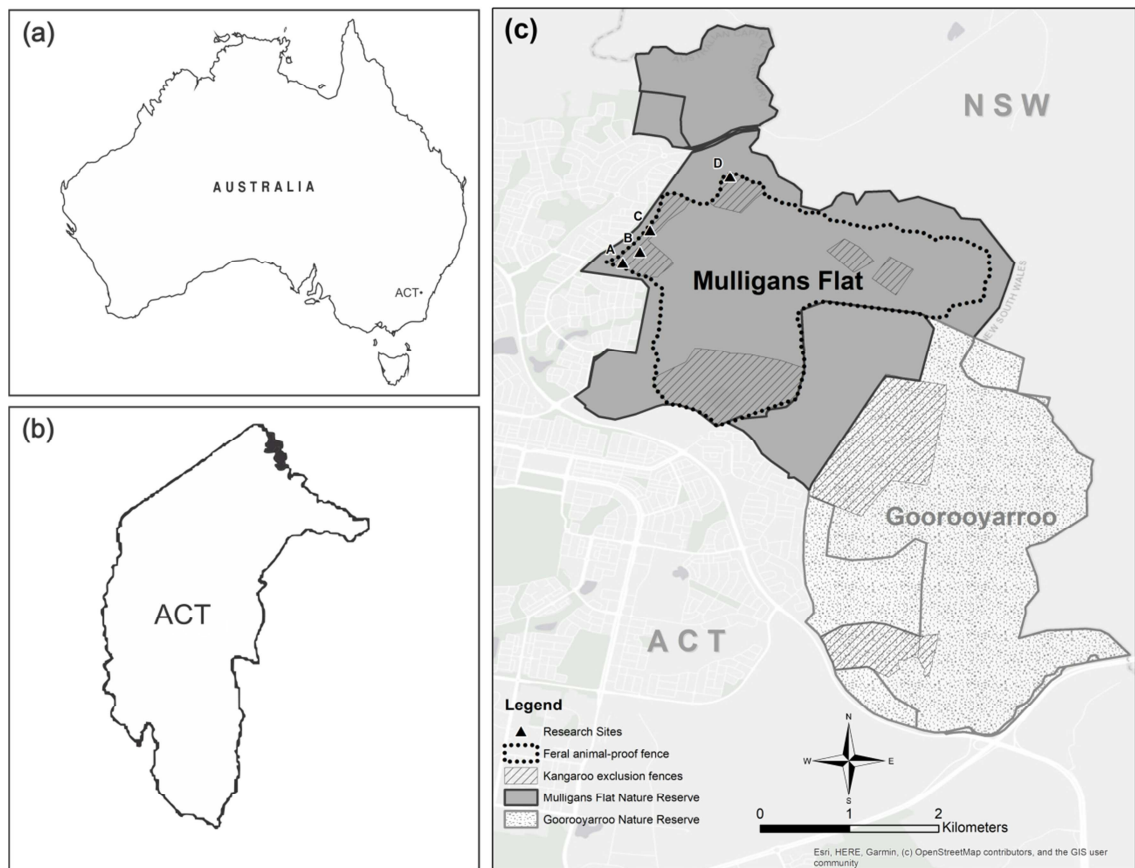


Figure 3.2. The location of Mulligans Flat Nature Reserve in north-eastern Australian Capital Territory (ACT). (a) The ACT within Australia (b) Mulligans Flat and Goorooyarroo Nature Reserves (shaded) within the ACT and (c) The experimental research sites A-D within Mulligans Flat Woodland Sanctuary. The coordinates for each research site were marked at the location of the control treatment of Plot 1.

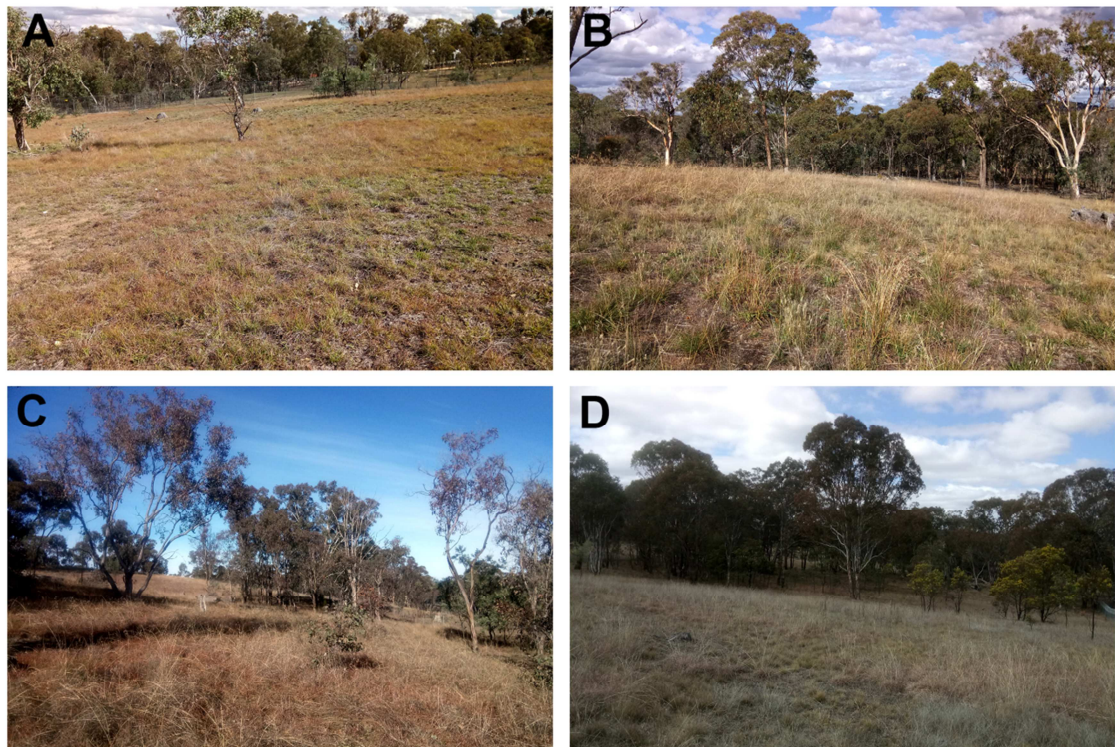


Figure 3.3. Research Sites A-D in Mulligans Flat Woodland Sanctuary. Photos taken by Rachael Robb (2018, 2019). A (April 2019), B (April 2019), C (August 2018), D (September 2018)

Rachael Erin Robb Engineering the regeneration niche for the restoration of temperate grassy woodlands

Due to the ecological importance of *Themeda* in grassy woodland ecosystems, my study sites are located in *Themeda* swards, the dominating grass cover of near-continuous tussocks (Barrett *et al.*, 2018) (Figure 3.4). The *Themeda* patch type was chosen as the study location following the findings by Ross *et al.* (unpublished a) that suggest the digging of the eastern bettong had a greater effect on seed germination in the denser *Themeda* grasslands when compared to *Rytidosperma* grassland. Additionally, all research sites have lower kangaroo grazing pressure than the rest of the sanctuary due to existing kangaroo exclusion zone experiments. The sites were placed in kangaroo exclusion zones because in the high grazing areas, the grass is too short and does not form a closed grass canopy.



Figure 3.4. Kangaroo grass (*Themeda triandra*) sward. Research site D, Mulligans Flat Woodland Sanctuary (MFWS). Photo taken by Rachael Robb (2019).

3.2.2 Treatments

The research by Ross *et al.* (unpublished a) suggests that soil chemistry in a bettong pit is not as important as the soil architecture in temperate grassy woodlands. Therefore, I focused my treatment variables on the physical attributes caused by bettong foraging. The experiment therefore tested treatments that may promote germination and establishment.

I applied the four treatments within each plot, separated by a minimum distance of 30 centimetres (Figure 3.5). I separated each plot by a minimum distance of one metre. I prepared the treatments with the use of: a tape measure (to ensure the minimum and maximum distances between plots and treatments), a ruler (to measure the depth of the pits), the chisel end of a brick hammer (to create the dimension of the artificial pit and loosen the soil of the scrape), and a

metal ring with a 75 millimetres diameter and area of 44.2cm^2 (for the dimensions of the control and scrape treatments).



Figure 3.5. The set-up of Plot 1, Site D, consisting of the four treatments. From left: natural pit, control, artificial pit, and scrape. Photo taken by Rachael Robb (2018), Mulligans Flat Woodland Sanctuary (MFWS).

Natural pit – Within the chosen sites, I selected natural eastern bettong pits. I ensured that they were relatively fresh, with a loose spoil and an absence of seedlings. The exact dimensions of each pit were measured to create the corresponding artificial pit. For reference, the average size of an eastern bettong pit, calculated from 1518 pits, is 50 by 40 millimetres and 35 millimetres deep (Munro *et al.*, 2019).

Artificial pit – The aim of the artificial pit treatment was to closely mimic the physical conditions of the natural pit and therefore assess the differences in seed germination. I created the pit according to the same measurements of a corresponding natural pit within the plot.

Scrape – I designed the scrape treatment to test whether the architecture of the pit was a factor in forb growth, or whether the removal of surface vegetation and creating a gap in the grass canopy were enough to create a regeneration niche for native forb seeds. This was tested by removing only the surface vegetation and the top 10 millimetres of soil. I then compared these to the natural bettong pit and to the control plots which only contained added seed.

Control – I selected the controls in areas of tussock density similar to where the natural bettong foraging pits were located. The treatment area was consistently measured at 75 millimetres (Figure 3.6).

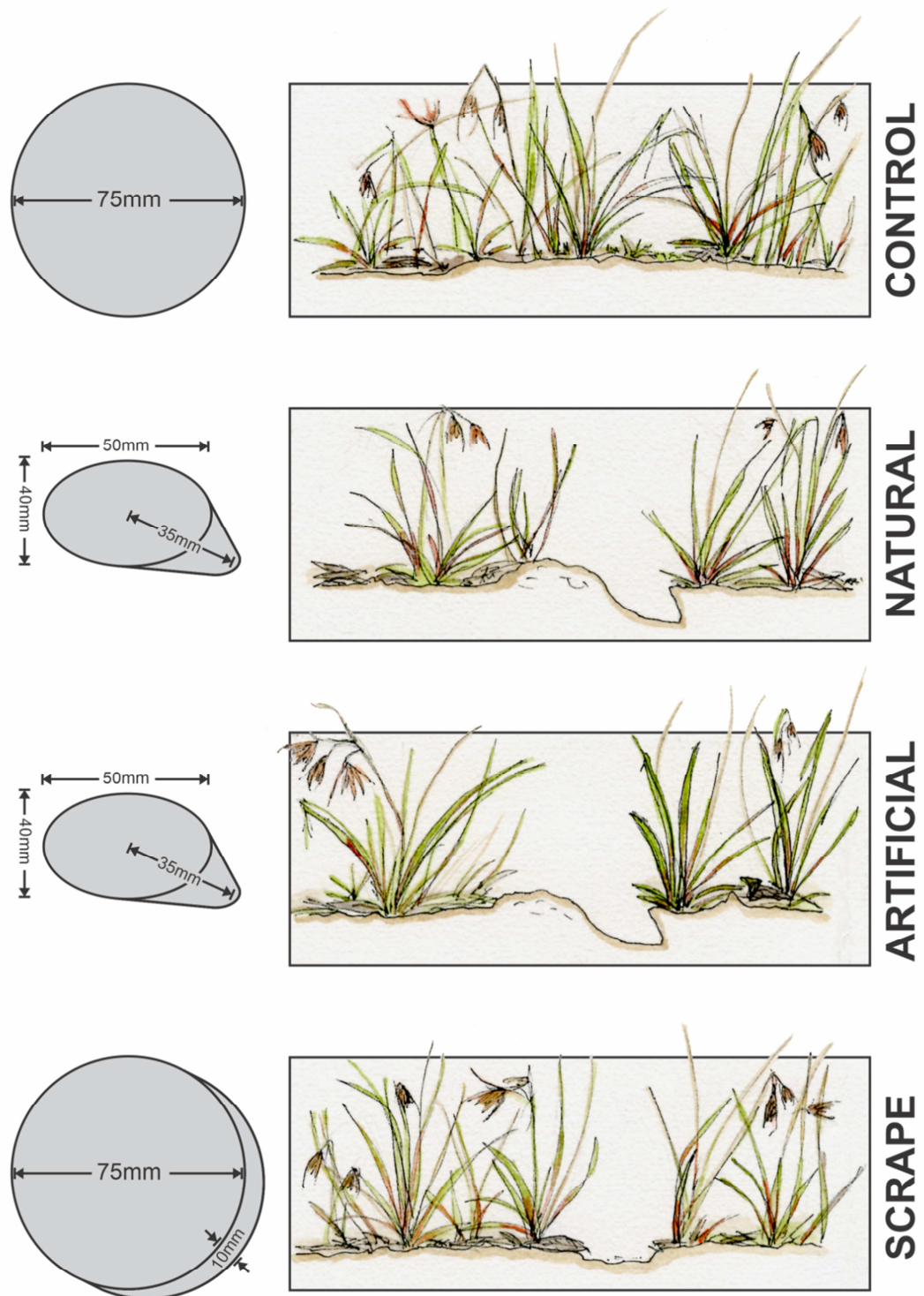


Figure 3.6. The method behind the four disturbance types measured for seedling emergence: a *control* with a fully shaded grass canopy, a *natural* bettong-created pit, an *artificial* pit replicating eastern bettong foraging, and an artificial *scrape* of vegetation removal. The diagram shows the dimensions and side profile of the treatment area, as a representation of the difference in treatments; it is not a quantitative depiction of the *Themeda triandra* grass density. Original artwork by Rachael Robb (2019).

3.2.3 Seed addition

I added 30 seeds of each of the three native forbs to each treatment, and monitored weekly for the next four months. I placed seeds on the surface of the treatment area. By dusting a fine layer of soil, combined with natural and manual disturbance to mimic natural accumulation of seeds and leaf litter, the issues identified in the study by Dowling *et al.* (1971) with seeding on non-cultivated soil surfaces were mitigated.

I chose a seed study for the experiment to mimic the natural fall and distribution of plant seed in the landscape, whether into prepared gaps in the grass canopy (pit or scrape) or into high competition tussock areas (control). Seed was added because I was interested in the effect of bettong digging on the chosen species, and replicating a restoration scenario where I added seed. Adding seed also meant I have direct comparison between plots, and can better assess the influence of the treatments on species germination and emergence.

3.2.4 Species selection

The species used during this experiment were chosen for their sensitivity to disturbance, their availability, and that their seeds were large enough to be manipulated and handled.

I selected three species of native perennial forbs that are present within the reserve, but relatively uncommon (likely because of their high sensitivity to past livestock grazing). Therefore, new germinants of the studied species were assumed to be from sown seed and not the existing seedbank. The forbs I used were yam daisy (*Microseris walteri*), blue devil (*Eryngium ovinum*), and bulbine lily (*Bulbine bulbosa*). I purposefully selected tuberous species from different families to see the individual response of each to the treatment conditions: daisy (Asteraceae), carrot (Apiaceae), and lily (Asphodelaceae). The species are active in winter and spring with shoots which die down in summer (McIntyre *et al.*, 2018). Hereafter, the study species will be referred to by their genus, as *Microseris*, *Eryngium* and *Bulbine* respectively.

Microseris flowers between September to February with a yellow flower (Barrett *et al.*, 2018), and has a large seed size and upright growth form (Smallbone, 2005) (Figure 3.7a). *Microseris* is a particularly palatable native forb genus and therefore sensitive to grazing especially when it is young (Lunt, 1991; Lunt, 1996). The grazing pressure and sensitivity of *Microseris lanceolata* and *M. walteri* is one of the reasons it is often studied (Farrington and Mitchell, 1966; Lunt, 1991). *M. walteri* was previously known as *M. lanceolata*, and there has since been a change to the naming convention which is not yet widely used (Walsh, 2016). This has separated the two *Microseris* species based on their altitude and their slight morphological differences, with *M. lanceolata* generally being sighted above 1000m and *M. walteri* below 1000m altitude. *Microseris* also has significance to indigenous cultural uses, and is one of the most important food plants of Aboriginal people of south-eastern Australia (Walsh, 2016; Silcock, 2018). This is due to the distinctive root system of *Microseris* that yields an annually replaced fleshy sweet-tasting tuber (Walsh, 2016).

Eryngium flowers between November and January with blue, spiky flowers in rigid compounds (Barrett *et al.*, 2018). The fruit is sized between 3 and 5mm long, and the leaves are stiff and fibrous, divided and can be tinged blue (Barrett *et al.*, 2018) (Figure 3.7b).

Bulbine flowers between September and October with a bright yellow flower (Barrett *et al.*, 2018). The lily has a fruit capsule with a 5-8mm diameter, fleshy green leaves and anthers which grow upright and clustered together (Barrett *et al.*, 2018) (Lunt, 1995). *Bulbine* also has Indigenous significance as a food source, because the roots can be eaten when cooked (Barrett *et al.*, 2018) (Figure 3.7c)

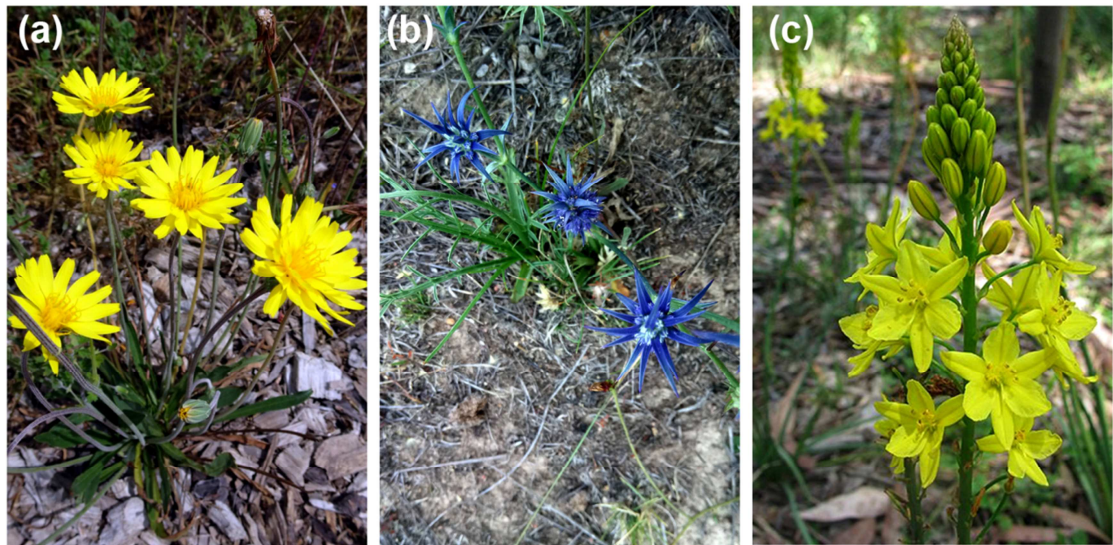


Figure 3.7. Native forbs in this study. (a) Yam daisy *Microseris walteri* (Canberra Nature Map, 2018), (b) Blue devil *Eryngium ovinum* (Robb 2019), (c) Bulbine lily *Bulbine bulbosa* (St Kilda Botanical Gardens, 2010)

I sourced seeds from Greening Australia, which were collected from the ACT Aranda Bushland on 26th October 2015 and 10th November 2017 (*Microseris*) and the Mulanggari Grassland (*Eryngium*). The *Bulbine* seeds were sourced from Gungaderra Nature Reserve, Gungahlin, in December 2010. The seeds received no pre-treatment, but were counted and separated using forceps into Eppendorf Tubes or envelopes based on the numbers needed for each treatment.

3.2.5 Measurement and germination count process

The experiment was set up over four days from the 13th to 16th of August 2018, and seeds were added to plots on the 19th of August 2018. I visited every treatment plot once a week for fifteen weeks, from the 27th of August to 6th of December 2018, and counted the number of seedlings of each species present. I also noted other species germinating in my study plots each week. Seed germination rates change over time as factors such as rain, climate and niche condition changes. I also wanted to see if there was an interaction between the disturbance treatments where, at a particular time, there was a strongest effect. Therefore, the measurement

process allowed me to observe whether this is the case, and account for the changes in germination over duration of my study.

3.2.6 Data Analysis

Do natural pits promote the germination and establishment of seedlings?

I tested the effect of the treatments, the effect over time and whether this effect varies at different times by comparing a set of generalised additive mixed models (GAMMs) and generalised linear mixed models (GLMMs) (Bolker *et al.*, 2009; Nakagawa and Schielzeth, 2013). I modelled each species separately to examine differences in response between species. My response variables for these models were the seedling counts of *Microseris* and *Eryngium* in each pit each week. My predictor variables were:

- *treatment* – a factor variable with four levels (control, natural bettong pit, artificial pit and scrape). This variable was treated as a linear term.
- *time* – fitted as a continuous non-linear variable ranging from Week 1 to Week 15. This variable was treated as a smoothed term; therefore each week's data was considered more related when closer in time (e.g. Weeks 1 and 2 were more related than Weeks 1 and 5). This differed from treating the data as discrete and independent between weeks.

I compared five models:

1. $response \sim 1 + random\ effects$ – This GLMM was the null model.
2. $response \sim treatment + random\ effects$ – This GLMM tested for the effect of the *treatments* regardless of *time*.
3. $response \sim smoothed(time) + random\ effects$ – This GAMM tested for the effect of *time* regardless of *treatment*.
4. $response \sim treatment + smoothed(time) + random\ effects$ – This GAMM tested for the effects of *treatment* and *time* without any interaction.
5. $response \sim treatment*smoothed(time) + random\ effects$ – This GAMM tested for the effects of the interaction of *time* and *treatment* i.e. whether the treatment effect changed over time.

I used plot replicates nested within a site as random intercepts to account for spatial and temporal correlation between samples. The plots were arranged in each site in ten plots of four in a blocked design, and therefore not randomly dispersed. The response variables were count data, therefore, I assumed a Poisson distribution for the models. Overdispersion can occur in Poisson models (Hilbe, 2011), and when there is clustering in the data (observations not truly independent), resulting in a poor fit to the data (Harrison, 2014). Overdispersion must be accounted for, or it can lead to errors in the conclusions made from research data (Harrison, 2014). Therefore, I checked all models for overdispersion in both species' response. I accounted

for the overdispersion of *Microseris* by using an observation-level random factor (Harrison, 2014). The *Eryngium* germination data were not overdispersed.

Each model was compared using second order Akaike's Information Criterion (AICc) for small sample sizes (Burnham and Anderson, 2002; Nakagawa and Schielzeth, 2013). I considered all models within two AICc scores of the highest ranked model to be appropriate fits to the data. If the null model was the highest ranked, then I considered none of the variables to be significant predictors of seedling germination. I plotted the linear effects on the link scale, and interpreted effects as significant if they did not cross the zero-effect line (du Prel *et al.*, 2009; Welsh, 2011). I plotted the smoothed non-linear effects (time) on the response scale. The models looked at all of the data as well as tested for differences between weeks. Differences only existed in the overall variation, allowing for the effect to be assessed.

Can artificial pits create a similar environment for germination and establishment?

To test whether there were significant differences in the effects of the artificial and natural pits, I fitted GLMMs to my response variables against the treatment variable as a predictor, again using the random effects mentioned above. The use of GLMMs for ecological data has been widely used as a flexible approach for analysing data with random effects (Bolker *et al.*, 2009). I then performed Tukey's honest significance *post-hoc* tests on the factor levels of treatment in each model (Hayter, 1984).

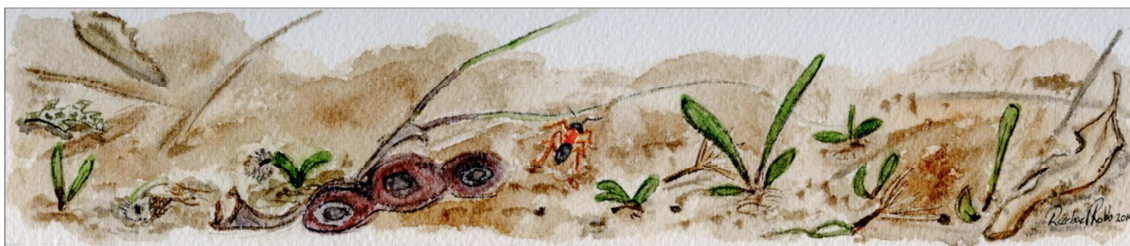
Is the possible facilitation effect of germination due to the removal of vegetation, or the structural effects of the pit?

To test whether there were significant differences in the effects of artificial deep pits and shallow scrapes, I followed the same procedure as question 2.

I conducted the analysis in R Studio version 3.4.0 (2017-04-21) and R version 3.4.4 (2018-03-15) (The R Foundation for Statistical Computing Platform). I used the 'gam4' package to fit the GLMMs and GAMMs (Wood *et al.*, 2017), the 'MuMIn' to calculate the AICc scores (Barton, 2009), the 'lme4' package to fit the GLMMs in questions 2 and 3 (Bates *et al.*, 2014) the 'multcomp' package for the post-hoc tests (Hothorn *et al.*, 2008) and the 'ggplot2' package for plotting (Wickham, 2016).

For my study, effect sizes were derived using GAMMs assuming a Poisson distribution. Due to the distribution, the effect sizes on the link scale are on the natural logarithm scale. Therefore the effect size is an abstraction of the raw data, describing the slope of the relationship between the controls and treatment on the link scale (log). It is used to clearly show the effect that the treatments had on the germination when compared to the reference of the control data.

Chapter 4: Results



4.1 Species germination results

I added 14,400 seeds into the research treatment sites. I recorded the observed germination of *Microseris* and *Eryngium* seedlings from the four sites and forty plots over fifteen weeks. No *Bulbine* seedlings were observed, possibly due to the seed being dormant or unviable. There were also seedlings observed emerging from the existing seed bank, a mix of exotic plants (e.g. quaking-grass *Briza*, common centaury *Centaureum erythraea*, wood-sorrels *Oxalis*, bromes *Bromus*) and native plants (e.g. early nancy *Wurmbea dioica*, *Haloragis*, sheep's burr *Acaena*).

The number of seedlings observed each week is shown in Figure 4.1a, 4.1b. In Week 2, germination of *Microseris* seeds was observed in both natural and artificial pits. During the following week, germination in the scrape treatment rose from 28 observed seedlings to 418 observed seedlings. Seedling emergence peaked during Week 4 with 480 seedlings across the four sites. The *Eryngium* seedlings were slower to germinate than the *Microseris*; emergence was first observed in the natural pit during Week 4, with a total of 37 seedlings over all sites by the end of Week 10.

When compared to the germination results, rainfall data over the duration of the study showed there was high rainfall in Weeks 2, 10 and 12, but very little between Weeks 3 and 9 (Figure 4.1c). Rainfall data for the study period can be found in Appendix I.

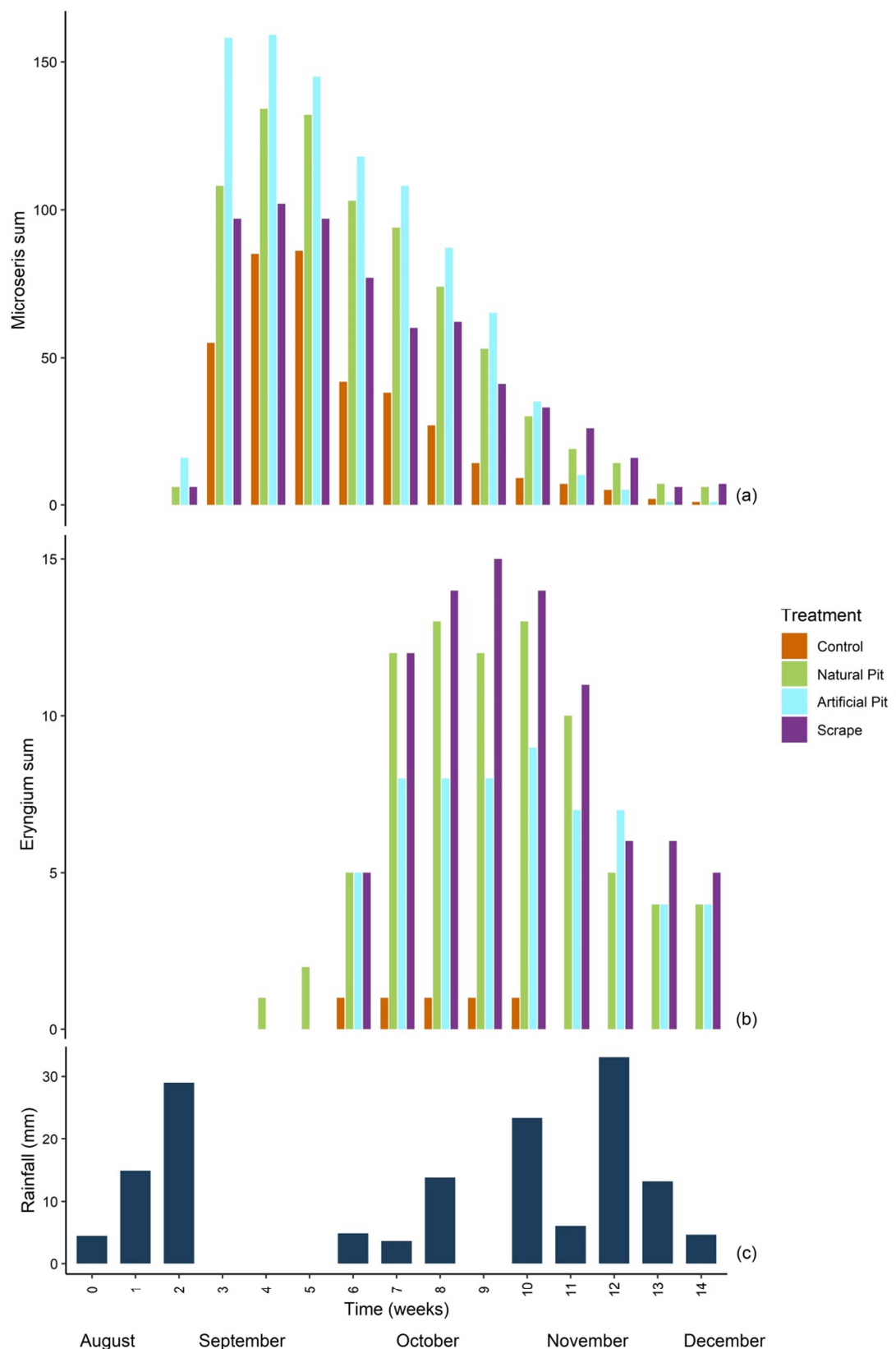


Figure 4.1. (a) Yam daisy (*Microseris walteri*) and (b) blue devil (*Eryngium ovinum*) seedling emergence over time. Data come from a seed germination field experiment over four sites within Mulligans Flat Woodland Sanctuary. Seedling emergence was measured in four disturbance types: control, natural pit, artificial pit, and the scrape. The data were collected in a period of 15 weeks from August to December 2018. (c) The rainfall data were sourced from the Bureau of Meteorology, location Nicholls (Gungahlin Lakes) station 70340 for the same time period, collating daily rainfall into the same weeks as the germination trial.

4.2 Do natural pits promote the germination and establishment of seedlings?

The first research question addressed the effect that natural foraging pits of eastern bettongs had on seed germination and establishment. After selecting the most appropriate model, I analysed the effects of the treatments and time on the germination of *Microseris* and *Eryngium*. Due to lack of germination, no analysis could be completed on *Bulbine* response to the natural and artificial pits and scrape treatments.

4.2.1 Model Selection

When I ran a model comparison using AICc for both *Microseris* and *Eryngium*, the top-ranked model contained both *treatment* and *time* (Model#3 in Tables 4.1 and 4.2). This suggested that seedling count differed significantly between the treatments and differed significantly through time. However, there was no interaction of these two predictors; this suggests that the difference in seedling counts between the treatments did not differ over time.

Table 4.1. *Microseris* statistical results for the AICc test comparison

Model	Predictor variables tested	df	AICc score	ΔAICc
Model#3	<i>~treatment+smoothed(time)</i>	9	4553.299	0.000
Model#2	<i>Smoothed(time)</i>	6	4603.665	50.366
Model#4	<i>~treatment*smoothed (time)</i>	12	4633.507	80.208
Model#1	<i>treatment</i>	7	5395.547	842.248
Null Model	<i>~1</i>	3	8476.056	3922.757

df=degrees of freedom, AICc = Akaike's Information Criterion

Table 4.2. *Eryngium* statistical results for the AICc test comparison

Model	Predictor variables tested	df	AICc score	ΔAICc
Model#3	<i>~treatment+smoothed(time)</i>	9	1078.802	0.000
Model#4	<i>~treatment*smoothed (time)</i>	12	1121.480	42.678
Model#2	<i>Smoothed(time)</i>	6	1175.793	96.991
Model#1	<i>treatment</i>	7	1304.058	225.256
Null Model	<i>~1</i>	3	1401.56	322.254

df=degrees of freedom, AICc = Akaike's Information Criterion

4.2.2 Effects of treatments

The model of best fit, Model #3, was used to calculate the effect that each treatment had on the overall germination compared to the control for both *Microseris* and *Eryngium*. Effect sizes represent the difference between the treatments and the control on the log scale. The error bars represent 95% confidence intervals (CIs). The zero line indicates no effect, and I interpreted effects as significant if the CIs did not cross the zero line. If the CIs of two effect sizes overlapped, I interpreted these as not significantly different from each other.

The effect sizes of the *Microseris* germination (Natural=0.89, Artificial=0.86, Scrape=0.68) compared to the control germination were significant (Figure 4.2). All the 95% confidence intervals of the artificial, natural and scrape treatments did not cross the zero effect line. Further, these treatment level effects were shown to be significant in the model output (Table 4.1). The artificial and natural bettong pit treatments showed the highest significant effect against the control.

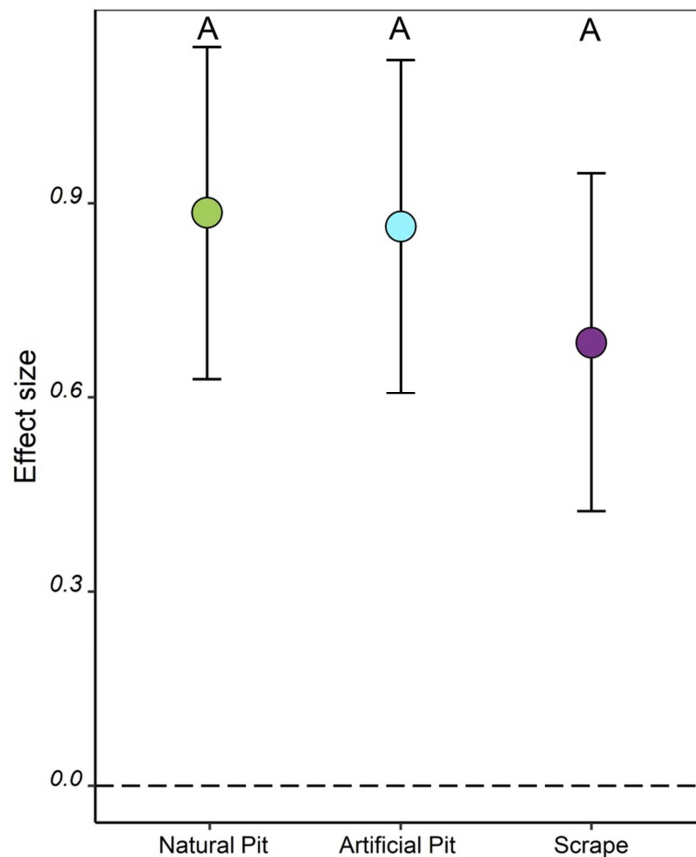


Figure 4.2. Effect of treatments on yam daisy (*Microseris walteri*) seedling emergence.

Data come from a seed germination field experiment over four sites within Mulligans Flat Woodland Sanctuary, ACT. Seedling emergence was measured in four disturbance types: control, natural pit, artificial pit, and the scrape. Effect sizes are derived using generalised linear mixed models assuming Poisson distribution. Effect sizes represent the difference between the treatments and the control on the log scale. The error bars represent 95% confidence intervals (CIs). The zero line indicates no effect, and I interpreted effects as significant if the CIs did not cross the zero line. If the CIs of two effect sizes overlap, I interpreted these as not significantly different from each other. Additionally, Tukey's honest significance *post-hoc* tests on the factor levels of treatment in each model showed no significance (A). The data were collected in a period of 15 weeks from August to December 2018.

The effects of the treatments on *Eryngium* germination (Natural=2.79, Artificial=2.48, Scrape=2.87) were statistically significant compared to the control (Figure 4.3). Further, these treatment level effects were shown to be significant in the model output (Table 4.2). Compared to the seedling emergence trend in *Microseris*, there was a trend of greater effect (but still not significant) in the scrape and the natural pit than in the artificial pit.

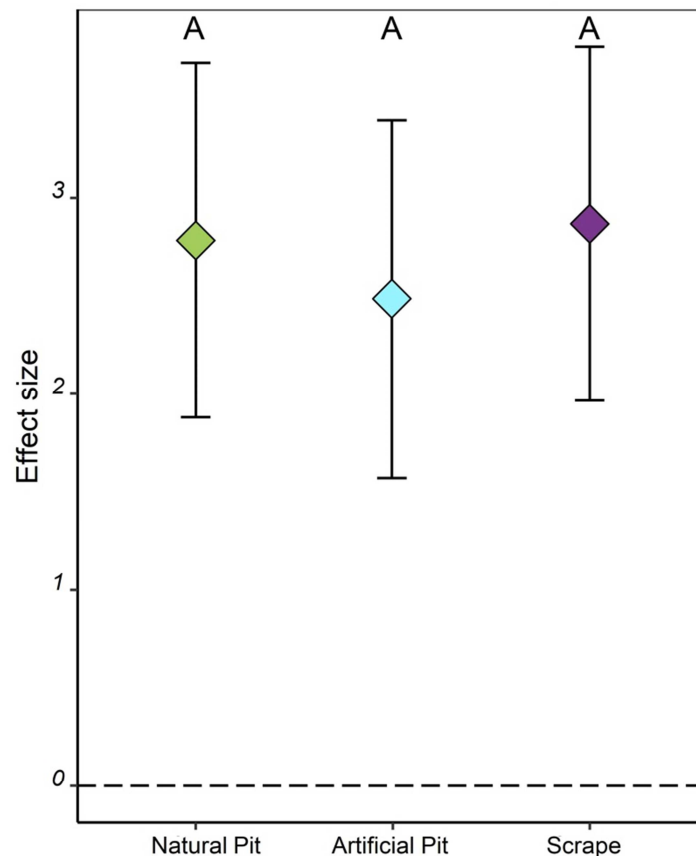


Figure 4.3. Effect of treatments on blue devil (*Eryngium ovinum*) seedling emergence.

Data come from a seed germination field experiment over four sites within Mulligans Flat Woodland Sanctuary, ACT. Seedling emergence was measured in four disturbance types: control, natural pit, artificial pit, and the scrape. Effect sizes are derived using generalised linear mixed models assuming a Poisson distribution. Effect sizes represent the difference between the treatments and the control on the log scale. The error bars represent 95% confidence intervals (CIs). The zero line indicates no effect, and I interpreted effects as significant if the CIs did not cross the zero line. If the CIs of two effect sizes overlap, I interpreted these as not significantly different from each other. Additionally, Tukey's honest significance *post-hoc* tests on the factor levels of treatment in each model showed no significance (A). The data were collected in a period of 15 weeks from August to December 2018.

4.2.3 Effects of time

By applying a Generalised Additive Mixed Model (GAMM) to each treatment over the weeks of the experiment, the predicted values showed the temporal differences in the germination peaks between species (Tables 4.3 and 4.4). When compared to rainfall, it also provided context to the germination patterns.

Table 4.3. Summary of best fit *Microseris* model ($\sim$ treatment + smoothed[time] $|I$).
Adjusted $R^2 = 0.063$, AICc = 4553.30

Predictor	Factor level	Estimate	Standard error	p value
Intercept	-	-3.533	0.418	<0.0001***
<i>Treatment</i>	Natural pit	0.886	0.131	<0.0001***
<i>Treatment</i>	Artificial pit	0.864	0.131	<0.0001***
<i>Treatment</i>	Scrape	0.685	0.133	<0.0001***

Approximate significance of smoothed term		
Smoothed term	Estimated degrees of freedom	p value
<i>Time</i>	7.735	<0.0001***

Table 4.4. Summary of best fit *Eryngium* model ($\sim$ treatment + smoothed[time] $|I$).
Adjusted $R^2 = 0.045$, AICc = 1078.80

Predictor	Factor level	Estimate	Standard error	p value
Intercept	-	-7.915	0.996	<0.0001***
<i>Treatment</i>	Natural pit	2.785	0.461	<0.0001***
<i>Treatment</i>	Artificial pit	2.485	0.466	<0.0001***
<i>Treatment</i>	Scrape	2.868	0.460	<0.0001***

Approximate significance of smoothed term		
Smoothed term	Estimated degrees of freedom	p value
<i>Time</i>	4.536	<0.0001***

The peak of the mean count of germination of *Microseris* was in Week 4, before decreasing again in a curve that drops to near zero by Week 10 (Figure 4.4). In contrast, the *Eryngium* showed a broader shaped curve, with a later start to germination and the peak around Week 9 or 10 (Figure 4.5).

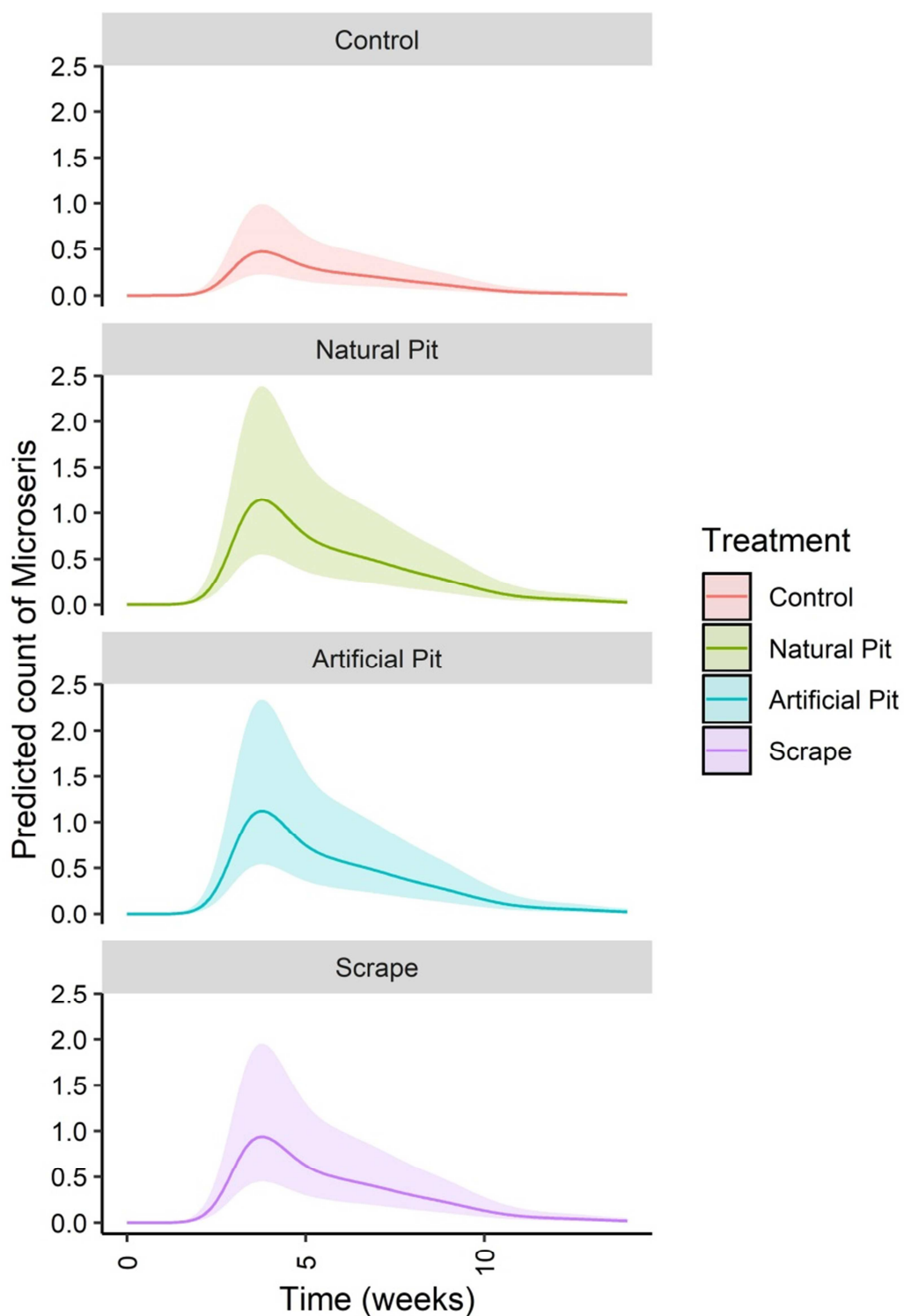


Figure 4.4. Generalised Additive Mixed Model (GAMM) of the predicted count of yam daisy (*Microseris walteri*) seedling emergence. Data come from a seed germination field experiment over four sites within Mulligans Flat Woodland Sanctuary. Seedling emergence was measured in four disturbance types: control, natural pit, artificial pit, and the scrape. The predicted values are shown by the solid line. The error shading represents the 95% confidence intervals. The data were collected in a period of 15 weeks from August to December 2018.

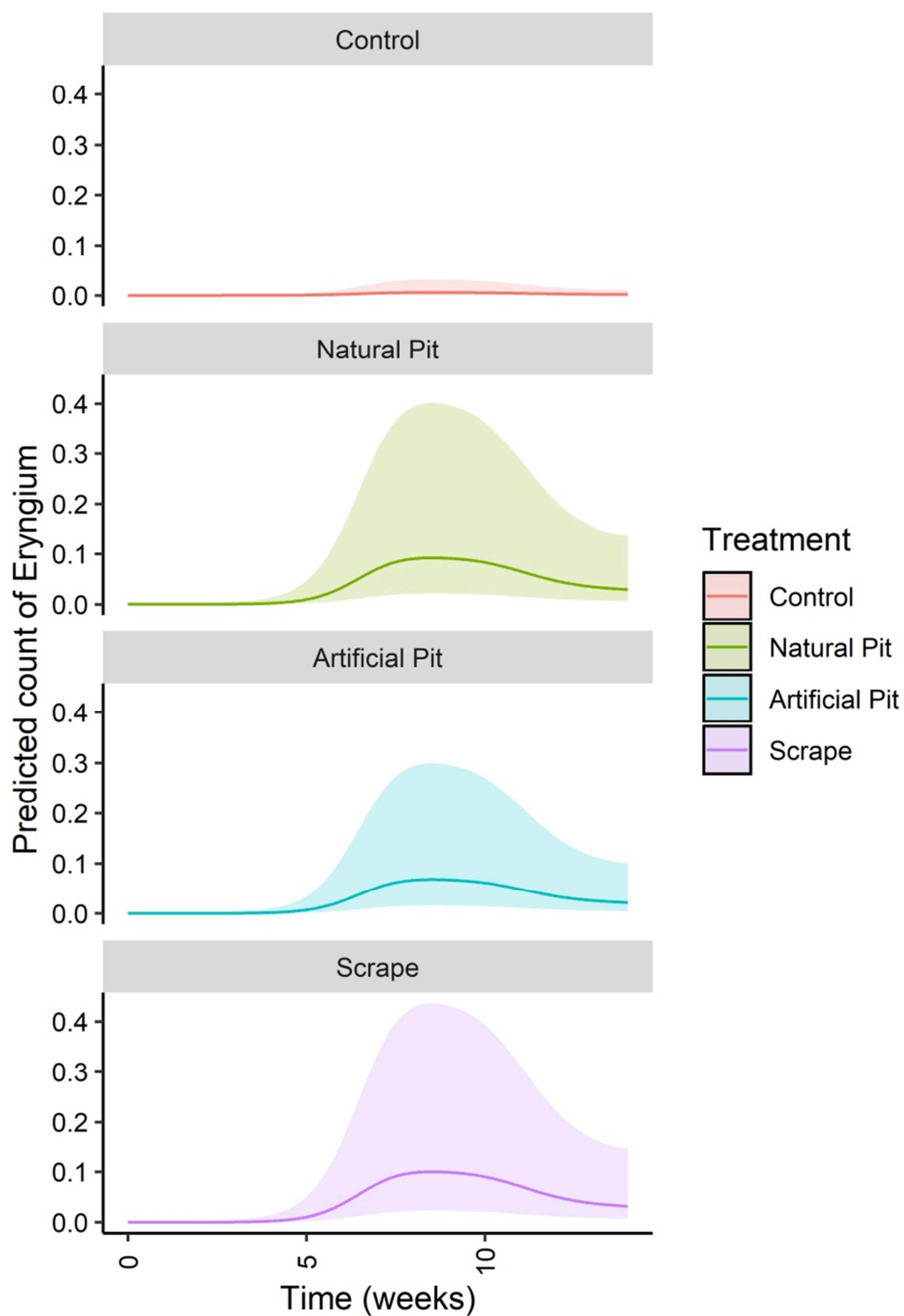


Figure 4.5. Generalised Additive Mixed Model (GAMM) of the predicted count of blue devil (*Eryngium ovinum*) seedling emergence. Data come from a seed germination field experiment over four sites within Mulligans Flat Woodland Sanctuary. Seedling emergence was measured in four disturbance types: control, natural pit, artificial pit, and the scrape. The predicted values are shown by the solid line. The error shading represents the 95% confidence intervals. The data were collected in a period of 15 weeks from August to December 2018.

4.3 Can artificial pits create a similar environment for germination and establishment?

Tukey's honest significance *post hoc* tests were run on a generalized linear mixed model on the treatment effects. This showed there was no significant difference between the natural and artificial pit treatments (Figure 4.2).

4.4 Is the possible facilitation effect of germination due to the removal of vegetation, or the structural effects of the pit?

Tukey's honest significance *post hoc* tests were run on a generalized linear mixed model on the treatment effects. These showed there was no significant difference between the artificial pit and scrape treatments (Figure 4.3).

Chapter 5: Discussion



5.1 Research questions

This thesis aimed to explore the influence of eastern bettong foraging pits on native forb germination, and the artificial creation of the diggings as a potential restoration technique for native grasslands. I argued that (i) the way bettongs dig and open the vegetation canopy in *Themeda* grasslands is beneficial to forb germination, and (ii) this benefit can be similarly gained through artificial engineering of a regeneration niche. The primary research question guiding this thesis is:

Do artificially engineered regeneration niches, based on bettong-created pits, provide equal forb germination when compared to the natural bettong foraging pit?

With this in mind, I will address and discuss the implications behind the answers to my focus questions:

- 1) Do natural pits promote the germination and establishment of seedlings?
- 2) Can artificial pits create a similar environment for germination and establishment?
- 3) Is the possible facilitation effect of germination due to the removal of vegetation, or the structural effects of the pit?

5.2 The influence of bettong digging

5.2.1 Do natural pits promote the germination and establishment of seedlings?

The first research question explored the beneficial influence of bettong digging on seed germination of native forbs. The results show that there is a significant effect, and therefore suggests that natural pits do promote the germination and establishment of seedlings. These effects were determined by comparing the control with seed germination over time in pits and scrape treatments.

Effects of treatments

The effects of the treatments were statistically significant from the control in both the germination of *Microseris* and *Eryngium* seedlings (Figure 4.2 and Figure 4.3). There was no result for *Bulbine* seedlings, due to a lack of germination. Significant differences to the germination of plant species has been found where other animals participate in soil engineering

behaviour e.g. in the cases of bettongs and bandicoots (Fleming *et al.*, 2014; Chapman, 2016; Valentine *et al.*, 2017; Valentine *et al.*, 2018), porcupines (Guterman and Herr, 1981), echidnas (Eldridge and Mensinga, 2007), and wild boar (Sandom *et al.*, 2013). For example, Sandom *et al.* (2013) found the reintroduction of wild boar into the Scottish moorlands reduced plant competition and aided re-establishment of woodland trees. Eldridge and Mensinga (2007) found short-beaked echidnas altered soil and resource heterogeneity by creating pits that acted as resource sinks.

This study is the first to directly compare seedling germination in natural and artificial eastern bettong pits. The use of artificially-created bettong pits has not been fully explored (Ross *et al.*, unpublished a; Ross *et al.*, unpublished b), although a study by Valentine *et al.* (2017) has used artificial plots paired to undug sites to investigate seedling recruitment and environmental characteristics (soil moisture content, hydrophobicity and litter composition) of foraging pits created by the southern brown bandicoot (*Isodon obesulus*). In open woodland of south-western Australia, they found that seedling recruitment for their three native plant species (Golden wreath wattle *Acacia saligna*; running postman *Kennedia prostrata*; and tuart *Eucalyptus gomphocephala*) was significantly higher in plots containing artificial diggings compared with undug sites. This was a similar result to the positive effect observed from my own treatments of artificially engineered pits compared to the control. However, Valentine *et al.* (2017) compared undug, or controlled, plots with artificially created pits based on the plaster moulds of natural pits, previously created when Valentine *et al.* (2013) used plaster moulds and water displacement to measure the width, depth and volume of the pits to estimate soil turnover. Therefore, unlike my study, this was not a direct comparison of seedling emergence response between artificial pit, natural pit, and undug control.

Effects of time

The different shapes of the species' GAMMs – *Microseris* with an earlier and higher peak, and *Eryngium* later with a smaller and broader peak – suggest species-specific responses to rainfall and temperature conditions, as well as germination timing and duration of growth (Austin *et al.*, 1981; Allcock and Hik, 2003). A study by Morgan (1998a) compared the germination responses of 28 temperate grassland species – three of which were my study species *Microseris*, *Eryngium*, and *Bulbine* – in response to a temperature regime, and darkness or light conditions. In that study, *Microseris* was shown to have rapid germination, within 7 days of the start of the experiment, whereas the germination lag of *Eryngium* was between 7 and 14 days (Morgan, 1998a). The relative germination times match those found in my study. The germination of *Bulbine* was shown to occur between 14 and 28 days of the experiment start (Morgan, 1998a). Therefore, because my study extended beyond 28 days, I would have seen germination within my own study period if the *Bulbine* seeds used in my study had been viable or not dormant. Based on the study by Morgan (2015), if the *Bulbine* had germinated, it would have had later germination than both *Microseris* and *Eryngium*, with fewer seedlings, resulting

in a GAMM curve with a shallow peak in the latter half of the time period. Due to the slower germination, *Bulbine* is predicted to have the potential to persist longer in the seedbank than more rapid germination forbs such as the *Microseris* (Morgan, 1998a). This is because species with slow and low germination have their germination inhibited by darkness or hard seed coats (Morgan, 1998a).

The shaded confidence intervals on Figures 4.4 and 4.5 show the uncertainty of the predicted count of seedling emergence, but they do not infer significance. In the *Eryngium* GAMM output, there was greater uncertainty and a lower predicted count than for *Microseris*. The exact cause of this is unknown, but may be due to weather variability and individual seed responses (Morgan, 1998a; Allcock and Hik, 2003). Seasonal changes in rainfall have been shown to affect herbaceous vegetation growth of plants and germination of seeds (Austin *et al.*, 1981; Allcock and Hik, 2003), with a lagging effect after the rainfall event. Although this effect can explain some of the germination count trends, other factors which were not measured also would have affected the trend. Additionally, seeds can remain viable in the soil seed bank waiting for favourable rainfall events and other conditions that create an appropriate regeneration niche. This includes not only spatial and temporal factors of grass canopy gap size and surface features but also the requirements of specific species for seed germination, establishment, and continued growth in respect to weather, disease, and pests (Grubb, 1986).

5.2.2 Can artificial pits create a similar environment for germination and establishment?

There were no statistically significant differences in the germination of forbs between the natural and artificial pits (Figure 4.2 and 4.3). The comparison and similarity between natural and artificial pits showed I could replicate the effects of a bettong pit, creating a similar environment for forb germination and establishment. Therefore, this indicated there is unlikely to be an additional benefit of a natural pit due to an unknown factor of bettongs behaviour, for example the spreading of mycorrhizae. This result also indicated that the primary benefit created by a foraging bettong is through the physical formation of gaps in the grass canopy.

A statistically significant effect in the seedling emergence of the artificial pit would have indicated that the benefit was not present in the artificial pit, perhaps from a biological change to the vegetation, soil architecture or microclimate. The artificial pit should have the same chemical effects as the natural pit. Changes, such as the spread of mycorrhizal fungi and seeds, improved nutrient cycles (e.g. soil nitrogen and phosphorous), and moisture retention, have been found to be influential in arid ecosystems (Martin, 2003; Fleming *et al.*, 2014; Mallen-Cooper *et al.*, 2019). The results of this study, however, do not indicate any such influence by bettongs in this temperate ecosystem.

The similarity in my results between the artificial and natural pit treatments are supported by a review by Mallen-Cooper *et al.* (2019), which found that similar animals tended to have a

similar disturbance effect. They compared rabbits and boars in native and non-native ranges, and determined that ecosystems tended to respond similarly to the same type of disturbance (Mallen-Cooper *et al.*, 2019). Therefore, this suggests artificial engineering of pits could be used to enhance regeneration niche conditions for soil architecture and forb growth. The difference between the results of this experiment could be because physical processes are more important in a temperate grassy woodland system because nutrient resources, rather than physical competition, is a limiting factor in arid landscapes (Crain and Bertness, 2006).

One advantage of artificial pit replication is that the age of the pit is known (Ross *et al.*, unpublished a). Natural foraging pits, by contrast, are difficult to age, and as a result have rarely been reported in existing studies (Mallen-Cooper *et al.*, 2019). The natural pits used in this experiment were all older than the artificial pits, which were created within a four-day period, and can be assumed to have variable age across the sites. Although seed was added to all sites, including both artificial and natural pits, on the same day, the age differences between the natural and artificial pits may have influenced the germination results. For example, if more recent pits are more likely to result in better germination than older pits, the natural pits could have been disadvantaged, and the results skewed in favour of the artificial pits. This could have been the difference seen in the raw total germination counts across the sites; in Week 4 there were 134 seedlings in the natural pit and 159 in the artificial pit. Statistical analysis, however, did take into account the variation of the physical attributes of the plots, and did not find a significant difference between the two treatments.

5.2.3 Is the possible facilitation effect of germination due to the removal of vegetation, or the structural effects of the pit?

Two artificial structures – pits and scrapes – were examined in this experiment. The pits recreated the physical shape and influence that the bettongs have on the soil architecture, vegetation and microclimate, while the scrape only affected the soil surface and an opening of a gap in the grass canopy. With both treatments, to restore the competitiveness of the native species, I used matrix suppression (creating a gap in the grass matrix) and nutrient removal (removal of top soil usually higher in nutrients).

The lack of statistically significant difference between the results of the scrape and artificial pit indicated either small scale disturbance that opened the grass canopy could result in higher germination. This lack of statistical difference in my results does not align with the conclusions of other studies, which compare the diggings of different animals (e.g. bettongs, bandicoots, rabbits, and echidnas), and indicate that having a depression in the soil seems to have an advantage over just removal of surface vegetation (Eldridge and Mensinga, 2007; Decker *et al.*, 2019; Ross *et al.*, unpublished b). This is because depressions caused by foraging animals accumulate organic matter (resource sinks) such as leaf litter and seeds and develop into

biological hotspots (Mallen-Cooper *et al.*, 2019). Observationally, the pits (both natural and artificial) seemed to retain more moisture than the scrape.

Additionally, other research in arid zones suggested that the pit has more than one function, representing a resource sink and not just a gap in resource competition (James *et al.*, 2009). This is likely due to different ecosystem functions and limiting factors in arid and semi-arid areas compared to temperate grasslands and grassy woodlands. For example, the research of James *et al.* (2009) on digging vertebrates (burrowing bettong, greater bilby, European rabbit and Gould's sand goanna (*Varanus gouldii*)) in the desert shrubland provided a good example of a different ecosystem study, where the theories and findings of different ecosystems are unlikely to hold in the temperate grassy woodland of my research sites. James *et al.* (2009) found litter was restricted to the foraging pits, with a greater effect in larger pits, and higher nutrients in the pits compared to surrounding area. The findings of James *et al.* (2009) were supported by other studies in desert shrublands ecosystem with the focus on the function of pits to collect litter and seeds (Martin, 2003; Chapman, 2016; Neilly and Schwarzkopf, 2018). Litter collecting in the treatment pits and scrapes was observed in my own study in *Themeda* grassland to a lesser extent (Figure 5.1), as expected in a more densely vegetated area compared to the arid desert environment. All of these studies, when compared, suggest physical processes were more important in a temperate grassy woodland system because nutrient resources are not as limited as systems of increasing aridity (Crain and Bertness, 2006).



Figure 5.1. Litter collected in treatment areas. Mainly leaf litter accumulated from the surrounding matrix species, kangaroo grass (*Themeda triandra*) in examples from (a) Site D, Plot 2, Natural Pit treatment (D2N), (b) Site C, Plot 6, Artificial Pit treatment (C6A), and (c) Site D, Plot 4, Scrape treatment (D4S). The scrape treatment area is indicated by the 75mm diameter metal ring. Lesuer's frog (*Litoria leseuri*) observed in (a). *Microseris* seedlings are present in (b) and (c). Photos taken by Rachael Robb (2018), Mulligans Flat Woodland Sanctuary (MFWS).

5.2.4 Species specific differences

Representing germination of the three species over time, the GAMM shows that *Microseris* germinated faster and more completely than *Eryngium* (which germinated later than the *Microseris*) and *Bulbine* did not germinate at all (Figure 4.4 and 4.5). The respective timing of germination, with *Microseris* quicker than *Eryngium*, has been found in a previous study by Morgan (1998a). *Microseris* and *Eryngium* showed differences in the highest mean germination between the artificial pit, natural pit, scrape and control (Figure 4.1). The results may relate to the natural responses of seed germination of *Microseris* and *Eryngium* (Morgan, 1998a), as well as the change in the species' growth through the season, active in winter and spring, and dying down in summer (McIntyre *et al.*, 2018).

While no statistically significant differences were identified between and within the treatments and control, the trends seen in the treatment effect sizes are different between species; *Microseris* has greater effect in natural treatment and artificial treatments, with the scrape treatment having a lower effect size. For *Eryngium* the scrape has the greatest effect (2.87), followed by the natural (2.79) and then artificial treatment (2.48) (Figure 4.3). The effect sizes were different; the effect of using pits was much larger in *Eryngium* which had fewer seedlings (Natural=2.79, Artificial=2.48, Scrape=2.87) (Figure 4.3), than in the *Microseris* seedlings which had more seedlings emerge (Natural=0.89, Artificial=0.86, Scrape=0.68) (Figure 4.2). The two species used the same statistical model, with the AICc score results indicating the same model, Model#3, had the best fit for both species.

The variation between germination count and effect size may be accounted for by the variation in spatial conditions. This was corrected for by spatial-autocorrelation using an observation-level random factor (Harrison, 2014). The variation between the sites may have been caused by differences in raw germination counts, where one site might have the highest germination response in a specific treatment whereas across all of the sites, another treatment performs better overall.

5.3 Viability of artificial restoration

The results suggest that artificial creation of small-scale disturbance, like a bettong pit, does have a positive effect on seedling emergence. This study is the first to directly compare seedling germination in natural and artificial eastern bettong pits. Although more research is necessary to determine full viability as a restoration technique, my results indicate artificial pits could be useful in wider grassy woodland restoration. Additionally, restoring ecosystem engineers like the eastern bettong to temperate woodland ecosystem is an effective way to restore forbs. There is a need for longer term studies to examine a wider range of plant species, and to explore cost-output analyses (Wilkerson *et al.*, 2014). My study marks a small but important step in the right direction, providing a valuable snapshot of what is possible if the

window of opportunity is increased for seedling establishment and seedling survival after emergence.

My study presents mixed results; there was a positive effect of the treatments on the germination of the native seedlings, which suggests that small-scale disturbance, either pit or scrape of vegetation and soil, benefits the initial germination of seedlings. Although many of the seedlings perished by the end of the time period, much of this can be accounted for by either the combination of natural senescence in seasonal growth, and/or the unfavourable weather conditions (low rainfall and high temperatures). Despite this, my results show that the seedlings in the natural and artificial treatments survived longer than those in the control treatments (Figure 4.1).

While my results showed both natural and artificial treatments can provide a similar effect to seedling emergence, artificial replication required a concentrated effort to recreate the same scope of the natural ecosystem engineering process. The rate of digging by eastern bettongs provides continual opportunities for seedling germination when the window of opportunity for ideal weather conditions aligns with the regeneration niche created by foraging pits. The germination cues are species-dependant, because no single set of conditions prompts optimal germination in all species (Morgan, 1998a). Some species' cues include response to light consistency, alternating temperatures, rainfall frequency, (Willis and Groves, 1991; Morgan, 1998a), lack of root and shoot competition (Wilson and Tilman, 2002), and chemical triggers e.g. smoke (Roche *et al.*, 1997). Extensive planning and monitoring would be necessary to avoid missing the opportunity for artificial methods to coincide with good rainfall and temperature.

Seedbanks can either have limited viable native seed (Lunt, 1997; Morgan, 1998a), or too much exotic seed (Willis and Groves, 1991; Buhler *et al.*, 1997). Active management addresses the issue of a poor seedbank through plant reintroductions (Morgan, 1999; McIntyre *et al.*, 2018), planting nursery seedling stock and cuttings, and through processes such as direct seeding (Morgan, 1999; Silcock, 2016). A question arising from this approach is whether to add seedlings or seed to establish recruitment. There is a range of literature on plant translocation which looks at the success of each of these (Commander *et al.*, 2018). The viability of natural and artificial engineering of soil disturbance and supplementing the seedbank is further explored by my study. This is through the aims to provide propagules for depleted species such as forbs, to have the species capable of regeneration in functional grassland with appropriate disturbance, examine the role of bettong digging in the regeneration of plant species, and promote the value of eastern bettong restoration.

5.4 Limitations to this study

Limitations to this study arose from three main factors: time, data and methods, which then influenced the scope of this study.

Limitations of time

A restricted timeframe led to a small, short experiment in a localised area, where I could examine a cross-section of possible data in the one season of native forb growth. Some of the knowledge about general function of plant growth and ecosystem function is available in the existing literature, but not directly applied to the context of my study. Another limitation of time is the restricted window of opportunity to study the growth stages of my forbs. I looked only at initial germination and the first few months of growth, which does not account for establishment in the grassland, regrowth or persistence through seasons or reproductive success.

Limitations of data

A limitation of data was the effect of the variation between natural treatments. The effects of natural pit size (e.g. depth, diameter, and area) and presence of vegetation should be further clarified, because the potential variation in pit size between plots could result in repetitions of the same treatments varying between plots. For context, the average size of an eastern bettong foraging pit, calculated from 1518 pits, is 50 by 40 millimetres and 35 millimetres deep (Munro *et al.*, 2019; Ross *et al.*, unpublished a). To accurately replicate natural variance in the occurrence of pits, the size of the natural pits I used in my study ranged from a length, width, and depth of 40 by 40 by 20 millimetres to 80 by 70 by 50 millimetres respectively. I addressed the intrinsic landscape variation through statistical analysis, by running a Poisson model corrected for overdispersion by observation-level random effects (Harrison, 2014).

Another limitation in the data that I collected was the lack of comprehensive data on the native and exotic seedlings that germinated from the existing seedbank. This would have helped provide context to unknown variables such as whether native and exotic seedlings responded differently to my specific treatments (Hayes and Holl, 2003), and if the reported seedling numbers (limited to only the study species) gave an accurate representation of all germination in the treatment area. Also, the observed germination that did form the dataset may not have included all germination. While I did not have comprehensive data on native and exotic interactions, a similar study in the same area by Ross *et al.* (unpublished a) did record the relative exotic to native seedlings ratio. They found that both exotic and native seedlings benefited from the treatments, with more native seedling emergence than exotic seedlings in the first year (Ross *et al.*, unpublished a). Even so, it is important to note that I cannot extrapolate results beyond the spatial extent my samples were selected (Hurlbert, 1984).

The data was potentially limited by an unknown variable of possible seed predation by ants with the removal of seed from the treatment areas (Valentine *et al.*, 2017). If significant theft of seeds occurred unobserved, it would have decreased the observed germination in the treatments.

However, lower predation in bettong pit structures has been found by Radnan and Eldridge (2017). Therefore, ant predation would have been at similar levels in both the control and scrape treatments. The results showed a significant difference in seed germination between the scrape treatment and the control, despite predation by ants, and therefore the findings indicated that there was another contributing factor influencing the final results beyond seed theft.

Limitations of methods

One of the limitations in the execution of my methods was the lack of result for the *Bulbine* seeds. The age and viability of the *Bulbine bulbosa* seeds I used was not known at the beginning of the experiment. The lack of germination of the *Bulbine* seeds may have been because of the seeds' older age or dormancy; the seeds were collected in December 2010. They were viable in 2016 with successful germination recorded (Ross *et al.*, unpublished a). Alternatively, another study found that the germination of *Bulbine bulbosa* seed was strongly temperature-dependant (Willis and Groves, 1991). This limitation is also linked to time: due to time and equipment restrictions within the project, no seed viability testing or pre-treatment was undertaken. In the future, I would recommend more extensive seed preparation.

One of the lesser factors in my study was potential bias in seed selection. While the selection of study species was carefully considered based on the wider literature, ultimately selection was constrained by seed availability. This was one of the concerns raised in Graff and McIntyre's (2014) paper; that selection process 'tends to be done on an *ad hoc* basis, with seed availability being a major constraint' (Graff and McIntyre, 2014). The choice of seed species in my study was due to the study forbs being grazing-sensitive species that have the potential to be more abundant at MFWS. There was also seed available, and the three species had large seeds suitable for manipulating and handling.

Limitations and expansion of scope

The scope of my study was necessarily focused due to time and the nature of the study. To reach further conclusions and provide accurate management recommendations, expanding the scope of my experiment would be essential for replication at multiple sites (Hayes and Holl, 2003). The scope of my research methods did not cover a comparison with alternative ecosystems conditions and classifications. While it is possible, to a limited extent, to compare the results of my specific study to experiments in other situations, it would be beneficial to re-run my experiment design. Further research could perform a similar experiment design in other sites, such as an area of poorer quality grassy woodlands than MFWS, and one that is also less accessible to large-scale disturbance restoration strategies such as scalping. This would be conceivable because my results show artificial pits can provide similar benefits to germination as provided by natural bettong-created pits. Assessing the effect that each of my treatments and species would have in a different quality grassland could contribute to the knowledge ecological managers use to restore poor-quality grassy woodlands.

This expansion of the study's scope could also encompass the question of shifting baselines (Manning *et al.*, 2006). Also called 'environmental generational amnesia', shifting baselines is the ongoing 'ratcheting down' of environmental knowledge and expectations in a continually degrading environment, as generations of people consider the quality and environmental function of their childhood environment as a new standard (Kahn and Kellert, 2002; Miller, 2005). This 'shifting baselines syndrome' should be considered in restoration projects, especially when the role looking to be restored (e.g. Australian digging ecosystem engineers) has not been present in living memory (Manning *et al.*, 2015). With this in mind, MFWS – as a sanctuary of a 'good quality' ecosystem – can be further restored to a new higher environmental baseline for continued ecological restoration (Manning *et al.*, 2015). Without new baselines, our current reference sites of 'good quality' grasslands could become only relatively better than the current mid- or poor-quality grasslands. It is important to incorporate baselines into management and policy with the recognition that over time there is uncertainty as to how a baseline will and has already changed (Miller, 2005; Manning *et al.*, 2006).

5.5 Significance of this study

This study showed that small scale disturbances such as those created by the eastern bettong can significantly increase germination of native forbs in the *Themeda*-dominated grasslands of MFWS. This research contributes an understanding of the influence that digging animals, such as the eastern bettong, have on the temperate ecosystem around them through the creation of regeneration niches. This is the first study to directly compare natural bettong-created pits, artificially-created pits, and scrape treatment, so by indicating that germination in artificially created disturbances is significantly higher than the control, with no significant difference from the natural foraging pit, the study also contributes uniquely to the wider knowledge of potential restoration techniques. The success of this study's technique does not suggest that bettongs are not required in an ecosystem to increase forb diversity, but rather, highlights the benefits of their approach to natural habitat management.

There is a lack of data from digging animals in native temperate grasslands and woodlands, and therefore my study contributes to this body of knowledge. This study has significance in the context of the existing literature because it explored a gap in ecosystem engineering research in Australian temperate grassy woodlands (Mallen-Cooper *et al.*, 2019). This study explored the influence of bettongs in a different environment to better understand their role in the function of the ecosystem of temperate grassy woodland, opposed to arid landscapes. The difference between the primary influences of bettongs may be due to a different limiting factor in the ecosystem: limited resources in arid areas and shoot and root competition in temperate grassy woodlands. The effects of soil disturbance generally intensifies with increasing aridity (Mallen-Cooper *et al.*, 2019), and therefore the major effect of digging animals differs because of the role they provide; creating nutrient sinks and collection of resources, compared to opening up

the grass canopy and creating a gap or regeneration niche, thereby decreasing the competition for space in the area of the small-scale disturbance (Munro *et al.*, 2019).

5.6 Future direction

There are still limits to our knowledge when it comes to the effects of soil disturbance on ecosystems, and the role of the reintroduction of locally extinct ecosystem engineers in ecosystem restoration (Mallen-Cooper *et al.*, 2019). Increasing the scope and scale of my study would offer more information on the influence of eastern bettong digging on the growth of native forbs, and in doing so allow more informed recommendations to management (Hayes and Holl, 2003). I suggest developing a landscape-scale replication of my methods, to include an additional site to MFWS, similar to the recommendation by Chapman (2016) for her own study, and to account for the risk in extrapolating conclusions from single-site studies (Hayes and Holl, 2003). The potential to re-scale is a consideration that would provide an avenue to assess whether my experiment design is applicable to a larger landscape project. It took five days for one person to set up four sites in a single geographical location of MFWS. This experiment could be up-scaled through more people creating pits and adding seed, over a larger spatial and temporal distribution, therefore increasing the time to compare artificial pits to existing eastern bettong pits. While this restoration strategy might be costly in terms of field hours and seed quantity, but it would be worth exploring the findings that suggest engineered pits can create a similar environment or niche for germination and establishment. Even more importantly, unlike my strategy, alternative strategies could not get forbs into ecologically sensitive woodlands successfully without causing damage. The question is whether this experiment works better than other cheaper options. Cost-benefit analysis could be undertaken to compare this study's technique with others, similar to the cost analysis performed to compare ground preparation and restoration techniques to the proposed wild boar rooting (Macmillan *et al.*, 1998; Sandom *et al.*, 2013). Expense is a factor in any restoration action, for example, the total cost associated with the nest box program intended to offset clearing of hollow-bearing trees in south-eastern Australia was AU\$199,688, including pre-establishment strategic planning, nest box construction, and post-establishment monitoring (Lindenmayer *et al.*, 2017). The elements associated with time, planning, work force, setting-up the experimental sites and post-establishment monitoring are also considerations for this study. Also, the cost of novel actions such as artificial replication of animal diggings would likely decrease the more the technique is applied and efficiencies are identified.

To assess seedling recruitment and establishment over more than one season, future research should include repeating the study experiment over a longer time period (Ross *et al.*, unpublished a). In the study by Ross *et al.* (unpublished a), they found the effect of bettong pits persisted beyond the first year, and that the plant species composition varied over the longer time period. Such a design would allow observation of the plants over their natural growing

seasons, and would be worth exploring further in the context of my engineered pit experimental design. Additionally, further research into temperate grassy woodland ecosystems could be undertaken to increase the body of literature, compared to the greater number of studies on the effect of soil disturbance in arid landscapes (Munro *et al.*, 2019).

I suggest further exploration into soil disturbance through fire because, similar to animal foraging, both create heterogeneity in the landscape, which in turn drives biodiversity across landscape scales (Mallen-Cooper *et al.*, 2019). This would compare and combine the effect of animal digging with other factors e.g. fire, grazing, and other restoration techniques to see how other forms of small scale soil disturbance influences seed germination (Johnson, 1994).

My findings provided a snapshot of only the studied species' emergence. Therefore, I suggest further investigation to determine the extent that these interventions of natural and artificial disturbances suppress exotic seedlings emerging from the seed bank. This would provide data on the potential decrease in emerging exotic species when compared to both hand-seeded native seedlings and natural regeneration, and could assist in the management of exotic species and promotion of native forb diversity.

The species I tested reacted differently in response to the experiment treatments. Therefore, when undertaking specific restoration action, further study is recommended to ensure the technique used is the best one for the target species. This is because what might work best for one species, would not necessarily work best for all species. However, both species that germinated in my study showed a significant effect in each treatment, suggesting that the treatments could maintain an effect on species other than those tested in my study.

My research is a small but unique contribution to the body of literature, and ongoing research can build from the understanding my research provides to explore more about how small Australian digging mammals, particularly in reserves where they are protected from predators (Martin, 2003), influenced the ecosystem in the past, and how they can be incorporated into restoration ecology (Seddon *et al.*, 2007).

Chapter 6: Conclusion



The diversity of native forbs in temperate grassy woodland ecosystems is threatened by anthropogenic or human-driven changes of the landscape. The intrinsic value of the Australian grassy woodlands, combined with the importance we place on the threatened ecosystem, motivates the conservation and restoration of both native flora and fauna. A holistic approach to ecosystem restoration is crucial for the continuation of these ecosystems, combining both biotic flora and fauna, and abiotic factors. My thesis therefore explored both the natural engineering by the eastern bettong, and the artificial engineering to mimic this influence, on the regeneration niche for the restoration of temperate grassy woodlands.

My thesis investigated (i) the germination response in bettong pits and (ii) artificial replication of bettong pits as a possible restoration technique. This was done through the research questions:

- 1) Do natural pits promote the germination and establishment of seedlings?
- 2) Can artificial pits create a similar environment for germination and establishment?
- 3) Is the possible facilitation effect of germination due to the removal of vegetation, or the structural effects of the pit?

In answer to the primary research question guiding this thesis (*Do artificially engineered regeneration niches, based on bettong-created pits, provide equal forb germination when compared to the natural bettong foraging pit?*), the results suggested engineered regeneration niches can create a similar environment for forb germination and establishment when compared to the natural bettong-created foraging pit. Firstly, artificially engineered disturbances modelled on the shape of the eastern bettong-created foraging pit did promote a significant increase to the germination of the native forbs *Microseris walteri* and *Eryngium ovinum*. This suggested the main influence bettongs have on seedling emergence is the engineering of a niche through physical manipulation of the soil, microclimate or vegetation. Additionally, there was no significant difference in germination between artificial disturbances mimicking bettong foraging pits, and the scrape removal of vegetation to create a gap in the grass canopy. This finding implied the main facilitation effect of forb germination is not due to the structure of the pit itself (which is not present in the scrape treatment) but rather the disturbance of the soil surface and vegetation to create gaps in the grass matrix canopy. Therefore, the study results implied there is potential to artificially engineer small scale disturbance events, such as digging animal

behaviour, to help restore diversity in temperate grassy woodland ecosystems such as found in Mulligans Flat Woodland Sanctuary.

My study is linked to a field of study beyond disturbance treatments in the temperate grassy woodland of MFWS, native forbs, and the eastern bettong. Significantly, the study offers an alternative restoration technique modelled on natural animal-created soil disturbance that could be applied to both a wider range of native forbs within grassy woodlands, and potentially extended to other ecosystems.

Extension of the research is needed on the ecosystem interaction between Australian native forbs and small digging mammals. Future recommendations include further investigation into the effects of bettong pits on the longer-term growth and establishment of native forbs, and in more than one site. Additionally, I suggest whole ecosystem management of intrinsically linked flora and fauna with monitoring of their interconnected relationships. My study is a piece of the puzzle, answering one part of a multifaceted question, and future studies will do the same to build knowledge and understanding of the interaction between native forb germination and digging animals like the eastern bettong.

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Appendix I: Rainfall data

The raw daily rainfall data for the months of my study was sourced from the Australian Government Bureau of Meteorology (2018).

(http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=136&p_display_type=dailyDataFile&p_startYear=2018&p_c=-989575702&p_stn_num=070340)

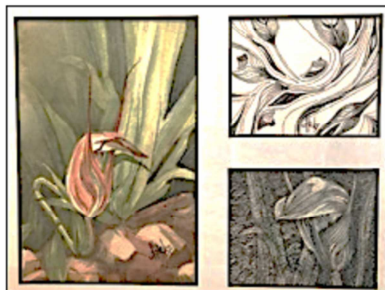
Site	Station number	Year	Month	Date	Week	Daily Rainfall (mm)	Daily Rainfall
Nicholls (Gungahlin Lakes)	70340	2018	August	19 to 26	0	Rainfall	4.4
Nicholls (Gungahlin Lakes)	70340	2018	August-September	27 to 2	1	Rainfall	14.9
Nicholls (Gungahlin Lakes)	70340	2018	September	3 to 11	2	Rainfall	29
Nicholls (Gungahlin Lakes)	70340	2018	September	12 to 18	3	Rainfall	0
Nicholls (Gungahlin Lakes)	70340	2018	September	19 to 27	4	Rainfall	0
Nicholls (Gungahlin Lakes)	70340	2018	September-October	28 to 2	5	Rainfall	0
Nicholls (Gungahlin Lakes)	70340	2018	October	3 to 10	6	Rainfall	4.8
Nicholls (Gungahlin Lakes)	70340	2018	October	11 to 18	7	Rainfall	3.6
Nicholls (Gungahlin Lakes)	70340	2018	October	19 to 25	8	Rainfall	13.8
Nicholls (Gungahlin Lakes)	70340	2018	October	26 to 31	9	Rainfall	0
Nicholls (Gungahlin Lakes)	70340	2018	November	1 to 8	10	Rainfall	23.4
Nicholls (Gungahlin Lakes)	70340	2018	November	9 to 15	11	Rainfall	6
Nicholls (Gungahlin Lakes)	70340	2018	November	16 to 22	12	Rainfall	33.2
Nicholls (Gungahlin Lakes)	70340	2018	November	23 to 28	13	Rainfall	13.2
Nicholls (Gungahlin Lakes)	70340	2018	November-December	29 to 5	14	Rainfall	4.6

Appendix II: Artist sketchbook stories

Tendrils Newsletter Issue 8, March 2019

Australian Botanical Artists Regional Network (ABARN)

Blue Sun Orchids and Cowslip Orchids, but unfortunately the Jug or Rabbit Orchids had recently finished.



Sketchbook Stories

By Rachael Robb

(Rachael's research project is: *Engineering the regeneration niche for the restoration of native grassy woodlands in Mulligans Flat Woodland Sanctuary*. Christine Fifield Scholarship/ANU Fenner School.)

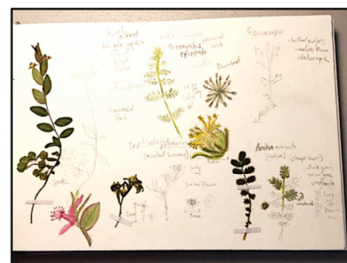
Triptilodiscus pygmaeus. How would you remember this plant's name? What are the defining characteristics? I found that in the scientific endeavor to improve my plant identification skills, my answer was through art.

Therefore, I combined my love for art and ecology to keep a nature sketchbook. I found the plants of interest to my area of study in native grassland forbs, taking samples where appropriate. I identified them with the help of experts or a plant guide, and then I sketched the main features and included colour notes with watercolour. Some, I worked up into more polished pieces but most were simple and used as a reference guide.

I found sketching the plant specimens helped to remember them, and the medium helps to emphasise features which a photograph cannot. It also allows for quick and easy annotation in the field. Often, I combined the sketched details with later research of the plants, reinforcing the initial contact.

It was an effective way of learning identifying features and names of the common forbs of my study area, and my sketchbook now forms a valuable record of plants. I have added to it each

time I volunteered with other field experiments, learning more from scientific and volunteers in the field, and will continue to expand the sketchbook as my experience continues to grow.



Two Sketchbook pages by Rachael Robb

Workshops and Events

Helen Fitzgerald

Botanical Illustration 5 Day Workshop

Next course: 15-19 April 2019 Fee: \$545

Location: Bungendore School of Arts

For workshop outline and to download enrolment form go to Helen's website:

<http://helenfitzgerald.com>

Tel.: 02 62972697

PO Box 125 Queanbeyan, NSW 2620 Australia

NatureArt Lab, Canberra

Intermediate Botanical Watercolour, with Cheryl Hodges

March 20 – April 10. Wednesday mornings from 9.30am to 12.30pm. A short course focusing on botanical art projects with mentored support from professional artist Cheryl Hodges.