The Diet and Habitat Use of a Mammalian Herbivore Guild

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In memory of Viktor and Josephine Rutar.

With love and gratitude.

Declaration of Originality

I declare that this thesis contains no material which has been accepted for any other degree or diploma in any university. Furthermore, the material presented in this thesis is my own original work and has not been previously published or written by another person, except where reference is made in the text.

Samantha Josephine Diana Shippley

July 2026

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Ethics statement

All studies within this thesis were conducted under the ACT Scientific Licence Number – LT20228 and approved by the ANU Animal Ethics Committee, protocol number – A2022/05

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I used ChatGPT (GPT-5.5; OpenAI) to: (1) troubleshoot and optimise coding in R, (2) support learning new analytical and statistical methods, and (3) act as a copy editor, using prompts and workshop materials provided by ANU Researcher Development, and following the guidelines for editing theses (ANUP_000407). The use of AI was complementary to and did not replace guidance from supervisors and traditional forms of learnings. The intellectual contribution of this thesis is my own and I drafted all original text. AI was not used to generate text.

Preface

My thesis is structured with four empirical data chapters which have been written and structured as stand-alone manuscripts and contain their own discussion and interpretation of the results, for the purpose of publication. There are therefore some unavoidable minor repetitions of the study site and some methods throughout.

Abstract

Large herbivores are fundamental drivers of ecosystem structure and function through their effects on vegetation, nutrient cycling, disturbance regimes, and seed dispersal. The loss of native herbivores and widespread introduction of domestic and exotic species have created novel herbivore assemblages with uncertain ecological consequences. Understanding how these contemporary herbivore guilds influence ecosystem processes is essential for effective grassland restoration. This thesis investigated the ecological roles of Australia's contemporary herbivore guild by integrating a global meta-analysis with field-based assessments of diet and endozoochorous seed dispersal. A global meta-analysis of grazing exclosure experiments demonstrated that introduced herbivores exerted stronger effects on plant diversity than native herbivores, while revealing substantial geographical and taxonomic biases in the available literature. These findings indicate that herbivore identity and evolutionary history are important determinants of vegetation responses to grazing. To examine these processes within an Australian temperate grassland, DNA metabarcoding of 883 faecal samples characterised the diets of native marsupials, domestic cattle, and feral deer over a 12-month period. Herbivore diets converged during periods of low resource availability but became increasingly partitioned when resources were abundant, indicating that seasonal resource dynamics facilitate coexistence. Greenhouse germination trials of 594 faecal samples identified 65 plant species, with exotic herbivores dispersing significantly more viable seeds and greater plant species richness than native herbivores. Integrating dietary and germination data further demonstrated that endozoochory acts as a selective ecological filter, with plant consumption alone failing to predict seed dispersal outcomes. Collectively, my thesis demonstrates that introduced herbivores shape Australian temperate grasslands not only through vegetation consumption but also as effective vectors of exotic seed dispersal. Rather than restoring lost ecological functions, introduced herbivores appear more likely to reinforce plant invasions and generate novel ecological disturbances, highlighting the need to consider the multiple interacting roles of entire herbivore guilds when managing and restoring temperate grassland ecosystems.

List of Abbreviations

ACT – Australian Capital Territory

ANOVA – analysis of variance

B – Levin's niche breadth

BP – base pairs

Cytb – Cytochrome b

EICAT – Environmental Impact Classification for Alien Taxa

EGK – eastern grey kangaroo

ENSO – El Niño–Southern Oscillation

FOO - frequency of occurrence

GCC – Ginninderry Conservation Trust

GPS – global positioning system

GLMM – generalized linear mixed model

ITS – Internal Transcribed Space

IUCN – International Union for Conservation of Nature

NCBI – National Centre for Biotechnology Information

NR – non-redundant

NSW - New South Wales

PCR – polymerase chain reaction

RRA - relative read abundance

*trn*L – transfer RNA Leucine

USA – United States of America

Table of Contents

The Diet and Habitat Use of a Mammalian Herbivore Guild i
Declaration of Originality iii
Acknowledgements v
Ethics statement vi
AI acknowledgement vi
Preface viii
Abstract ix
List of Abbreviations x
Table of Contents xi
Thesis Introduction 1
Introduction 1
Niche Theory and Resource Partitioning 2
Evolutionary context 4
Australia's contemporary temperate grassland large herbivore assemblages 7
Dominant native species 7
Exotic herbivores 8
Domestic herbivores 10
Rewilding 10
Knowledge gap 11
Thesis aims 11
Introduction Reference list 14
Chapter 1 29
Grazing the Globe: A Review of Large Herbivore Impacts on Plant Diversity 29
Introduction 30
Methods 34
Literature search and compilation of dataset 34
Diversity indices 35
Meta-analysis 37
Results 38
Herbivore guild by study 40
Herbivore nativeness and plant nativeness 42
Impact of herbivore type 44
Potential publication bias 46

Gaps in study representation 47
Discussion 48
Domestic herbivores 50
Does herbivore nativeness matter? 51
Missing empirical knowledge 53
Conclusion 54
Key findings 54
Grazing exclosures 54
Major knowledge gaps 54
Temperate grasslands 54
Australian Context 55
Chapter 1 References 56
Chapter 2 64
Dietary overlap among native and exotic herbivores in a temperate grassland ecosystem 64
Introduction 65
Methods 69
Site and study species 69
Study design 71
Sample collection 71
DNA barcoding 72
Sample homogenization 72
DNA extraction 72
PCR Amplification 72
Data filtering and bioinformatics 73
Herbivore Species Identification 73
Statistical analyses 74
Statistical models 74
Species richness 75
Relative Read abundance and Frequency of occurrence 75
Niche breadth and dietary overlap 75
Results 76
Sequence data 76
Herbivore species identification 76
Relative read abundance and frequency of occurrence 77

Dietary overlap 79
Plant Species richness 82
Model outputs 83
Discussion 85
Niche Partitioning 87
Environmental impacts 88
Drought and resource limitation 89
Evolutionary context 89
Conclusion 90
Chapter 2 Reference list 92
Chapter 3 100
Seeds on the move 100
Introduction 101
Methods 104
Site and study species 104
Study design 106
Sample collection 106
Sample processing and greenhouse planting 107
Plant identification 108
Herbivore Species Identification 110
Statistical analyses 110
Herbivore samples 110
Statistical models 110
Species richness 111
Results 112
Herbivore species identification 112
Plant species identification 112
Most common plant species 112
Modelled effects of plant nativeness and season 114
Species richness 115
Seed Density 118
Rarefaction curves 120
Discussion 122
Not all herbivores are equal. 123

Exotic herbivores reinforce exotic plant communities. 125
Reinstating native grazing systems 126
Conclusion 127
Chapter 3 Reference list 128
Chapter 4 136
What goes in doesn't always come out 136
Introduction 137
Methods: 140
Site and study species 140
Data collection 141
Diet dataset 141
Germinated seed dataset 141
Dominance index 141
Germination persistence 142
Mapping and statistical analysis 142
Results 143
Spatial patterns 143
Exotic species proportions 145
Germination persistence 147
Plant nativeness 149
Plant functional groups 151
Discussion 153
Invasion meltdown and homogenization 154
Plant traits linked to invasion success 156
Grazing in grasslands 158
Management implications 161
Future directions and limitations 162
Conclusions 163
Chapter 4 References 164
Chapter 5 175
How similar is similar enough? 175
Introduction 176
Are all herbivores ecologically equal? 178
Domestic herbivores 180

Pathway to invasion meltdown 185
Climate change 187
Is evidence biased or limited? 189
Limitations in germination studies 190
Management implications 191
Define the objective 192
Strategic management 192
Integrated management 193
Conclusions 194
Appendix A – Chapter One ccxl
Appendix B – Chapter Two ccxliii
Appendix C – Chapter Three ccxlviii

Thesis Introduction

Introduction

Large herbivores play vital roles shaping vegetation structure, community composition, biodiversity and ecosystem processes Pringle et al. (2010), (Pringle et al., 2023). These processes include nutrient cycling, disturbance, seed dispersal and biomass consumption (Janzen, 1984, Persson et al., 2000, Bakker et al., 2004, Pakeman and Small, 2009, Van Der Waal et al., 2011). However, the magnitude and direction of their impacts are highly variable, and dependent on multiple variables including body size, environmental factors, and sympatric interactions with other species (Forbes et al., 2019, Atkinson et al., 2024, Trepel et al., 2024, Trepel et al., 2026).

Large herbivores have evolved independently across continents, resulting in functionally diverse assemblages often comprising of multiple sympatric species (Janis, 1982, Codron, 2019). The coexistence of multiple species exploiting similar resources presents a fundamental ecological challenge (Levins, 1979). Our understanding of the ways in which different species resolve this issue has been challenged and well-debated and studied for many decades (Vesey-Fitzgerald, 1960, Bell, 1971, Chesson, 2000, Hillerislambers et al., 2012, Letten et al., 2017). The competitive exclusion principle is the pre-curser to niche theory, and surmises that two species inhabiting the same niche, cannot truly co-exist in equilibrium because there is a constant competition for limited resources or energy (Gause, 1932, Hardin, 1960), with the likelihood that the more aggressive species will result in the displacement of the weaker or smaller (Levine, 1976, Finke and Snyder, 2008). Evidence to support this theory includes the contemporary herbivore assemblage across the Indian Trans-Himalaya region, where the low diversity of wild herbivores is likely due to competitive exclusion by domestic grazing animals over the past 300 years (Mishra et al., 2002). Despite some evidence to support the theory of competitive exclusion, many regions of the world are host to high biodiversity and multi-species assemblages indicating some resource partitioning must be occurring (Schoener, 1974, Finke and Snyder, 2008).

Niche Theory and Resource Partitioning

Classical niche theory explains these patterns of diversity by hypothesizing that different species use different components of a habitat to partition resources (Hutchinson, 1959, Macarthur and Levins, 1967, Schoener, 1974). There are many ways in which this can occur, such as diet specialisation or spatial and temporal partitioning of resources, both of which have been recorded in many guilds as a mechanism to reduce interspecific competition (Roughgarden, 1976, Gordon and Illius, 1988, Kleynhans et al., 2011a, Kartzinel et al., 2015, Davis et al., 2018, Kartzinel and Pringle, 2020, Pansu et al., 2022). This is evident in an assemblage of five sympatric Bornean felids, where coexistence was facilitated through the use of different elevational habitats, as well as seasonal and peak diel activity periods, which refers to the time of day or night in which an animal is active (Carothers and Jaksić, 1984, Hearn et al., 2018).

Resource and niche partitioning has also been shown to occur based on differences in body size and morphology (Belovsky, 1986, Illius and Gordon, 1993). Resource partitioning according to body size is well documented, including between cervids in the Rocky Mountains (Jenkins and Wright, 1988), sympatric predators in the Iberian Peninsula (Carvalho and Gomes, 2004), and terrestrial frugivores in tropical forests of Brazil (Akkawi et al., 2020). The African savannah for example, supports a highly diverse assemblage of herbivores all relying predominantly on grasses, yet resource partitioning is partially maintained through differences in body size (Djagoun et al., 2016, Kihwele et al., 2025). During dry seasons, larger herbivores use lower-quality, fibrous forage by consuming greater quantities of biomass, resulting in differences in habitat selection (Kleynhans et al., 2011b). This pattern follows the Jarman-Bell Principle, a well-documented mechanism in large ungulate co-existence, which surmises that larger herbivores can survive on lower-quality, but more abundant, forage diets because of their gut capacity to process fibrous food more efficiently in contrast to smaller bodied herbivores which require higher-quality resources to meet their energy requirements (Bell, 1970, Bell, 1971, Geist, 1974, Jarman, 1974, Owen-Smith, 1988, Codron et al., 2007, Potter and Pringle, 2023).

A further driver allowing for diverse assemblages of sympatric species, is the evolution of trophic specialisation (Shipley et al., 2009, Price et al., 2012), which has arisen independently across a wide range of taxa and ecosystems. By partitioning food resources, species reduce interspecific competition and facilitate long-term co-existence. Dietary specialization has been documented in numerous animal groups, including New World leaf-nosed bats (Family: *Phyllostomidae*) (Rex et al., 2010), many assemblages of birds (Harmáčková et al., 2019, Remeš and Harmáčková, 2025), coral reef fishes (Delecambre et al., 2025), and small mammals inhabiting Chilean semi-arid thorn scrub, where species partition resources into herbivorous, insectivorous and granivorous feeding guilds (Meserve, 1981). Many large mammalian herbivore guilds have been shown to use dietary specialisation to partition resources, which prompted the concept of the grazer, browser and mixed feeder continuum, as first proposed by Lamprey (1963). The concept has become a central contributor to theories of herbivore coexistence (Bell, 1971, Sinclair, 1975, Belovsky, 1986, Mcnaughton and Georgiadis, 1986, Codron et al., 2023) and helps to explain the separation and co-existence of herbivores within a guild, by describing them as either eating grass (grazer), or woody plants (browser) at the extreme ends of the continuum, with mixed feeders having a more plastic diet and falling somewhere in between.

The differences in feeding strategies of grazers or browsers, are closely linked to behavioural and morphological adaptations, including digestive physiology and dentition, influencing a species' ability to exploit plants that differ in defensive traits and nutritional quality (Shipley, 1999, Gordon and Prins, 2008a, Janis, 2008, Codron et al., 2019, Huntley, 2023). Such adaptations provide the foundation for optimal foraging theory, which predicts animals should forage in ways that maximise their net energetic gain by balancing food choice, patch selection and time spent using different resource patches, while minimising the energetic costs (Macarthur and Pianka, 1966, Emlen, 1968, Schoener, 1974, Pyke et al., 1977, Hofmann, 1989).

Considerable differences in large herbivore gut morphologies is a notable adaptation linked to both optimal foraging theory and the Jarman-Bell principle because it heavily affects digestibility

of plant material and therefore diet choice (Van Soest, 1996). The broad categories of herbivore guts are; hindgut fermenters, including horses, tapirs and rabbits, foregut fermenters (multi-chambered stomachs), including macropods and old-world monkeys, and the most common gut type in herbivores, ruminants, including deer and cattle (Hume, 1989, Johnson et al., 1993, Hume, 1997, Sneddon and Argenzio, 1998, Dehority, 2002).

Although resource partitioning is widely recognised as an important ecological process, our understanding of the mechanisms that drive it, and its implications for ecosystem diversity and stability remains the subject of ongoing debate (Roughgarden, 1976, Abrams, 1983, Walter, 1991, Chesson, 2000, Chase and Leibold, 2009). It is however likely that there are interchangeable and ever-changing elements effecting guild formation and co-existence, especially in the context of ever-changing environmental factors (Lawton, 1999).

Redundancy can be thought of as a surplus, whereby several species provide the same ecological functions (Lawton and Brown, 1994). Redundancy and high levels of biodiversity are thought to enhance ecological resilience and stability through the maintenance of critical ecosystem functions despite species loss (Walker, 1992, Fonseca and Ganade, 2001, Biggs et al., 2020). A contrasting body of research supports the idea that complex and diverse ecosystems are indeed more stable, but theorise this is due functional complementarity rather than redundancy (Hooper et al., 2005, Poisot et al., 2013, Barry et al., 2019). Complementarity posits that by contributing different ecological functions, different species maintain ecosystem productivity and diversity more effectively than a single species or functional group alone, better supporting niche partitioning theory (Loreau, 1998, Burkepile and Hay, 2008).

Evolutionary context

Sahul, the combined continent of Australia and New Guinea was geographically isolated for 40 million years (Long, 2017), culminating in the evolution of unique mammalian fauna, dominated by soft-footed marsupials, with a notable lack of ungulate herbivores (Johnson, 2006). Historically, the Australian continent had a diverse range of large (>45kg) and mega herbivores (>100kg) (Peters,

1986, Gordon and Prins, 2019), including the *Sthenurus* kangaroos, weighing up to 200kg, the largest hopping mammal to exist, *Procoptodon goliah*, weighing up to 232kg (Helgen et al., 2006) and the largest ever marsupial and the largest mammal in the Australian fossil record, the *Diprotodon optatum* weighing over two metric tonnes (Wroe et al., 2004a, Sharp and Rich, 2016). Interestingly, the *Diprotodon* was only one third the size of many extant mega herbivores such as the African elephant (*Loxodonta Africana*) and the Indian rhinoceros (*Rhinoceros unicornis*) (Owen-Smith, 1988, Webb, 1998, Milewski and Diamond, 2000a, Licht, 2016). This further emphasises the uniqueness of Australian ecosystems, in which both plant and herbivore traits have been shaped by plant-herbivore interactions that differ fundamentally from those on other continents.

A global mass extinction event at the end of the Pleistocene resulted in the extinction of most Australian mega-faunal between 40,000 – 36,000 years ago (Prideaux et al., 2007, Wroe et al., 2013, Long, 2017). There has been a long and ongoing debate as to the precise cause of Australian mega faunal extinctions, with three predominant theories (Johnson, 2014). Firstly, the "blitzkrieg" or overkill model suggests that the arrival of early humans caused rapid extinctions because of over-hunting (Martin, 1973, Mosimann and Martin, 1975, Martin and Klein, 1984, Wroe et al., 2004b, Smith et al., 2016). Secondly, rather than over-exploitation there is the theory that extensive use of fire by indigenous Australians rapidly altered the landscape, making it unsuitable for many species (Johnson, 2016, Van Der Kaars et al., 2017). Lastly, natural climatic shifts are hypothesized to have played a role in Pleistocene extinctions in the Northern Hemisphere (Barnosky et al., 2004), however the Eurasian mega faunal extinctions seem to predate the last maximum glacial climate shift which occurred between 35,000 – 12,000 years ago (Prideaux et al., 2007, Wroe et al., 2013, Hocknull et al., 2020). Evidence is most suggestive of multiple factors, with extinctions linked to both changing climate and increasing anthropogenic influence (Stuart, 1991, Roberts et al., 2001, Miller et al., 2005).

Regardless of the cause, the Pleistocene extinction event led to the loss of all native mega-herbivores on the Australian continent (Desantis et al., 2017). The remaining extant herbivore assemblages are dominated by much smaller generalist species, with the largest native herbivore, the red kangaroo (*Osphranter rufus*), weighing less than 100 kg (Hopwood, 1981, Woolnough and Steele, 2001). In response to expanding grasslands and the associated increase in suitable habitat, the rapid expansion of extant herbivores such as the eastern grey kangaroos (*Macropus giganteus*), red kangaroos and western grey kangaroos (*Macropus fuliginosus*) across the Australian continent represents the ecological equivalent of artiodactyl ungulates found in other continents (Johnson, 2006, Prideaux et al., 2009b, Jackson et al., 2015, Couzens and Prideaux, 2018, Freedman et al., 2020). Contemporary Australian ecosystems therefore function without the large herbivores that previously shaped vegetation for millions of years, possibly representing missing ecological functions (Johnson et al., 2016).

Indigenous land management has been occurring across the Australian continent for over 50,000 years: including frequent low-intensity fires that maintained grassland biodiversity by promoting herbaceous regeneration and by creating a heterogeneous vegetation mosaic (Flannery, 1990, Yibarbuk et al., 2001, Burrows et al., 2006). However, European invasion in the 18th Century elicited a rapid cessation of Indigenous land management practices, that were supplanted by the introduction of managed livestock grazing (Parsonson, 1998, Gordon and Prins, 2008b, Bradshaw, 2012, Fletcher et al., 2021), creating profound and unpredictable changes to habitats, guild structures and vegetation structure. These major changes ultimately resulted in a severe reduction in the size and condition of critically important grassy-woodland habitat that once covered millions of hectares of South-Eastern Australia (Prober and Thiele, 1995, Yates and Hobbs, 1998). Consequently, Australian temperate grasslands now occupy less than 1% of their former range and are listed as critically endangered under the Australian Government's Environmental Protection and Biodiversity Conservation Act 1999 (Committee, 2008, Zimmer et al., 2010, Williams and Morgan, 2015).

Australia's contemporary temperate grassland large herbivore assemblages

Domestic and introduced grazers represent a completely novel disturbance to Australian grasslands, predominantly due to the lack of pre-adaption to ungulate grazing mechanisms, but also due to the associated land conversion to agricultural pasture (Mcintyre and Lavorel, 1994c). Thus, contemporary, temperate grassland large herbivore assemblages are fundamentally different to pre-extinction fauna and now consists of native marsupials, domestic ungulate livestock and introduced exotic ungulates.

Dominant native species

The most dominant sympatric native herbivore grazers in Australian temperate grassland system are kangaroos, specifically the eastern grey kangaroo, common wallaroo (*Macropus robustus*), and the western grey kangaroo. All crepuscular and nocturnal grazing marsupials, with females weighing from 22 – 40 kg and males from 40 – 90 kg, depending on the species (Kaufmann, 1975, Dawson, 1995). Large macropod grazers are considered ecosystem engineers (Jones et al., 1994) in woodland and grassland ecosystems, because they modify the structure and composition of grassy vegetation, thereby altering habitat conditions and resource availability for other species (Frawley, 2010, Howland et al., 2014, Mcintyre et al., 2015). However, the lack of large natural predators and provision of artificial watering points has resulted in a drastic increase in large macropod abundance in many native ecosystems across south-east Australia (Viggers and Hearn, 2005, Mills et al., 2020, Read et al., 2021). There is growing concern that these high-density populations will contribute to overgrazing and consequential negative consequences for ecosystem composition and function, as well as potential loss of species diversity (Coulson, 2007, Lunney et al., 2007, Foster et al., 2014, Rees et al., 2017, Mills et al., 2020, Morgan, 2021). Both the eastern and western grey kangaroos are species currently under active management in many parts Australia due to over-abundance including urban areas as well agricultural lands and in national parks (Adderton, 2004, Mawson et al., 2016, Kerle, 2019, Lucas et al., 2021). The other large native macropods occur at lower densities across south-east Australian grasslands but are still considered common, and have the

potential to become over-abundant (Dexter et al., 2013): swamp wallabies (*Wallabia bicolour*), red-necked wallabies (*Notamacropus rufogriseus*).

In addition to macropods, contemporary herbivore assemblage also includes the common wombat (*Vombatus ursinus*) and the less abundant, southern hairy-nosed wombat (*Lasiorhinus latifrons*), which contribute a distinct ecological role to temperate grasslands (Taggart et al., 2020). Wombats are the largest burrowing marsupials on earth, weighing up to 40 kg and occurring predominantly in hilly, riparian habitats in the temperate regions of south-east Australia (Evans et al., 2006, Borchard et al., 2008). As burrow ecosystem engineers, wombats modify their environment by acting as bioturbators, contributing an important ecological function which effects nutrient exchange, soil properties and vegetation dynamics (Halstead et al., 2020). There is further evidence showing that their large burrows also provide critical refuge to many other native species (Linley et al., 2024). However, wombat populations have been declining due to multiple factors, including high road mortality, habitat modification and the increasing prevalence of the parasitic disease, sarcoptic mange (*Sarcoptes scabiei*) which disproportionately affects wombats (Martin et al., 1998, Roger et al., 2007, Fraser et al., 2016, Old et al., 2018).

Exotic herbivores

Large populations of exotic ungulates have established across the Australian continent, including water buffalo (*Bubalus bubalis)* in North Queensland, feral horses (*Equus caballus*) in the Alpine regions (Driscoll et al., 2019, Mihailou and Massaro, 2021) and feral pigs (*Sus scrofa*), sambar (*Rusa unicolor*) and fallow (*Dama dama*) deer, all of which have inhabited much of south-eastern Australian for several decades (Hone, 2020, Mccarthy et al., 2025). High-density deer populations are known to affect plant community structure, therefore, significantly reducing plant species diversity (Gill and Beardall, 2001, Burns et al., 2021). Furthermore, high intensity and selective browsing place strong selective pressure on native fauna (Zhu et al., 2012) and cause other ecological damage through their digging and tree-rubbing behaviour (Côté et al., 2004). It is also likely that feral deer are facilitating the spread of invasive weeds, such as the European blackberry

(*Rubus fruticosus aggregate*), as is evident by the large quantities of seed previously found in their faeces (Vellend, 2002, Forsyth and Davis, 2011). Despite differences in habitat type and species interactions, the problem of over-abundant deer populations is not restricted to Australia but is in fact a global issue. In Patagonia, Argentina, non-native deer species, (red deer *Cervus elaphus*) and fallow deer) have been a wild population for 80 years, living in sympatry with several other native deer species (Relva et al., 2010). Despite a habitat that has evolved with ungulate grazers, a study by Relva et al (2010) showed that only non-native deer produced strong negative effects on forest tree growth, vegetation cover, and the facilitation of invasive weed species. North American forest habitats are similarly threatened by the over-population of deer, particularly the white-tailed deer (*Odocoileus virginianus*), which is a native species in this context (Rawinski and Square, 2008, Habeck and Schultz, 2015). Shifts is successional forest communities and a reduction in herbaceous and woody plant cover are the two most harmful impacts of deer in these habitats (Liang and Seagle, 2002, Rossell et al., 2007) because plant cover is critical habitat for many ground-dwelling mammalian and bird species in North American forest ecosystems (Hunter et al., 2001, Litvaitis, 2001, Converse et al., 2006). A study by Rossel et al (2007) showed a 47% reduction in woody plant cover in control plots when compared to deer exclusion plots. Further studies contradicted these findings showing that due to their selective browsing, deer can also expediate native plant germination at the same time (Claridge et al., 2016), with research suggesting that it is an over-abundance of deer that causes drastic and sometimes irreversible changes to ecosystems (Côté et al., 2004). However, the limited research into their impact on Australian grassland habitats makes it difficult to know what constitutes ‘over-abundance’. To better inform management, there is a need for greater knowledge about the true complexity of the ecological impacts of feral deer on Australian grasslands, especially in the context of their sympatric relationship with other herbivores (Burns et al., 2021).

Domestic herbivores

Domestic animals, particularly cattle and sheep (*Ovis aries*), remain the most widespread large-bodied non-native herbivores across much of Australia's rangelands and temperate grazing systems (Mcivor, 2005, Reid, 2019). Although cattle are primarily managed for agricultural production, they are increasingly being incorporated into conservation and restoration programs to reduce biomass, suppress invasive plants, to maintain open vegetation structure and to increase biodiversity (Lunt et al., 2007, Gordon et al., 2021d).

Rewilding

There is a growing recognition of the importance of large herbivores and the ecological processes that they provide, likely encouraged by a growing interest in rewilding initiatives (Navarro and Pereira, 2015, Jepson, 2016, Carver et al., 2021). Rewilding is a plastic term (Jørgensen, 2015), but the over-arching vision is the restoration of self-sustaining ecosystems and ecological processes while minimizing human interactions (Soulé and Noss, 1998, Lorimer et al., 2015, Jepson, 2016, Fernández et al., 2017, Svenning, 2020, Svenning et al., 2024). Rewilding encompasses a range of different approaches such as trophic rewilding, which is the (re)introduction of missing keystone species, of which Pleistocene rewilding falls under (Bakker and Svenning, 2018, Carver et al., 2021, Schmitz et al., 2023, Ejrnæs et al., 2024, Svenning et al., 2024). Broadly described as: the (re)introduction of large herbivore species or their close relatives, with the aim to restore lost ecological processes following the global extinction of megafauna during the Late Pleistocene (Donlan et al., 2006, Perino et al., 2019, Lundgren et al., 2020). In many cases, cattle or other domestic species are being used as ecological analogues for species that have become extinct centuries ago (Jørgensen, 2015, Svenning et al., 2016, Fernández et al., 2017, Gordon et al., 2021b, Gordon et al., 2021c, Manning et al., 2024). Many studies demonstrate that large non-native herbivores can restore ecological functioning when managed appropriately, though much of the evidence originates from Europe, Africa and North America (Zimov, 2005, Svenning et al., 2016, Overend and Lorimer, 2018, Garrido et al., 2019, Selwyn et al., 2025). Whether these concepts

translate to Australian ecosystems remains largely unknown and there remains considerable debate as to whether introduced herbivores should be used to achieve conservation outcomes (Lunt et al., 2007). Some argue that domestic herbivores may partially replace ecological functions that were lost with the extinction of megafauna if managed appropriately (Fensham, 1998, Waters et al., 2017, Teague and Kreuter, 2020). In contrast, many more assert that grazing by domestic herbivores further drive ecosystem degradation and species loss, in part due to Australia's unique evolutionary history (Mcintyre and Lavorel, 1994c, Robertson and Rowling, 2000, Ford, 2011, Eldridge et al., 2016, Lindenmayer et al., 2018). Resolving this uncertainty is central to evaluating the potential role of herbivores in restoring ecological processes and improving biodiversity outcomes. However, first this requires an understanding of the ecological roles performed by the current herbivore guild.

Knowledge gap

Despite the widespread occurrence of medium to large, native, domestic and exotic herbivores across Australia, relatively little is known about how these species function collectively in a temperate grassland habitat. There is limited recent evidence describing partitioning of resources, the degree of dietary overlap and composition (Braithwaite et al., 1985, Dawson and Ellis, 1994, Garnick et al., 2016) or their potential as seed dispersers through endozoochory (Davis et al., 2010, Quin et al., 2023b, Murray and Nevard, 2024). By studying patterns of resource use and partitioning across a contemporary guild, we may gain a greater understanding of the functional roles and ecological significance of these species in the Australian grassland system (Kelly et al., 2016).

Thesis aims

The broad aim of my thesis was to evaluate the sympatric nature of an Australian contemporary herbivore guild comprised of native, domestic, and exotic herbivores, and further assess their impact on plant community dynamics and ecosystem function.

Chapter One – Grazing the Globe: A Review of Large Herbivore Impacts on Plant Diversity

For this chapter I conducted a global meta-analysis, synthesising the effects of grassland grazing exclosures on plant species richness, diversity, and evenness. Specifically, I tested whether vegetation responses could be predicted by (1) herbivore nativeness (native, domestic, exotic, or mixed guilds) and (2) plant nativeness (native or exotic). I also examined the distribution of moderator variables to identify potential biases and gaps within the available literature.

Chapter Two - Dietary overlap among native and exotic herbivores in a temperate grassland ecosystem.

This chapter explores the dietary composition and overlaps of six large herbivores using DNA metabarcoding of 883 faecal samples collected over a 12-month period.

The main objectives of this chapter were to: (1) asses the degree of dietary overlap and partitioning between the herbivore species, (2) determine any seasonal differences in the species richness and diet of the herbivore species, and (3) test whether exotic herbivores were more likely to consume native plants

Chapter Three - Seeds on the move

This chapter investigated the seed dispersal capabilities, via endozoochory potential, of six large herbivores. Endozoochory potential was determined using 594 faecal samples in a greenhouse experiment.

The main objectives of this chapter were to: (1) evaluate whether there was a difference between native and exotic herbivores, in their potential to transport viable seeds via endozoochory: (2) determine if species richness and abundance of seeds found in faecal matter varied, (3) analyse seasonal differences in the diversity and quantity of viable seeds being dispersed, and (4) test whether exotic herbivores were more likely to disperse exotic seeds.

Chapter Four - What goes in doesn’t always come out

For this chapter I analyzed how plant consumption may influence seed germination persistence through endozoochory across six herbivore species,

Based on the hypothesis that exotic herbivores are more adept at dispersing exotic seeds, I asked: (1) if compared to diet composition, do exotic plant species disproportionately represent germinated assemblages? (2) If plant functional groups are more adept at dispersal by endozoochory than others, relative to consumption? (3) Is there evidence to suggest that one can predict risk factors associated with highly invasive plant species?

Chapter Five - How similar is similar enough?

This concluding chapter integrates the findings of each chapter with broader ecological and management implications, while also addressing the major limitations and future directions of this research

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Chapter 1

Grazing the Globe: A Review of Large Herbivore Impacts on Plant Diversity

Introduction

The world is in what many consider to be a sixth global extinction event (Pimm et al., 2006, Pievani, 2014, Ceballos et al., 2015, Ceballos et al., 2017, Cowie et al., 2022), predominantly due to anthropogenic influence (Mccauley et al., 2015, Young et al., 2016). There is evidence suggesting that herbivores, whether mammalian, bird or reptile, have the greatest proportion of species at risk of extinction, when compared to other trophic groups (Atwood et al., 2020). Herbivores play a pivotal role in shaping and maintaining ecosystems functions and as a result (Trepel et al., 2024), the continued loss of native species will have profound ecosystem impacts (Rule et al., 2012).

Furthermore, the large-scale introduction of novel species may further alter fundamental ecological processes, and is now considered one of the top threats to global biodiversity (Lovejoy, 2002). One example is the native pudu deer (*Pudu pudu*) and huemul (*Hippocamelus bisulcus*) of Argentina. They have become extremely rare, whilst the introduction of red (*Cervus elaphus*) and fallow deer (*Dama dama*) have resulted in abundant numbers, strongly affecting native plant communities by reducing understory cover and modifying plant composition (Relva et al., 2010). Similar trends have been recorded globally (Bescond-Michel et al., 2025) with the introduction of exotic or domestic ungulates having the most detrimental impacts (Holmgren, 2002, Lowney et al., 2005, Borchard et al., 2008, Porter et al., 2014, Davis et al., 2016, Boyd et al., 2017). This is concerning considering the use of domestic grazing animals is so extensive, that there is one domestic herbivore for every two people on Earth (Mottet et al., 2018), far out weighing the combined number of all wild mammals (Ripple et al., 2015, Smith et al., 2016, Greenspoon et al., 2023). The ongoing loss of native species paired, with an increase in exotic herbivores, creates shifts in historical grazing guilds with far reaching consequences for ecosystems processes.

Grasslands cover 40% of the earth's land mass, and are found on every continent on earth except for Antarctica (White et al., 2000). Grassland biomes are home to many endemic species, they sequester large amounts of carbon, have considerable cultural value for indigenous groups, are used extensively for pastoralism, commercial grazing and harvesting (Heidenreich, 2009, Prach et

al., 2017), making them incredibly important for human life. Due to grasslands being heavily shaped by herbivores, the domestication and subsequent overgrazing by large ungulate herbivores, coupled with the replacement of native species, has contributed to severe grassland modification and altered plant communities (Bai et al., 2002, Hilker et al., 2014, Gonzalez and Ghermandi, 2021). Furthermore, despite being outside the scope of this study, the importance of invertebrate herbivores and their significant contribution to ecosystem functions such as: nutrient cycling and pollination services, is important to note, particularly in the context of modified grasslands having caused catastrophic declines in invertebrate diversity (Littlewood et al., 2012, De Gracia et al., 2025). Consequently grasslands, particularly those in the temperate zones, are considered the most threatened terrestrial ecosystems on earth (Henwood, 2010).

Conservation initiatives have highlighted the importance of restoring grassland biodiversity and ecosystem functions, but the extinction and replacement of large mammalian herbivores have created ecological (including trophic) gaps, resulting in further declines in biodiversity (Campbell et al., 1994, Valiente-Banuet et al., 2019, Pringle et al., 2023, Garrido et al., 2025). The need to fill these gaps has been a significant component of rewilding, with the belief that simply protecting existing ecosystems is insufficient and instead we need to focus on restoring processes (Soulé and Noss, 1998, Sandom et al., 2013, Lorimer et al., 2015, Corlett, 2016, Pettorelli et al., 2019, Carver et al., 2021, Mutillod et al., 2024). Although the broad definitions of rewilding differ, the key underlying principle is that the focus is restoring lost ecosystem functions, rather than species reintroduction (Naundrup and Svenning, 2015, Prior and Brady, 2017, Carver et al., 2021) and includes the restoration of the frequency of events such as fire and predation, increasing the dispersal capabilities of species and restoring trophic webs (Svenning et al., 2016, Perino et al., 2019, Svenning et al., 2019, Schmitz et al., 2023).

The importance of large herbivores in grassland processes and community structure makes them essential in restoring lost processes. However, a global mass extinction event at the end of the Pleistocene resulted in most native megafauna being lost by 13’000 years ago (Martin, 1973, Martin

and Steadman, 1999, Barnosky et al., 2004, Lundgren et al., 2018). Here, megafauna is defined as terrestrial mammals with an adult body mass greater than 45kg (Roberts et al., 2001, Barnosky, 2008, Moleon et al., 2020). The continued loss of large herbivores and associated degradation of habitats (Ripple et al., 2015), has led to the suggestion that the use of non-native and domestic herbivores may be effective as ecological substitutes to restore these missing ecological functions (Gordon et al., 2021d, Pérez-Barbería et al., 2023, Rey Benayas et al., 2025). For example, the concept of rewilding-lite was developed in recognition that the restoration of native herbivore assemblages is not always practical or possible and advocates the strategic use of traditional domestic livestock to restore lost ecological functions (Carver et al., 2021, Gordon et al., 2021b). Furthermore, Lundgren et al. (2018) highlighted the fact that the inclusion of currently distributed exotic megaherbivores, increases global megafaunal richness significantly. They go on to suggest that a reassessment of conservation attitudes toward introduced megafauna is needed because they may be overlooked as species able to perform desirable ecological roles (Schlaepfer et al., 2011, Lundgren et al., 2018, Lundgren et al., 2020). However, the use of exotic herbivores in this manner assumes that they can replicate former native herbivore functions; yet there is significant uncertainty as to whether they do (Parker et al., 2006, Hempson et al., 2017, Gordon et al., 2021a, Young et al., 2021, Pringle et al., 2023, Manning et al., 2024).

There have been extensive studies looking at the impacts and effects of large herbivores plants, but they often focus on biomass reduction, productivity, and single or total plant species responses such as exotic plants only or not differentiating plant responses by nativeness (Frank, 2005, Burns et al., 2009, Bernes et al., 2018). There are some reviews that compare species richness and diversity metrics in response to herbivores, but they include only ungulate grazing herbivores (Diaz et al., 2007, Schieltz and Rubenstein, 2016, Filazzola et al., 2020, Price et al., 2022), exclude domestic livestock (Lundgren et al., 2024, Trepel et al., 2024), overlook native herbivores, or present data as total plant species response rather than identifying native and exotic plant responses

(Albon et al., 2007, Herrero-Jáuregui and Oesterheld, 2018, Koerner et al., 2018, Staver et al., 2021).

Furthermore, the use of grazing simulation data whether sourced through computational models, application of mechanical damage to plants to mimic natural herbivory damage, or through the use of slashing or mowing as substitutes for actual herbivory, is quite common (Jorritsma et al., 1999, Hjältén, 2008, Olofsson, 2009, Song et al., 2023, Guo et al., 2024). Although simulation experiments have their merits, there are some fundamental limitations. Dynamic simulations utilize models that are mathematically complete but biologically incomplete (Loewer, 1989) and often lack the integration of animal and plant-focused approaches in equal consideration with environmental variables, which is critical because each introduce a suite of complex interactions (Weisberg et al., 2006). Furthermore, the emulation of grazing and herbivory through moving or slashing experiments similarly ignores critical interactions (Eckard et al., 2014). Further evidenced by the processes of natural foraging which involves decisions made by the animal, which will change according to temporal and spatial scales (Dumont and Iason, 2000). The uncertainty of how true and accurate simulation data in comparison to real-world ecological processes drove my decision to reject any studies of this nature for my meta-analysis.(Bergström and Edenius, 2003, Remler and Van Ryzin, 2021)

The limited understanding of the comparative effects of native, exotic, and domestic herbivore impacts, on native and exotic plant species responses is alarming. Globally, there are over 3.5 billion domestic ungulate herbivores, which represents one domestic herbivore for every two people on the planet (Mottet et al., 2018). Our knowledge of the ecosystem impacts of domestic, and, increasing spread of large exotic herbivores across temperate grasslands, (Holmgren, 2002, Mcgeoch et al., 2010, Lundgren et al., 2018) is insufficient and represents essential knowledge for the ongoing conservation and restoration of these critical grassland biomes (Wisdom et al., 2006, Vavra et al., 2007).

To address these knowledge gaps, I conducted a global meta-analysis synthesising the effects of grazing exclosures on plant species richness, diversity, and evenness. Specifically, I tested whether vegetation responses could be predicted by: (1) herbivore nativeness (native, domestic, exotic, or mixed guilds) and (2) plant nativeness (native or exotic). Based on the hypothesis that herbivores lacking a shared evolutionary history with the resident flora exert stronger ecological impacts, I predicted that domestic and exotic herbivores would have more negative effects on plant communities than native herbivores, with native plant richness being disproportionately reduced. I also examined the distribution of moderator variables to identify potential biases and gaps within the available literature.

Methods

Literature search and compilation of dataset

I used Web of Science (www.webofscience.com) to find studies relating to the presence of terrestrial herbivores and their impact on plant species diversity and richness. On the 25 November 2024, I used the following search terms “(Graz* OR brows* OR herbivory) NOT (arthropod OR invertebrate) AND (forest* OR Woodland* OR Grassland* OR Steppe* OR Agricultural OR “Alluvial Plain” *) AND ("species richness” OR biomass)” and added the following key words, grazing, grazing intensity, grazing exclusion, herbivory, livestock grazing, grassland, grassland management, exclosure, sheep grazing, cattle grazing. Biomass was included in the search terms to ensure I captured all relevant exclosure experiments that may have relevant diversity or species richness metric results.

I only included publications in my analysis if they reported the effects of terrestrial herbivore presence on the following variables: *study design*; full exclosure experiment with an appropriate control or high versus low density experiments if the low density was zero. No greenhouse or simulated grazing experiments were included, as discussed above. The terms ‘open’ and ‘grazed’ were used throughout the following analysis and discussion and is in reference to

experimental plots that were not herbivore exclosed and therefore experienced herbivory. Exclosure plots in contrast, were experimental plots that were exclosed from herbivores and therefore experienced no herbivory. *Richness unit*; mean plant species richness and any plant diversity indices (Shannon-Weiner, Simpson's diversity, Pielou's evenness Index, Alpha diversity or Beta diversity). Where there were more than one plant richness units or spatial variables evaluated in the same study, I handled them as separate observations (Rossetti et al., 2017). The moderator variables tested were *habitat type;* grasslands, temperate, montane, coastal, tropical or savannahs, woodlands and mosaic landscape with a majority comprising of grassland, *herbivore/guild type;* native, exotic, domestic or mixed, *feeding strategy;* browser, grazer, mixed, *plant nativeness;* native, exotic, all. Only studies that reported mean or median values with either standard error, standard deviation or confidence intervals were included in the analysis. The R package 'revtools' (Westgate, 2019) was used to remove duplicates. Titles were initially screened for relevance, followed by abstracts and finally the full paper was downloaded and screened. All articles were screened by a single person (SS), with a subset reviewed by another (LEN) to check for consistency. The data from each of these studies was then assessed and extracted where appropriate using the Plot Digitizer software (Plotdigitizer, 2026) for figures. (See Appendix A. for the full list of papers and associated effect sized used in this meta-analysis)

Diversity indices

The diversity indices included in my meta-analysis were statistical representations of biodiversity, whether they be richness, evenness or dominance (Shannon, 1948, Simpson, 1949, Pielou, 1966, Whittaker, 1972, Smith and Wilson, 1996, Heip et al., 1998). Different diversity indices are often used based on individual study questions and aims because some will be better suited than others (Peet, 1974). Biodiversity is difficult to quantify, and indices are effective at describing different general community properties (Morris et al., 2014), therefore the most effective way to examine broad trends is by comparing effect size changes across all diversity indices.

Simpson's index measures the number of species, and how evenly individuals are distributed among species. Higher values indicate more diverse communities (Simpson, 1949). Simpson's index is calculated using:

$D = \sum_{i=1}^{S}(\frac{n_i}{N})^2$

Where n_i = number of individuals per species *i*, N = total number of individuals of all species, n_i/N = p_i (Proportion of individual species *i*), and S = species richness (Peet, 1974).

Shannon-Weiner index also measures the number of species and how evenly individuals or distributed among species. Higher values indicate more diverse communities (Shannon, 1948, Macarthur, 1955). Shannon-Weiner index is sometimes denoted as *H'* and is calculated using:

$$H = -\sum_{i=1}^{S} pi * ln\, p_i$$

Where p_i = the proportion of individual species *i*, *ln* = natural logarithm and *s* = species richness.

Pielou's evenness index measures the distribution of individuals across species. Values closer to 1 indicate greater diversity and equal abundances between species (Pielou, 1966). Pielou's evenness index is calculated using:

$$J = \frac{H}{H_{max}}$$

Where *H* = Shannon-Weiner diversity and H_{max} = the maximum possible Shannon-Weiner diversity and calculated as H_{max} = *ln(s)*, where s = number of species.

Alpha (α) diversity is the diversity within a single site or community and can be calculated using species richness or Shannon-Weiner diversity, whereas Beta (β) diversity represents the change in species composition between sites or communities and similarly, is often derived from species richness or Shannon-Weiner (Whittaker, 1972, Jost, 2007). Lower values are equal to a similarity between the measured sites. Beta diversity is calculated using:

$$\beta = \frac{\gamma}{\alpha}$$

Where γ = total regional diversity and α = average of the site or community diversity.

Meta-analysis

I calculated effect size using Hedges' g (Hedges, 1981, Hedges and Olkin, 2014), a standardized mean difference metric corrected for small sample size bias (Gurevitch et al., 1993). A negative effect size indicated open sites have a greater effect than exclosed sites. All analyses were performed using R Studio (Rstudio, 2023).

Publication bias is the tendency for studies reporting statistically significant, positive or novel results to be published preferentially. This can cause an ever estimate in effect sizes, leading to a distortion in the available scientific literature (Dickersin, 1990, Joober et al., 2012, Song et al., 2013). To assess for publication bias, and to detect any potential gaps in the literature, I used the metafor (Viechtbauer and Viechtbauer, 2015) package to perform a random effects model (rma). This model was used to estimate the overall pooled effect size across studies focusing on the interaction between herbivore type (exotic, native, domestic or mixed) and plant nativeness (native, exotic, all) while accounting for sampling variance and heterogeneity. This method produced a weighted average, whereby studies with a lower variance or larger sample size exert more influence. Using the same package, I then performed a funnel asymmetry test (regtest) to determine if the effect sizes were related to study precision. This is often used to help determine if there is publication bias present in the dataset.

Finally, I used the trim-and-fill method and funnel plots (Ligrrr and Pillemer, 1984, Duval and Tweedie, 2000) in which the study effect sizes were plotted against their precision. In the absence o publication bias, studies should form a symmetrical inverted funnel, with the larger and more precise studies clustered near the top (Liu, 2011, Song et al., 2013). The trim-and-fill method estimates the number of potentially missing studies required to restore symmetry and recalculates the overall effect size accordingly (Duval and Tweedie, 2000). For the primary meta-analysis statistics, still using the metafor package (Viechtbauer and Viechtbauer, 2015) I used random effects

models (rma) and multi-level mixed-effects models (rma.mv) to test moderator variables and their interactions and ANOVAs to test omnibus moderator significance I included random effects to all models to account for multiple effect sizes from the same study and tested whether the methodological diversity metrics influenced the results (Fisher and Fisher, 1966, Becker, 1992, Hedges and Vevea, 1998, Schmidt et al., 2009). I used the rnaturalearth (South and South, 2017) and sf (Bivand, 2022) packages to produce mapping plots.

Results

My searches returned 7,652 peer-reviewed articles. After screening titles and abstracts and removing articles that were obviously unsuitable for my study, 355 studies remained and, after reviewing the full papers, I extracted the data from a total of 62 papers (Figure 1).

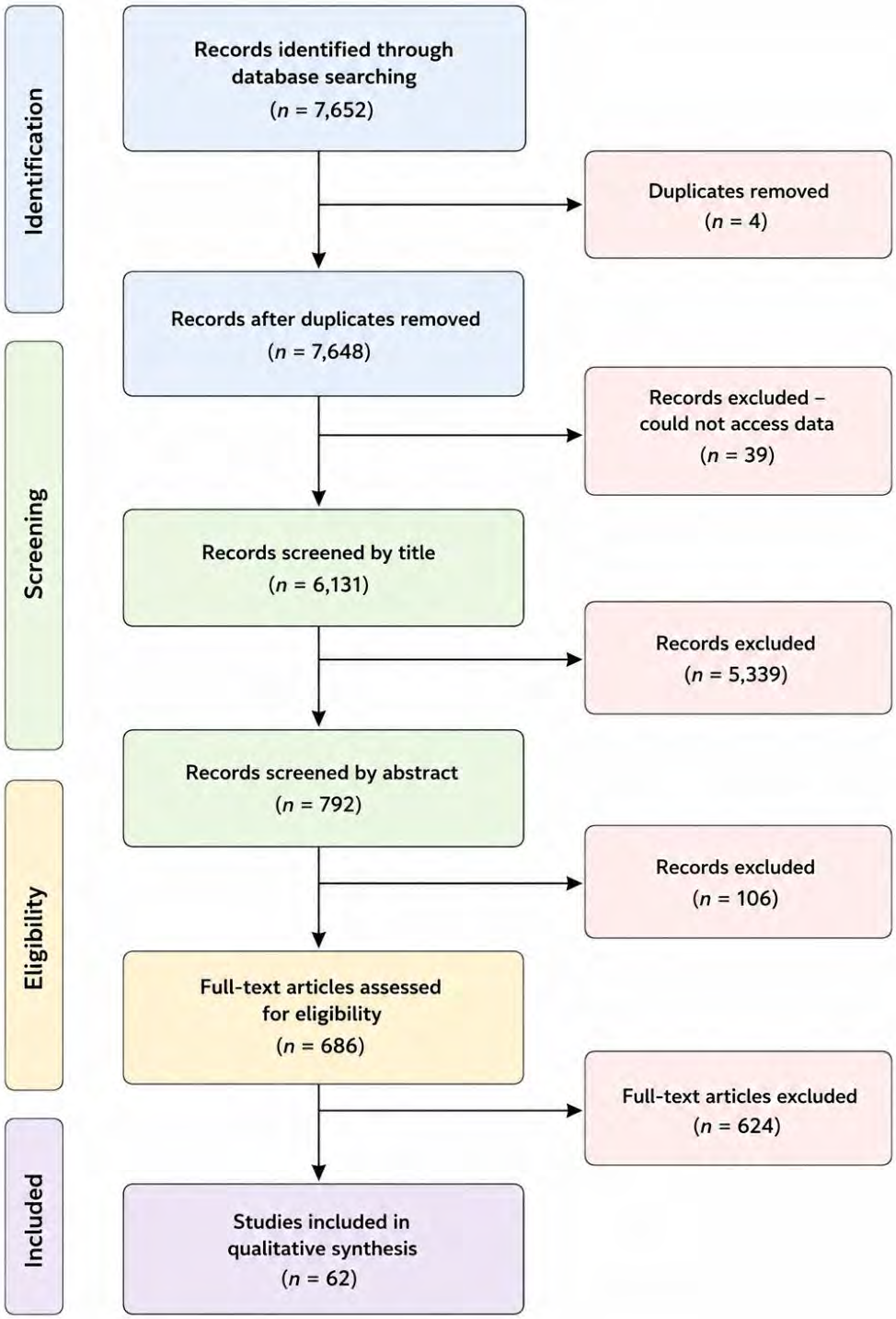


Figure 1. Flow chart depicting the number of articles after the initial search (7,652) and the subsequent screening process with 62 studies included in the final meta-analysis.

The random effects model indicated the total heterogeneity of the dataset was significantly high ($p = <0.0001$), confirming that there was an extremely high degree of variation in both the magnitude and direction of the effects. ANOVAs signified that the two moderators, habitat type and feeding

strategy (grazer, browser, mixed) did not significantly influence effect sizes, nor the interaction between them.

Herbivore guild by study

I found considerable variation in the effect size of the different herbivore guilds or herbivore species as reported represented studies (Figure 2). Of the 35 different guild assemblages and species studied, 35% reveal significant effect sizes. However, significance shown in the forest plot did not necessarily correspond to significance in the overall mixed-effects meta-regression model, which simultaneously accounted for heterogeneity, variance structure, random effects, and moderator interactions. For some guilds, their impact on effect size differed by study, as either a positive or negative effect, which is reflective of the high heterogeneity. The meta-regression model analysis indicated that the exclosure of the following herbivores by study, had a greater effect on plant diversity ($p = all < 0.05$); (sheep (*Ovis aries*) and eastern grey kangaroo (*Macropus giganteus*)), (horse (*Equus ferus caballus*)), (cattle (*Bos taurus*), horse and sheep), and (cattle and sheep). Of these assemblages, both (horse) and (cattle and sheep) had equally significant effect sizes in open/grazed plots.

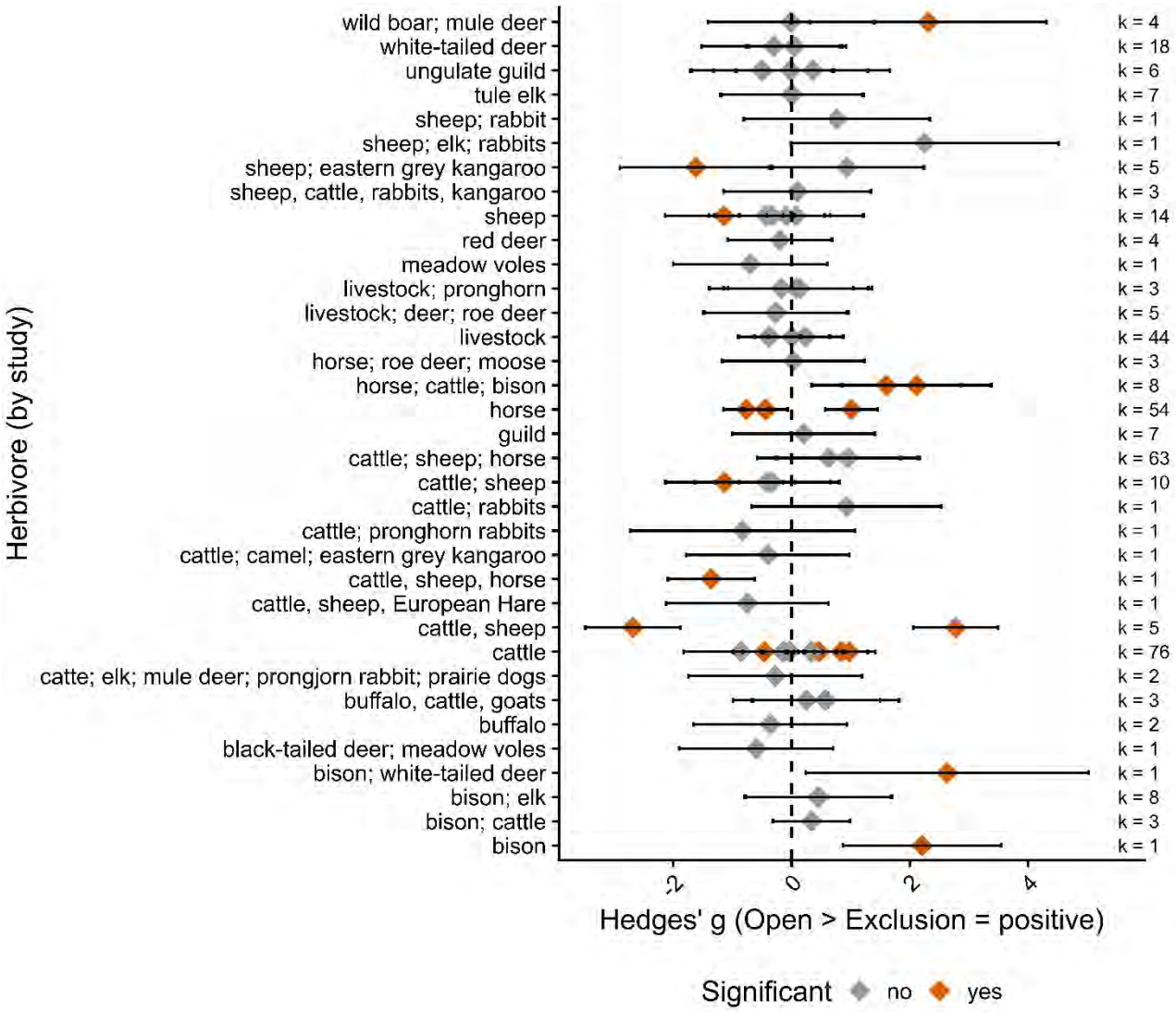


Figure 2. Forest plot depicting Hedges' g effect sizes (n = 62 studies; 368 effects) of the individual herbivores or mixed guilds investigated across individual studies included in the meta-analysis. The combined effect sizes contributing to each herbivore group is denoted by k. Positive effects indicate a greater plant diversity in grazed plots relative to herbivore exclosures, whereas negative values indicate reduced diversity under grazing. Points represent individual study effects and error bars represent 95% confidence intervals. Orange points denote statistically significant effects (confidence intervals that do not cross the zero line), while grey points indicate non-significant effects. The dashed vertical line at zero represents no difference between open and exclosure treatments.

Herbivore nativeness and plant nativeness

The multi-level mixed-effects models (rma.mv) testing the moderators herbivore type and plant nativeness and their interaction, signified that both moderators were significant contributors to the variation in effect sizes ($p = all < 0.0001$, Figure 3), both with and without the addition of diversity index into the model. Furthermore, beta diversity significantly explained variation in overall effect sizes ($p = < 0.0001$), whilst the interaction between Shannon-Weiner diversity and plant nativeness significantly explained some of the variation in effect sizes ($p = < 0.0001$). The model output (Figure 4) signified that overall, exotic plants were significantly, positively affected by open/grazed plots ($p = < 0.001$), as was the interaction between exotic herbivores and exotic plants ($p = < 0.001$). However, the model output also indicated that open/grazed plots had a significantly negative effect on exotic plants when the herbivores comprised a mixed guild ($p = 0.018$).

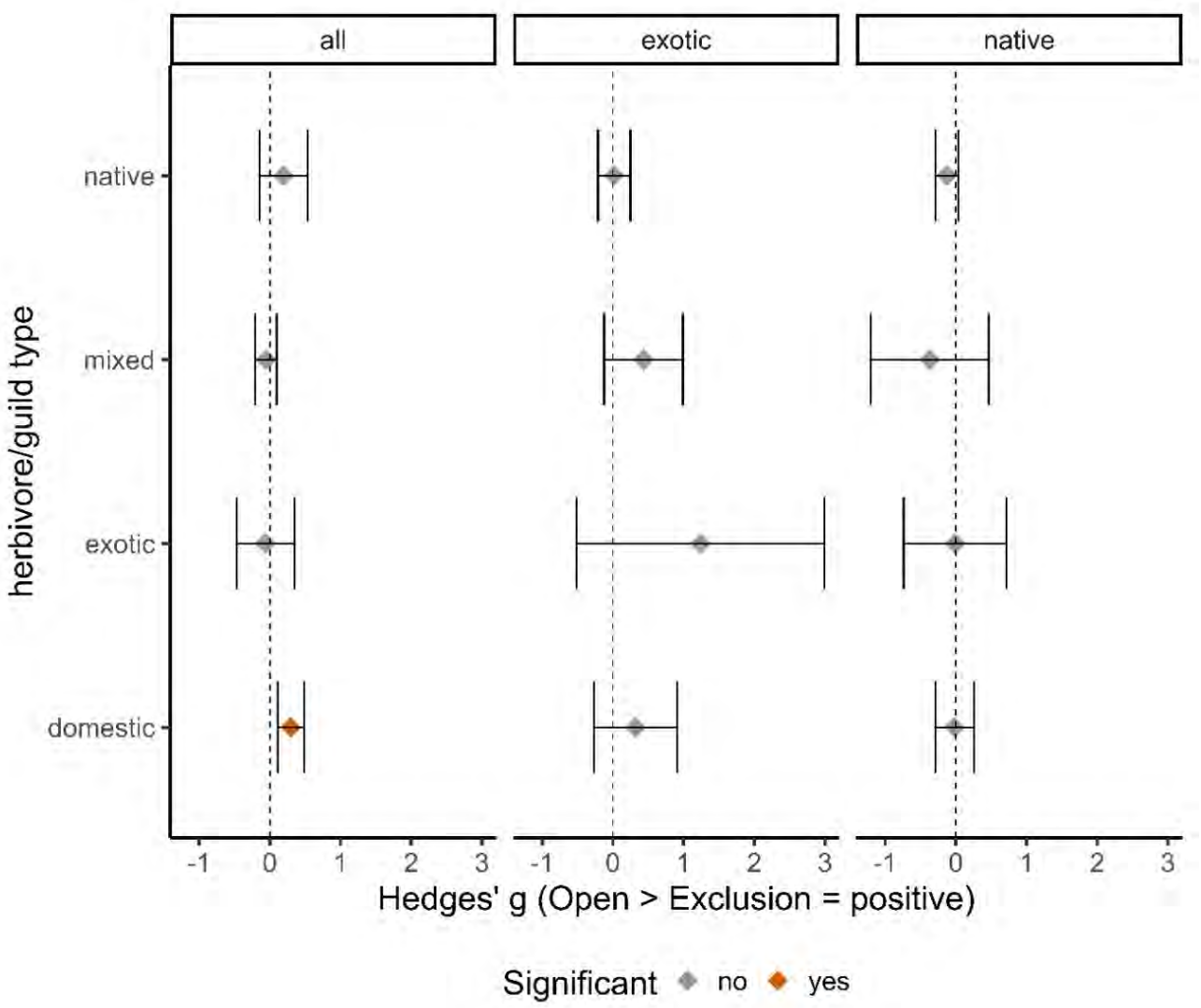


Figure 3. Forest plot depicting model-estimated Hedges' g effect sizes (n = 62 studies; 368 effects) for interactions between herbivore or guild type (native n =35, exotic n = 69, domestic n = 224, mixed n = 46) and plant nativeness (native n= 85, exotic n = 39, all n = 250). Positive effects indicate a greater plant diversity in grazed plots relative to herbivore exclosures, whereas negative values indicate reduced diversity under grazing. Points represent predicted mean effect sizes and error bars represent 95% confidence intervals. Orange points denote statistically significant effects (confidence intervals excluding zero) while grey points indicate non-significant effects. The dashed vertical line at zero, represents no difference between open and exclosure treatments.

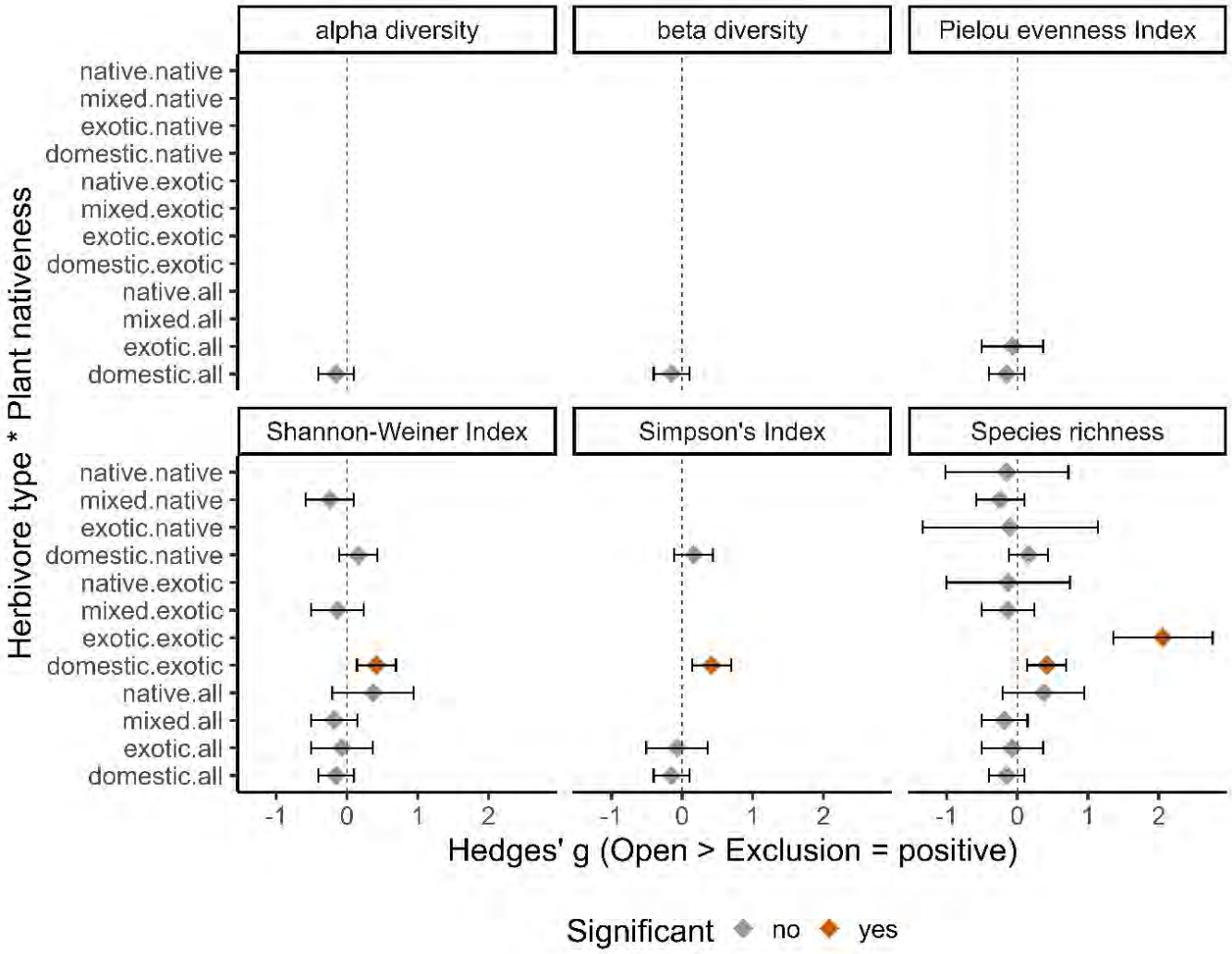


Figure 4. Forest plot depicting model-estimated Hedges' g effect sizes (n = 60 studies; 368 effects) for interactions between herbivore or guild type (native n =35, exotic n = 69, domestic n = 224, mixed n = 46) and plant nativeness (native n= 85, exotic n = 39, all n = 250) across six diversity metrics: Pielou's evenness (n = 28), Shannon-Weiner diversity (n = 97), Simpson's diversity (n = 10), species richness (n = 228), alpha diversity (n = 9) and beta diversity (n = 3). Positive effects indicate a greater plant diversity in grazed plots relative to herbivore exclosures, whereas negative values indicate reduced diversity under grazing. Points represent predicted mean effect sizes and error bars represent 95% confidence intervals. Orange points denote statistically significant effects (confidence intervals excluding zero), while grey points indicate non-significant effects. The dashed vertical line at zero, represents no difference between open and exclosure treatments.

Impact of herbivore type

The distribution and variability of effect sizes differed between herbivore/guild types, with the most variation in effect sizes contributed by domestic and exotic herbivores (Figure 5). Both domestic and exotic assemblages or species had values distributed across the extreme positive and negative

effects sizes, whereas native herbivores/guilds, and to a lesser extent, mixed guilds, had values concentrated around an effect size of zero, signifying many studies showed no effects of grazing. Furthermore, the little variation contributed by native herbivores/guilds predominantly concentrated around positive values, signified greater plant diversity in open/grazed plots.

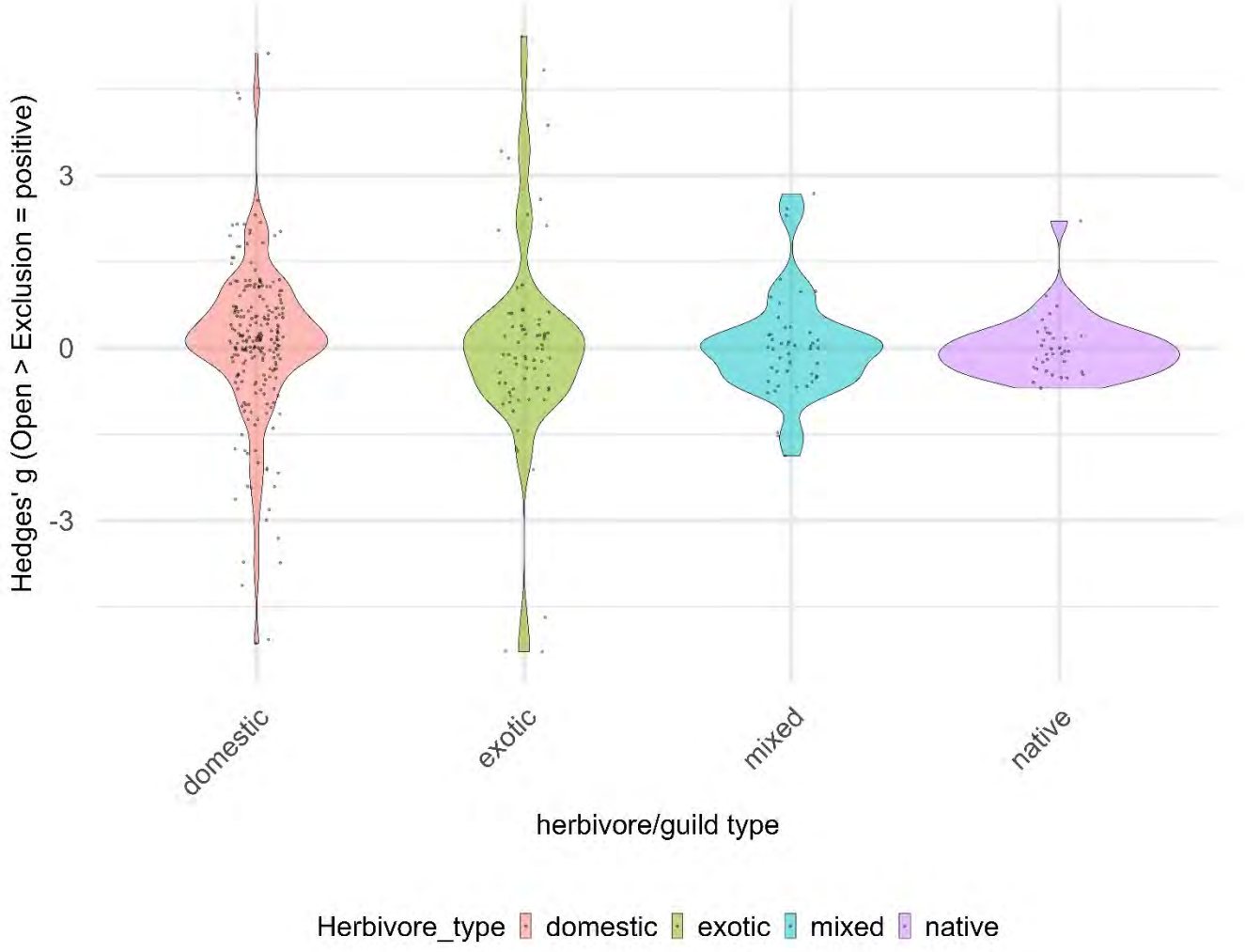


Figure 5. Violin plot depicting the distribution of Hedges g effect sizes (n = 62 studies; 368 effects) among herbivore types (native n =35, exotic n = 69, domestic n = 224, mixed n = 46) across all studies included in the meta-analysis. Positive effects indicate a greater plant diversity in grazed plots relative to herbivore exclosures, whereas negative values indicate reduced diversity under grazing. Violin widths represent the density of distribution of effect sized within each category, and overlaid points represent individual study effects.

Potential publication bias

The funnel plot of residual effect sizes of the meta-analysis was slightly asymmetric, showing extreme values on both the positive and negative side, particularly in the smaller studies (Figure 6), suggesting substantial variation between the studies. High heterogeneity in ecological variation contributed to these patterns. The trim-and-fill analysis for both the domestic herbivore-exotic plant (n = 17 studies; 28 effects) and native herbivore-native plant (n = 2 studies; 13 effects) subgroups, suggested asymmetry. The greater number of residual effect sizes were represented on the negative value side, which indicates that there are statistically inferred missing studies on the positive effect side. This may indicate that there is a publication bias favouring studies that report increases in plant biodiversity in response to herbivore exclusion, with a particular bias towards studies with small sample sizes. However, substantial ecological heterogeneity and small subgroup sample sizes contributed to these observed patterns.

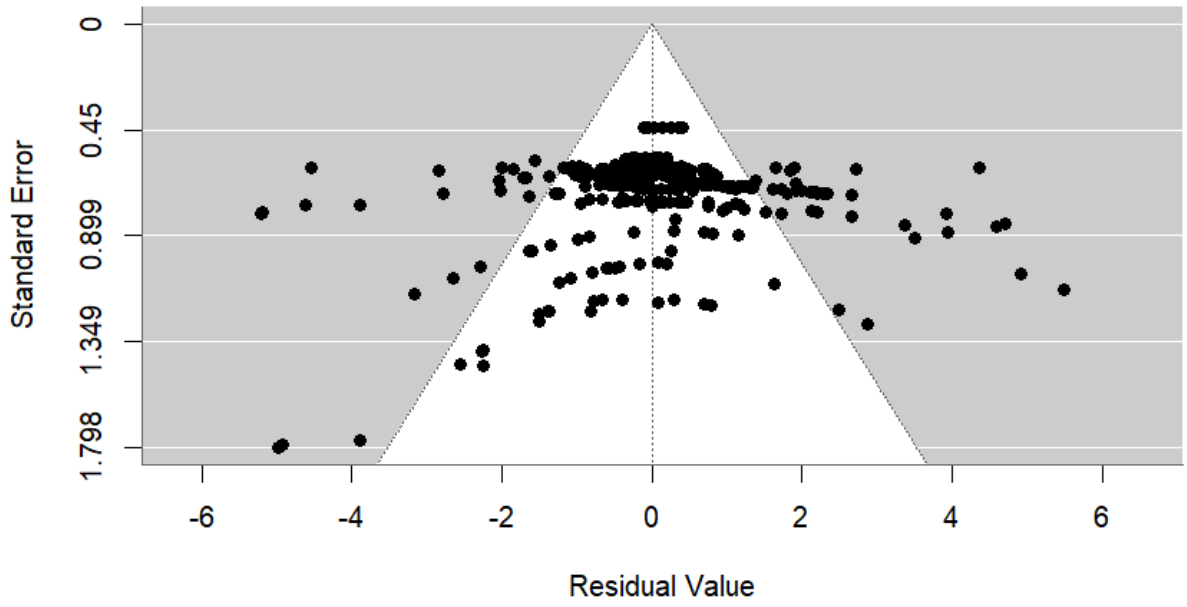


Figure 6. Funnel plot depicting residual Hedges' g effect sizes from a random-effects meta-analysis examining herbivore impacts on plant diversity metrics across all studies in the dataset (n = 62 studies; 378 effects). Each point represents an individual effect size, with the y-axis showing the standard error, values closer to the top represent larger or more precise studies. The dashed vertical line indicates the pooled overall effect size, and the triangular region represents the expected 95% pseudo-confidence limits under a symmetrical distribution.

Gaps in study representation

Heatmaps depicting the distribution of studies across moderators showed that some moderators had a disproportionately high study density. Domestic herbivores were the most represented herbivore type in all studies in the meta-analysis, with most of the studies comparing them to all plant types (Figure 7) across both the USA and African continents (Figure 8) with the majority conducted in temperate grassland habitats. The heatmaps further illustrated the disproportionate under-representation of both native and exotic plant diversity responses to both native and exotic herbivores. Furthermore, the USA was the only continent within this meta-analysis that has studies looking at plant diversity responses to native herbivores.

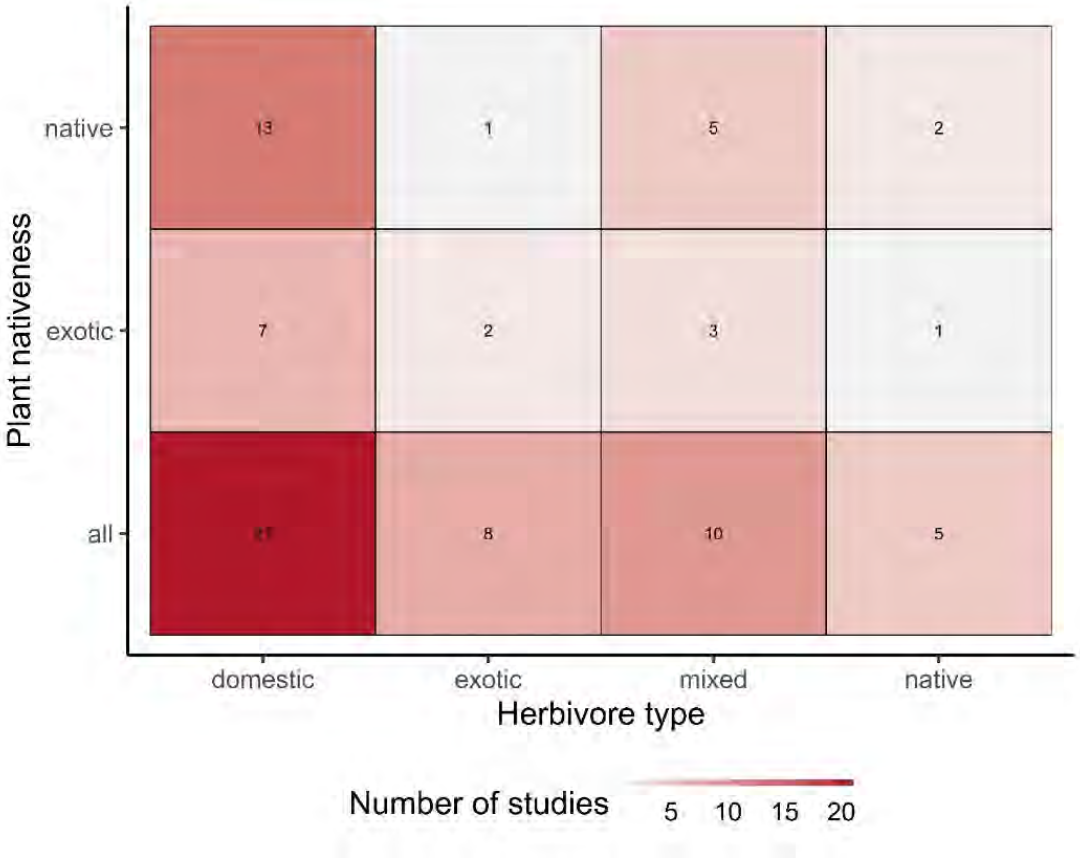


Figure 7. Heatmap depicting the distribution of studies across herbivore type (native, exotic, domestic and mixed) and plant nativeness (native, exotic, all) categories included in the meta-analysis. Numbers within the cells represent the number of independent studies included in each subgroup, and colour intensity corresponding to study density. Categories with low study numbers highlight potential knowledge gaps and underrepresented herbivore-plant interactions requiring further investigation.

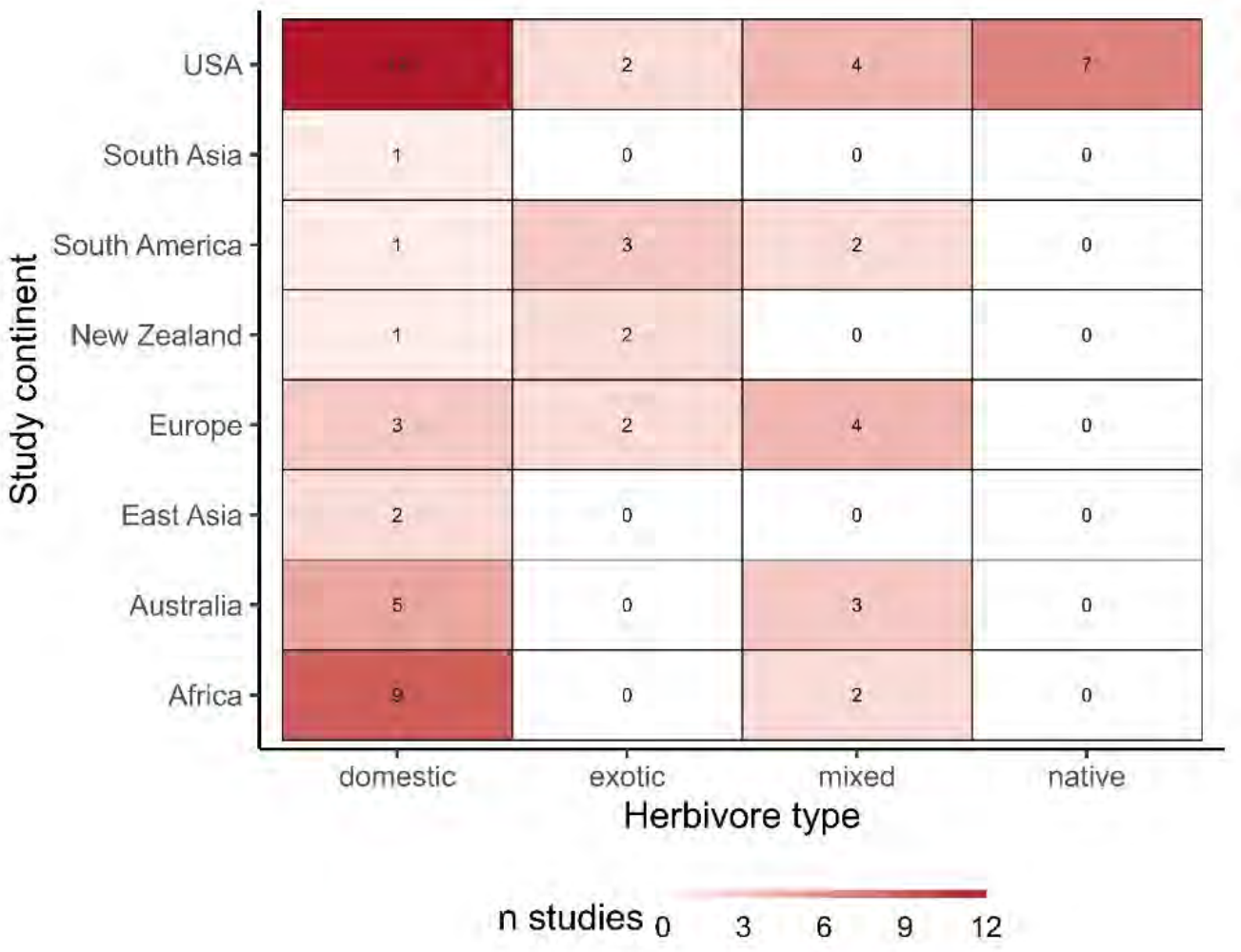


Figure 8. Heatmap depicting the distribution of studies across herbivore type (native, exotic, domestic and mixed) categories and the corresponding continents included in the meta-analysis. Numbers within the cells represent the number of independent studies included in each subgroup, and colour intensity corresponding to study density. Categories with low study numbers highlight potential knowledge gaps and underrepresented continents requiring further investigation

Discussion

My meta-analysis results indicated that both exotic and domestic herbivores exerted the strongest effects on overall plant diversity, driver greater changes than native herbivores. In some instances, these changes were positive and plant species diversity increased in response to herbivory, and in others the trend was reversed and plant species diversity decreased in response to herbivory. The meta-analysis further indicated that both exotic and domestic herbivores alter the evenness (Pielou's

index) of plant assemblages, showing marginally negative effects. The evenness metric is often used to measure species dominance, with a reduction in evenness signifying a loss of diversity.

Despite representing a small number of studies, these results align with expectations, considering that my meta-analysis also illustrated a significant positive increase in exotic plant species richness and diversity (Shannon-Weiner and Simpson's), in response to both exotic and domestic herbivores. My findings align with many other studies that suggest herbivory, and the associated plant responses, are highly dependent on both the geographic variation between different study sites and the differences in local herbivore assemblages, and no predictable based solely on the herbivore species (Kuglerová et al., 2019, Pringle et al., 2023, Sommer et al., 2025).

Overall, my findings are indicative of herbivore evolutionary background playing an influential role in driving diversity responses. The importance and value of a co-evolutionary history between native plants and herbivores is reflected in the fact that native herbivores maintain an ecosystem equilibrium, showing the least amount of impact on plant richness and diversity. This is supported by a study in southcentral California that showed weak effects of herbivory by native ungulates when compared to the addition of livestock, which resulted in reduced vegetation cover and an increase in bare ground (Orr et al., 2022).

The overall heterogeneity in the dataset was partly due to the ecological variation present across different variables, but the extreme effects sizes driven by herbivore type further highlights the dynamic uncertainty of exotic and domestic herbivores and their impact on novel ecosystems. My findings contrast with many studies that show evidence of increased overall plant diversity and species richness in response to domestic and exotic herbivore grazing (Stahlheber and D'antonio, 2013, Jauni et al., 2015, Eldridge et al., 2018).

However, I posit that studies reporting increases in overall plant diversity may, in some instances, be unintentionally misleading. As demonstrated by my meta-analysis, increases in total plant richness or diversity may be driven primarily by an increase in the richness or abundance of

exotic plant species, despite no corresponding increase—or even a decline—in native plant diversity. The responses of exotic and native plants have been shown to differ significantly to: fire (Alba et al., 2015), soil disturbance (Mcintyre and Lavorel, 1994b), elevated nutrient levels (Driscoll, 2017) and temperature (Welshofer et al., 2018). It therefore makes sense that studies reporting only total plant responses risk obscuring ecologically significant differences between native and exotic plant communities.

This interpretation is further supported by the substantial gaps in the available literature identified during this review (Figures 7 and 8). Several moderator interactions contained insufficient data to estimate model parameters, reflecting a lack of empirical evidence rather than an absence of ecological effects. These knowledge gaps were particularly evident for the interaction between herbivore type and continent. The United States was the only continent with published studies examining changes in plant diversity in response to native herbivores, while most studies focused on the impacts of domestic herbivores. Consequently, my understanding of how native herbivore guilds influence plant diversity remains geographically biased and comparatively limited.

Domestic herbivores

The reduction of grassland biomass by grazing pressure is often a desired effect for land managers, due to an increase in agricultural productivity (Kemp and Michalk, 2007, Lemaire et al., 2023), and is sometimes used for restoration purposes (Guo, 2007). As demonstrated by the introduction of de-domesticated herbivores into the Oostvaardersplassen nature reserve the Netherlands, to prevent willow (*Salix cinereal*) encroachment (Lorimer and Driessen, 2014). A further example is the introduction of European bison (*Bison bonasus*), cattle (*Bos taurus*) and Exmoor ponies (*Equus ferus caballus*) onto abandoned xeric grasslands in the Czech Republic to reduce biomass and avoid further successional changes (Dvorský et al., 2022). However, reduction in biomass creates disturbance both through grazing and digging behaviours (Khalil et al., 2019), leading to temporary open space and reduction in plant competition (Green & Kauffman 1995), allowing for the colonisation of new species (White & Jentsch 2004). It would be expected that under the heavy or

novel grazing pressure exerted by over abundant exotic and domestic animals, that colonisation would occur by plant species that are grazing tolerant, or have qualities that make them invasive, particularly due to their ability to out-compete native species (Kulmatiski, 2006)(Coughenour 1985). The facilitation and reinforcement of exotic plant dominance, particularly in already disturbed ecosystems, may be a consequence of introduced herbivores, even when the aim is to increase diversity and ecosystem health (Hobbs, 1996)

Does herbivore nativeness matter?

Large-bodied mammalian species face a higher risk of extinction compared to small, bodied mammals (Hilton-Taylor, 2000, Duffy, 2003, Fisher and Owens, 2004, Cardillo et al., 2005), with 60% of the worlds large herbivores currently threatened, ecosystems are left with simplified herbivore assemblages and consequentially, missing trophic interactions and ecosystem functions (Ripple et al., 2015, Schowanek et al., 2021). In response, restoration initiatives to replace these missing ecological roles are growing in interest, with a particular focus on the use of introduced species as ecological replacements (Suding, 2011, Svenning et al., 2016, Gordon et al., 2021d, Atkinson et al., 2024, Jepson, 2025, Søndergaard et al., 2025).

Many studies support my findings that exotic and domestic herbivores elicited more variable plant responses and facilitate exotic invasion (Holmgren, 2002, Parker et al., 2006, Vavra et al., 2007, Young et al., 2013, Travers et al., 2018). However, to further evidence the lack of empirical knowledge on herbivore impacts on plant richness and diversity, I highlight the fact that some studies showed completely contradictory results (Boltovskoy et al., 2021). A paper by Schowanek et al. (2021) suggested that even with the return of all extant native herbivores to their previous ranges, most ecosystems would remain trophically downgraded and still require conservation intervention (Schowanek et al., 2021). This idea is supported by a meta-analysis by Lundgren et al. (2024), which found no evidence that herbivore nativeness changes the effects of megafauna (>45kg) on plants, but posited that herbivore functional traits, such as dietary selectivity, were more influential factors (Lundgren et al., 2024). While this is potentially the case in some instances,

functional traits are linked to evolutionary history, making it difficult to separate the two in some instances.

My results contradict their conclusions and instead suggest that in some instances, exotic and domestic herbivores promote novel community compositions, rather than restoring historical structure. I further suggest that the conclusions reached by Lundgren et al. (2024) failed to highlight one of their key findings, in which, introduced and native deer showed strong evidence of influencing a decrease in native plant diversity (Lundgren et al., 2024). Many traits are innately linked to ungulate herbivores, such as hard hooves, foregut rumination and incisor arrangement (Janis, 1979, Mckenzie, 1990), and on continents and islands where native ecosystems have no historical analogue for these traits, such as New Zealand, Australia, Madagascar and Hawai'i, it is difficult to separate trait effects and species nativeness (Cumming et al 2003, Leopold et.al 2017, Fraser et al. 2017, McGlone et al. 2014, Goodman et al. 2014, Forsyth et al. 2019).

Additionally, Lundgren et al. (2024) classified herbivores as co-evolved or native, if they would theoretically remain in a landscape without human-induced extinction. This position assumes that previously existing herbivores will act in the same manner as if they had never left. I posit that there is not enough data available to support this, as in herbivore absence, ecosystems, plant communities, and ecosystem processes have likely changed (Briggs et al., 2005, Bremm et al., 2016, Borer et al., 2017, Stewart et al., 2021). My concerns are shared by others (Caro, 2007, Nogués-Bravo et al., 2016), including studies that support unexpected outcomes and behaviours from a species' re-introduced into previously native ranges. Examples include the reintroduction of the eastern quoll (*Dasyurus viverrinus*) in Australia (Shippley et al., 2025), which included changes in niche utilisation and diet, and the tule elk (*Cervus elaphus nannodes*) re-introduction into California, with observed complex and unexpected positive and negative effects on both exotic and native plant communities (Johnson and Cushman, 2007, Bremm et al., 2016). Unlike the analysis by Lundgren et al. (2024), my study focused on grassland habitats only, and I additionally analysed

domestic herbivore impacts, both likely contributed to some of the contradictory results, but further highlights the knowledge gaps in the literature.

Missing empirical knowledge

The lack of empirical studies examining the effects of native, introduced, and domestic herbivores on plant diversity makes it exceedingly difficult to understand their impact of on grassland ecosystems. Currently, broad scale meta-analyses may not be the appropriate tool for ascertaining mammalian herbivore effects on richness and diversity, simply because there is not enough data to account for the variability between habitats, continents, species interactions, and behaviours in novel environments. More research is needed examining individual native and exotic plant responses to both native and exotic herbivores. Furthermore, there needs to be an increased focus on these responses on a global scale, because most studies looking at herbivore impact in grassland diversity and richness were conducted in the USA, where there is a long evolutionary history of large ungulate herbivores.

My meta-analysis highlighted the extreme variability in the direction and effect sizes of plant responses driven by exotic and domestic herbivores, leading to the notion that the changes in global grasslands are complex and impossible to predict with the current literature available. Furthermore, there is a dire need for more research on plant responses to novel herbivore/s guilds to fill the local knowledge gaps which are required to inform land manager and conservation policy decisions. With evidence suggesting that exotic and domestic herbivores have a high potential for reinforcing exotic plant invasion, I advocate for land managers to reassess the desired outcomes of herbivore grazing when used as a conservation or restoration tool and to consider the potential long-term consequences.

Conclusion

Key findings

My meta-analyses suggest that herbivore identity and, in many cases, herbivore nativeness, does matter for plant diversity. This was evidenced by the herbivore assemblage comprised of cattle and sheep, whereby depending the study location, I saw both significant positive effects and significant negative effects on plant diversity. Evidence is suggestive of domestic and exotic herbivores exerting stronger effects on plant diversity than native herbivores. Furthermore, responses differed depending on plant nativeness, highlighting the importance of distinguishing native and exotic plant response, rather than solely reporting on total plant diversity

Grazing exclosures

Grazing exclosure experiments remain one of the most powerful approaches for isolating ecological effects of herbivory on plant communities. By comparing grazed and ungrazed plant responses, they provide direct evidence for how herbivores influence diversity. The continued use of well-designed exclosure experiments will be essential for the management of grassland, particularly in the context of exotic plant species management and climate change.

Major knowledge gaps

The distribution of Studies reporting the impacts of large herbivores on plant diversity remains geographically biased, with a considerable proportion of all studies analysed coming from the USA. Furthermore, native herbivores were poorly represented in the literature compared to domestic herbivores and many of the moderator combinations lacked sufficient data for robust inferences to be made.

Temperate grasslands

Temperate grasslands represent the habitats most heavily influenced by domestic grazing worldwide. Despite this, few studies have investigated how diverse herbivore guilds shape temperate grassland communities. Because these ecosystems are extensively modified by large domestic herbivores, understanding whether different herbivore assemblages may produce different

ecological outcomes will be critical for conservation and restoration of grassland ecosystems, particularly in the context of climate change and increasing anthropogenic influences.

Australian Context

Australia represents a particularly interesting case study of contemporary herbivore guilds due to its the long evolutionary separation. Consequently, Australia has no history of large-bodied ungulates therefore there are very few extant herbivore analogues capable of restoring ecological roles once performed by extinct megafauna. Contemporary large herbivore guilds now consist of native marsupials, introduced livestock and exotic ungulates and therefore provides an opportunity to examine how novel herbivore assemblages influence ecosystems that evolved without large placental herbivores.

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Chapter 2

Dietary overlap among native and exotic herbivores in a temperate grassland ecosystem

Introduction

Large Herbivores (considered >45 kg) are key drivers of plant community structure and ecosystem functions (Peters, 1986, Huntly, 1991, Suzuki et al., 2013, Gordon and Prins, 2019). Through selective foraging, they influence species composition (Coverdale et al., 2024), ecosystem productivity and nutrient cycling (Dubeux Jr et al., 2007, Frank et al., 2018). In temperate grasslands, there are three major overlapping factors that function as dominant ecological processes shaping biodiversity: herbivore identity, grazing intensity, and vegetation type (Török et al., 2018, Török et al., 2024). Herbivore diet comprises all three of these processes to some degree and therefore, represents important knowledge for biodiversity conservation. Their diets are shaped by many factors, firstly by environmental factors such as resource availability, plant nutritional quality and plant defence traits (Iason and Villalba, 2006, Potter et al., 2022). Secondly by morphological factors including herbivore body size (Pineda-Munoz et al., 2016), diet strategy (whether a grazer or browser) (Hofmann and Stewart, 1972), and digestive system (ruminant or hind-gut fermenter) (Hume, 1989, Illius and Gordon, 1993). Lastly herbivore diet can be shaped by optimal foraging theory (Macarthur and Pianka, 1966, Emlen, 1968) which posits that animals must balance the energy gained from eating, with associated energy costs such as search time and competition. Therefore, diet choice is non-random and is reflective of the biological and environmental constraints present.

Guilds are made up of multiple species that provide similar ecosystem functions and there are several ways in which they manage to co-exist within the same environment. The theory of niche partitioning surmises a process by which multiple species can coexist within an ecosystem by utilizing different resources (Grinnell, 1917, Hutchinson, 1953, Vandermeer, 1972). For mammalian herbivores, partitioning can occur across different plant taxa (Pansu et al., 2022), the consumption of different plant parts (Mata et al., 2024) and the use of different spatial or temporal scales. This has been recorded in an African guild, where the plains zebra (*Equus quagga*), buffalo (*Syncers caffer*), and sable antelope (*Hippotragus niger*) all rely on savannah tall grass, yet through

utilization of different areas, they mostly evade range overlap, reducing competition pressure (Macandza et al., 2012). However, it has been shown in some predator and generalist guilds that high dietary overlap can occur when shared resources are in abundance (Gordon and Illius, 1989, Zurdo et al., 2023). As evidenced by the white-footed mouse (*Peromyscus leucopus noveboracensis)* and woodland deer mouse (*Peromyscus maniculatus gracilis*), both generalists with large diet breadths. Though, in times of beech masting, a synchronised, massive seeding event by beech trees occurring every two- six years, both species become specialists, resulting in high dietary overlap (Stephens et al., 2019).

Resource partitioning among species within a guild can also be understood in the context of optimal foraging theory, which predicts how individuals maximise resources under given constraints. The theory posits that species must select food and resources that maximise the energy intake, while minimising the costs associated with searching for resources, predator vigilance, and the processing of food (Macarthur and Pianka, 1966, Schoener, 1974, Pyke et al., 1977). However, species are strongly influenced by multiple traits and environmental factors. Differences in gut morphology – such as ruminant or hindgut fermenters - plays a vital role in a herbivores ability to process different plant materials and cope with chemical defences, strongly influencing diet choice. This is demonstrated through the diet preference of beavers (*Castor canadensis*), where forage choice was selected based on digestibility and shorter gut-retention times rather than solely choosing based on nutrition (Doucet and Fryxell, 1993). Research also suggests that body size drives diet choice (Belovsky, 1986), with many large herbivores having long gut-retention times, allowing them to tolerate low quality food and therefore leading to a quantity of quality strategy (Illius and Gordon, 1990).

Native herbivores have co-evolved with locally native plant communities, which may result in the development of traits that are adapted to particular plant taxa (Garrido et al., 2012), and the local variation that occurs with seasonal resource availability (Abraham et al., 2022). Conversely, exotic herbivores have an evolutionary history that is separated from the local flora, which may

allow them to exploit naïve plant communities (O'reilly-Wapstra et al., 2002, Sakata and Craig, 2021). The competitive advantage of exotic herbivores in a novel environment can have major detrimental effects on ecosystems. Examples include: the role of domestic cattle in creating a shift in habitat type from forest to open savannah in central Chile (Holmgren, 2002), livestock and rabbits strongly reducing native species richness in South-eastern Australia (Travers et al., 2018), the ecosystem homogenisation of plant and animal communities by black-tailed deer (*Odocoileus hemionus*) on the Canadian islands of Haida Gwaii (Martin et al., 2010), and the reinforcement of exotic plant dominance in a forest ecosystem by back-tailed deer (*Odocoileus hemionus colombianus*) and Roosevelt elk (*Cervus canadensis rossevelti*) (Stokely et al., 2020). Despite these potential impacts, most grassland ecosystems now contain novel herbivore assemblages, made up of both native, exotic, and domestic grazing animals. These shifts in herbivore assemblages have been shown to disrupt historical niche partitioning (Arumoogum et al., 2023) with the expectation that competition between herbivore species would increase (Wegge et al., 2006). This is best illustrated by the Rocky mountain elk (*Cervus elaphus nelsoni*), where they were shown to utilise different spatial elevations in avoidance of domestic cattle to maintain resource partitioning structure (Stewart et al., 2002).

Temperate grasslands are considered the most altered and endangered terrestrial ecosystem on earth (Henwood, 2010), yet they are incredibly important as they support a high biodiversity of plant and animals (Carbutt et al., 2017). Australian temperate grassland range and ecological communities have been most heavily affected by the introduction of both domestic herbivore grazers and subsequent release of feral exotic ungulates over the past 150-years (Prober and Thiele, 2005). Further, the severe fragmentation and exotic plant invasions of these critical ecosystems caused by anthropogenic impacts, have been exacerbated by the fact that all eastern Australian grasslands now support a mixed guild.

Despite their importance and potential impacts on ecosystems, there are limited studies looking at the diet overlap across a novel herbivore guild in temperate grassland systems (Dawson

and Ellis, 1994, Davis et al., 2008), and none, to my knowledge, using high resolution methods such as meta-barcoding. It is unclear as to whether exotic herbivores occupy a distinct niche from natives, and how this relates to invasion dynamics and overall ecosystem function. Traditional methods, such as microhistology, used to conduct diet analysis require the visual identification of plant material. This method is effective at detecting abundant prey species and determining abundances, but less likely to identify rare items and likely to produce high incidences of false negative and positive identifications (Holechek et al., 1982), in comparison to genetic methods. However, it is important to note that like all methods, there are caveats with genetic techniques around the interpretation of raw read counts. The most conservative approach to taxa detection using diet data is to use presence-absence data, which is extremely reliable (Valentini et al., 2009). However, the use of presence-absence data as an indicator for biomass consumed is less reliable since equal weighting is given to both rare and common taxa (Deagle et al., 2019), with the complementarity of both approaches recommended.

The aim of this study was to quantify and compare the diets of a novel large herbivore guild comprised of two herbivore groups, native and exotics (one feral and one domestic), using an Australian temperate grassland habitat as a case study. The main objectives of the study were to: (1) asses the degree of dietary overlap and partitioning between the herbivore species, (2) determine any seasonal differences in the species richness and diet of the herbivore species, and (3) test whether exotic herbivores were more likely to consume native plants. To address these objectives, I conducted a diet analysis study on 883 faecal samples, collected from six herbivore species over a 12-month period. The results from my study may reveal critical knowledge of the outcomes of shifting herbivore guilds and the degree to which herbivore identify influences resource use and potential competition in a temperate grassland ecosystem.

Methods

Site and study species

The study took place in the Ginninderry Conservation Corridor (GCC) in the Australian Capital Territory (ACT), Australia (35°13’54.8” S, 148°58’35.7” E, Figure 1 (Ginninderry Conservation Trust et al., 2018)). This 580-ha site had a mean elevation of 570m and is bordered by the Murrumbidgee River on one side and urban development on the other (Figure 1). Historically, much of the GCC was used as pasture, but is now comprised of a mosaic of different habitat types, including riparian woodland, open grasslands, woodlands, pasture grass, and remnant patches of critically endangered box-gum grassy woodland (Figure 2). Dominant native herbivore species across the site are all marsupials and include the eastern grey kangaroo (*Macropus giganteus*), common wallaroo (*Osphranter robustus*), red-necked wallaby (*Notamacropus rufogriseus*), swamp wallaby (*Wallabia bicolor*), and the common wombat (*Vombatus ursinus*), with annual macropod counts averaging at 162 animals. Domestic cattle (*Bos taurus*) herds of 40-80 individuals are rotated across the site throughout the year as a vegetation biomass control measure, and a population of feral fallow (*Dama dama*), and to a lesser extent sambar (*Rusa unicolor*) deer, exist in large numbers throughout the surrounding Namadgi National Park (Mulvaney et al., 2017, Kennedy,

2025), with significant mobs (herds) regularly using or passing through the GCC.

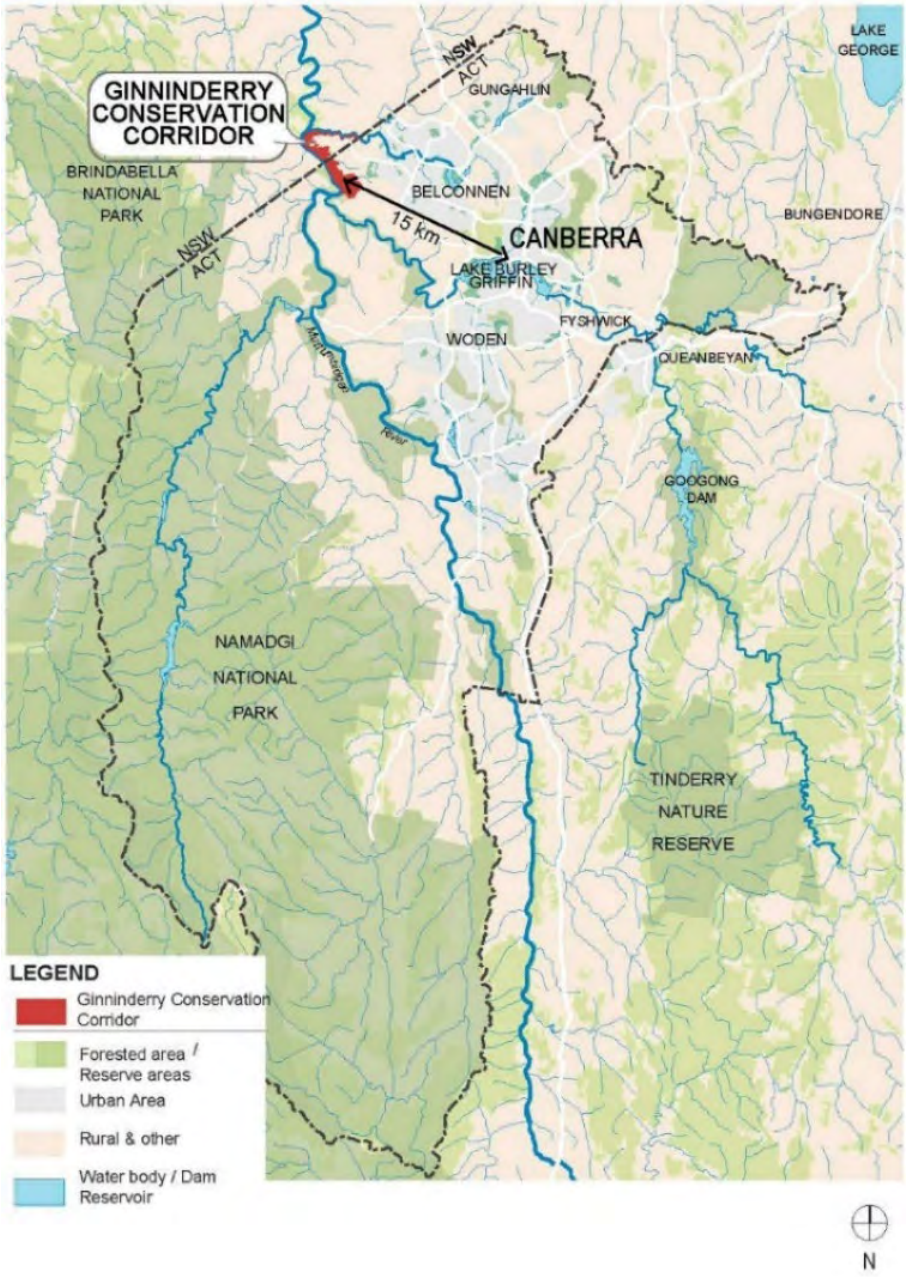


Figure 1. ***Ginninderry Conservation Corridor in the Australian Capital Territory, Australia -*** *(35°13’54.8” S, 148°58’35.7” E) in relation to the ACT (top left) and Australia (top middle). Image*

adapted from Ginninderry Conservation Trust et al. (2018).

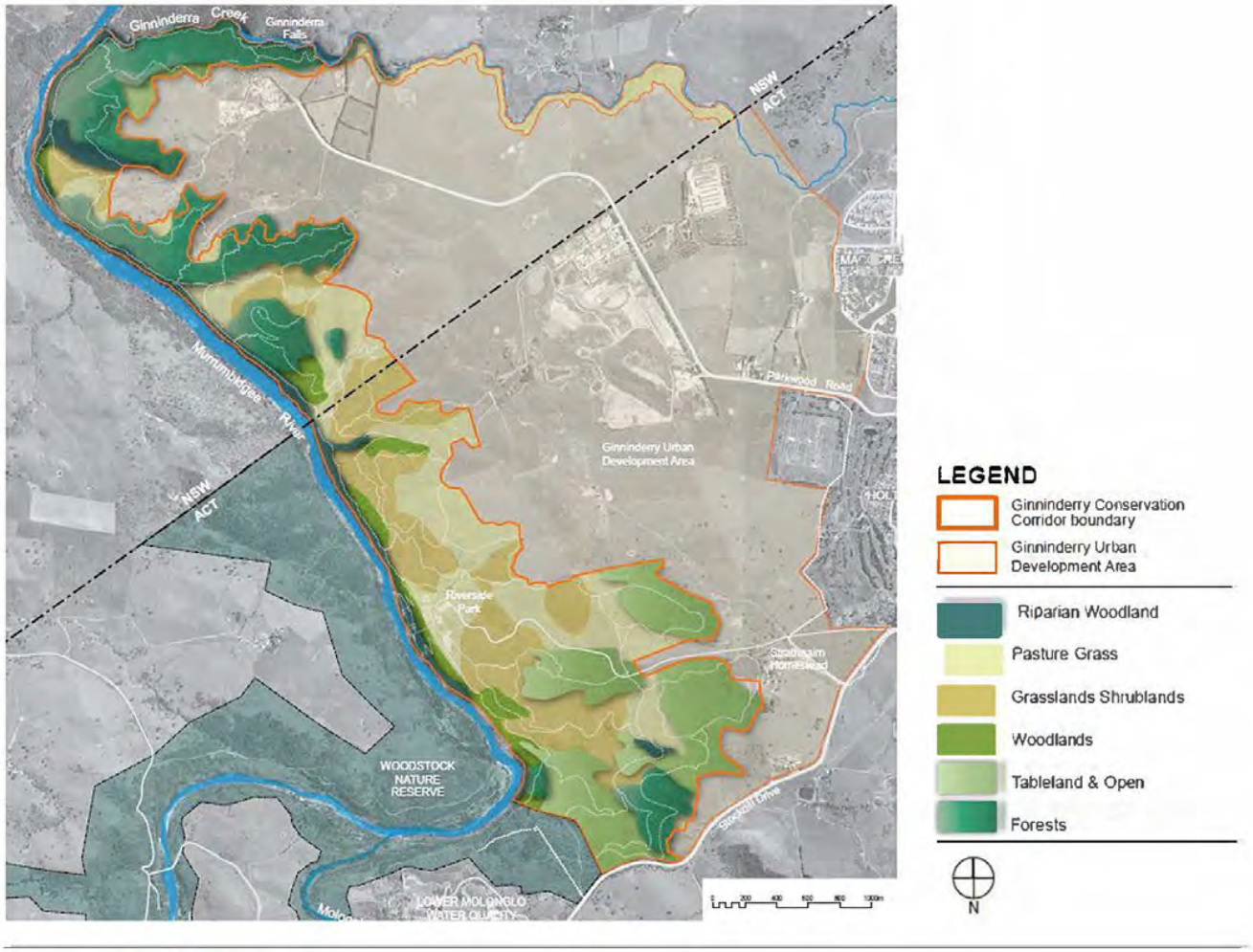


Figure 2. ***Ginninderry Conservation Corridor in the Australian capital Territory, Australia*** *- (35°13'54.8" S, 148°58'35.7" E) with habitat types and borderlines based in a 2015 vegetation survey. Image adapted from Ginninderry Conservation Trust et al. (2018).*

Study design

Sample collection

I divided the entire GCC area into ten zones for the purpose of random sampling. I covered as much of the zone by foot as possible and collected all fresh (glossy and wet) faecal samples of the target species. Samples were given a unique code, and a Global positioning system (GPS) position was recorded. All faecal samples within 10 cm were collected and treated as a single sample. To ensure the samples were fresh, no collection was performed during or within 24 hours after a rain event.

Each location was visited twice per season between October 2022 and July 2024 (Spring; 18 October - 17 November, Summer; 22 January –16 February, Autumn; 10 – 24 May, Winter; 4 – 22 September ’23 & 25 June – 16 July ‘24). An additional sampling period was added for winter because I could not find enough samples in the first sampling period. All efforts were made to identify the species of origin for faecal samples in the field, which was achievable for all cattle and wombat samples. Macropods were identified to species at the time of collection if a mob was visually present at the time (mixed mobs were not observed). For all macropod and deer samples, where species could not be obtained in the field, identification of the source herbivore species was attempted using DNA analysis. All samples were stored in silica and stored in ambient temperatures to dry out. Silica was changed regularly to ensure optimal conditions for samples to dry without compromising the DNA quality.

DNA barcoding

Sample homogenization

I subsampled a total of 883 samples by placing all the faecal material available, excluding the outer-surface, into 15ml TeenPrep Lysing Matrix E and homogenized using a FastPrep-24™ 5G (MP Biomedicals, USA). Homogenized samples were then sub-sampled into a 2ml tube, with weights ranging between 0.5 – 1.5g.

DNA extraction

The modified TNES Buffer used for this process was prepared in my laboratory under optimum conditions. DNA was extracted using a modified version of Sunnucks and Hales (1996) and purified using Sera-Mag™ SpeedBeads (Cytiva, USA). Extraction blanks were included for every DNA extraction batch.

PCR Amplification

I amplified a 150 bp region between the *trnT* (UGU) and *trnF* (GAA) *trn*L chloroplast RNA genes using the trnL_c (CGAAATCGGTAGACGCTACG) and trnL_h (GGGGATAGAGGGACTTGAAC) primers (Taberlet et al., 1991). I performed all polymerase

chain reactions (PCR) in a 12.5µl reaction, using Q5 High-Fidelity 2X Mastermix (New England BioLabs, USA). The PCR reaction conditions were denaturation at 95°C for 5 minutes, followed by 35 cycles of 94°C denaturation for 30s, annealing at 50°C for 30 seconds, extension at 72°c for 60 seconds and a final extension at 72°c for 8 minutes. I used a second round of amplification to attach sample specific combinations of NEBNext Multiplex Oligos for Illumina i5, i7 indexes (New England BioLabs, USA). Amplicons were then purified using Sera-Mag™ SpeedBeads (Cytiva, USA). Indexing PCR amplicons were pooled in equimolar concentrations. I performed paired end 150bp sequencing on a NovaSeq X 10B at the Biomedical Resource Facility, Australian National University.

Data filtering and bioinformatics

I assessed the quality of all raw sequence data using 'FastQC' (Andrews, 2010) and trimmed adapter and primer sequences using 'cutadapt' (Martin, 2011). I deduplicated reads, checked for errors, merged the forward and reverse reads and combined samples into unique Amplification Sequence Variants (ASV) using the *dada2* pipeline in R Studio (Fu et al., 2012, Rstudio, 2023). The resulting ASVs were then matched to a local reference database for the study region, which contained sequences for all plant families and as many genera and species as possible, using the 'assignTaxonomy' function in *dada2*. The reference database was based on previous plant surveys for the region, and was comprised of 34 exotic, and 47 native plant species. Where matches were identified in negative controls, I removed the corresponding read counts from all potentially effected samples (Drake et al., 2022). To further negate the potential for false positives, I removed any read counts from the main data that had less than ten read counts (Drake et al., 2022). In total, I deleted 2929 sequences (likely chimeras) that did not match to any plant in my database or gene bank, and 20 PCR replicates with zero read counts after filtering.

Herbivore Species Identification

Using the same macropod and deer DNA products as previously extracted, I added a column clean-up using the DNeasy® PowerClean® Clean-up Kit (Qiagen, USA) to further remove inhibitors.

Species specific primers were designed to differentiate macropod and deer species, targeting the cytochrome *b* (*cytb*) mitochondrial gene (1146 bp). For macropods I targeted: a 250 bp section for eastern grey kangaroos, a 150 bp section for wallaroos, a 450 bp section for swamp wallaby, and a 220 bp section for red-necked wallaby. For the deer: I targeted a 161bp section for sambar deer and a 197bp section for fallow deer (Appendix iii; Table 2). I performed all PCRs in a 20µl reaction using Platinum™ Direct PCR Universal Mastermix (Invitrogen™, USA). I performed PCR cycling according to Koehler et al. (2020b), modified to an extension temperature of 68°C. Some problematic samples were applied up to 45 cycles. The amplicons were visualised on 2% agarose gels stained with SYBR Safe (Invitrogen™, USA), using TAE as the buffer and using 50bp DNA ladder (Invitrogen™, USA).

Statistical analyses

Statistical models

Diet read counts were converted to presence-absence data and analysed using generalised mixed-effects models (GLMMS). Due to the nature of count data exhibiting overdispersion, models were fitted using a negative binomial error distribution with a log link function (Zuur et al. 2012) rather than a Poisson distribution. The models included herbivore species, plant nativeness, and season, and their two-way interactions were included as fixed effects.

Sample identity was included as a random effect which accounted for any variation among individual faecal samples.

Model diagnostics were assessed using simulated residuals generated with the DHARMa package (Dormann, 2020). Analysis of variance (ANOVA) were performed on all fitted models, and statistical significance was assessed using TYPE II Wald chi-square tests. Estimated marginal means were calculated using the emmeans package (Searle et al., 1980, Lenth, 2025) and used to visualise model predictions in RStudio (Rstudio, 2023).

Species richness

Species richness was calculated from presence-absence data and analysed using a generalised mixed-effects model (GLMM). Due to the nature of count data exhibiting overdispersion, models were fitted using a negative binomial error distribution with a log link function (Zuur et al. 2012) rather than a Poisson distribution. The model included herbivore species, plant nativeness, and season were included as was the two-way interaction between herbivore and plant nativeness, as fixed effects. Sample identity was included as a random effect which accounted for any variation among individual faecal samples. Statistical inference was based on the negative binomial model, with p-values derived from the model outputs. Graphical representations show observed data, rather than model-predicted values.

Relative Read abundance and Frequency of occurrence

The relative read abundance (RRA) was calculated as the proportion of sequence reads assigned to each plant taxon, relative to the total number of reads per sample. RRA is not a direct measure of biomass consumed, but when used cautiously, it is a useful tool in understanding diet composition and dietary overlap that cannot be gained from presence absence data alone (Deagle et al., 2019). Due to many genera detected, the 50 most abundant were used for descriptive analysis and the remaining genera were grouped into the category ‘other’. Frequency of occurrence was calculated using presence absence data to determine how frequently invasive or problematic native plants occur in the diet.

Niche breadth and dietary overlap

Both indices were calculated using relative read abundance (RRA) data derived from metabarcoding, under the assumption that RRA provides a proxy for relative dietary contribution. All calculations were performed at the genus level.

Niche breadth was quantified for each herbivore across seasons to asses seasonal variation, using Levin’s index (Levins, 1968), calculated as:

$$B = \frac{1}{\sum Pi^2}$$

Where *Pi* represents the relative read abundance (RRA) of plant taxon (*i)* within each herbivore species. Higher values of B indicate broader diets, while lower values indicate greater specialisation.

Dietary overlap was calculated using Schoener's index (Schoener, 1974):

$$D = 1 - \frac{1}{2}\sum | pi - qi |$$

Where *pi* and *qi* represent the relative read abundances (RRA) of plant taxon *i* by two different herbivore species. Schoener's index values range from 0 (no overlap) to 1 (total overlap).

Results

Sequence data

I obtained 718,633,268 raw sequence reads after demultiplexing and filtering; 98.4% of those reads were from sample PCR products and 1.6% were from negative controls. Any ASVs with read counts less than 10 were removed. A total of 703,254,349 reads were assigned to plant taxa and read counts ranged from 10 to 5,166,931, with a mean of 5622 reads. The final plant species table consisted of 187 unique plants (Appendix B; Table 1). I endeavoured to identify plants to the highest taxonomic resolution possible; I successfully identified all plants to family level. In total I assigned 56 plant families (for 26 plants, this was the lowest taxonomic resolution possible), which comprised of 118 genera and 102 species. Of the native plant, one was a considered problematic native plant, according to the New South Wales (NSW) Government (2018) Land Management Code and of the exotic plants, nine were considered invasive pest species according to the Australian biosecurity ACT (Orr, 2025).

Herbivore species identification

A total of 148 unknown deer samples, and 285 unknown macropod samples were collected. I was able to successfully identify 95 macropod samples, 21 as eastern grey kangaroo, and 74 as common

wallaroo, and 71 deer samples, all as fallow deer. Despite best efforts and the amplification of positive controls, I found no positive matches to either red-necked wallaby, swamp wallaby, or sambar deer, despite the primers successfully amplifying positive controls. Both native macropod species exist in small, isolated patches across the study site, making it possible that some of my unidentified macropod samples comprise of these species. Therefore, I treated these 188 samples as unknown macropod species. Although I didn't observe any, it is possible that some of the unknown deer samples comprise of sambar deer, because of their similar use of the landscape and same gut morphology, I categorised all samples as having originated from one of the two species and referred to them simply as deer. A total of 161 cattle, and 75 wombat faecal samples were collected and visually identified at the time of collection.

Relative read abundance and frequency of occurrence

Relative read abundance (RRA) was generated using plant genera but included family in the instances where genera were unknown (Figure 3). Of the 187 plant IDS included in the RRA, 118 were unique genera and 19 were family level classification. The 30 most abundant plants were plotted, and all remaining plants were merged into "other" (for a full list of plants, see appendix B; Table 1). The most common genera were the same across all herbivores; however, the composition varied between herbivores and across seasons. Of the genera presented in Figure 3, nine were classified as invasive species and one as a problematic native, with the frequency of occurrence of this subset of invasive and problematic taxa presented in Figure 4. There was minor variation in the occurrence of invasive plant species between herbivores.

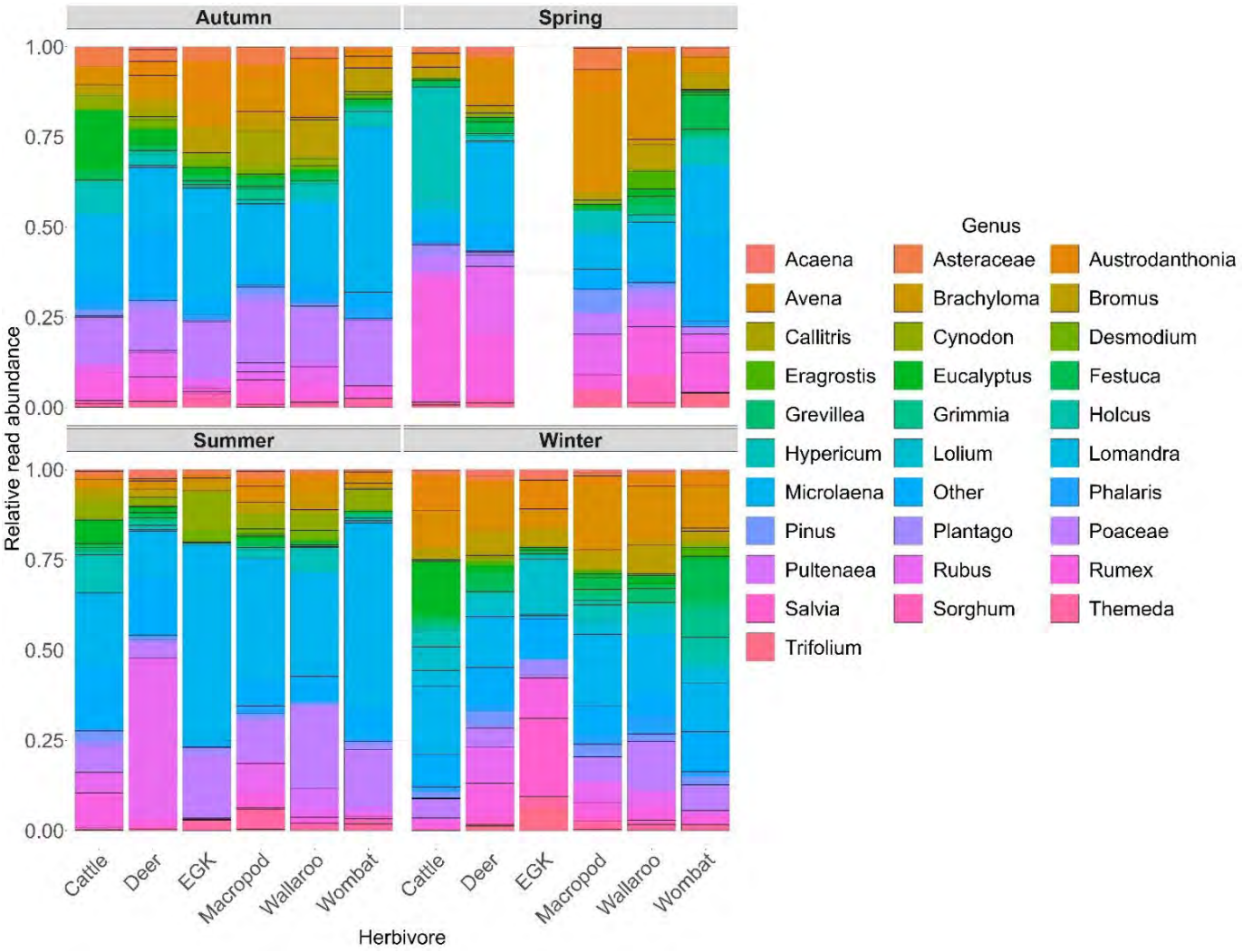


Figure 4. ***The relative read abundance (RRA) of the 30 most abundant genera (the remaining 40 grouped into 'other' category) present in the diet of herbivores.*** *Herbivore faecal samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between October 2022 and July 2024; exotic herbivores n = 309; (cattle n = 161 and deer n = 148) and native herbivores n = 360; (eastern grey kangaroo n=21, unknown macropod species n = 190, common wallaroo n = 74, and the common wombat n = 75). There were no samples for eastern grey kangaroo in spring.*

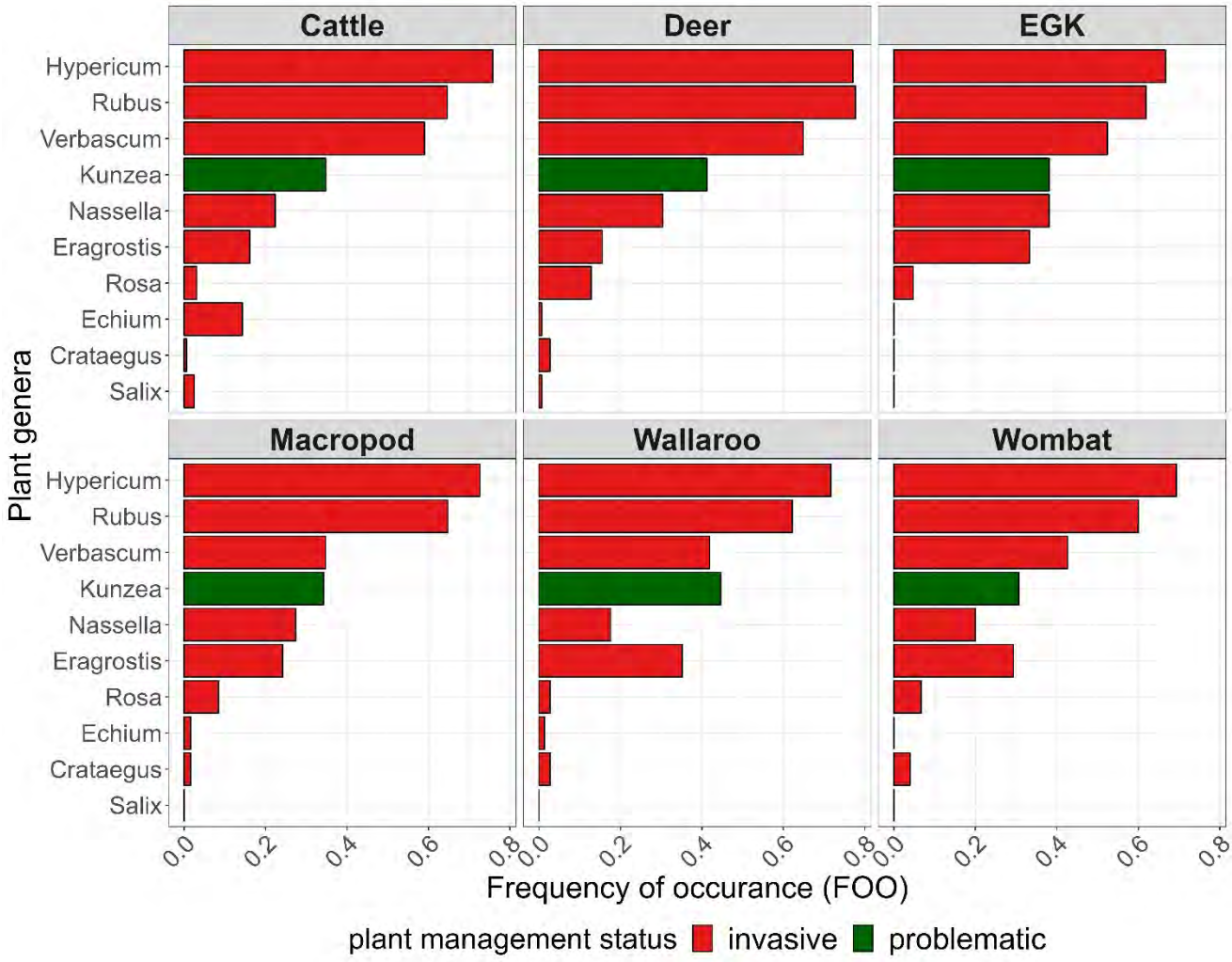


Figure 5. ***The frequency of occurrence (foo) of genera within each nativeness category (native, exotic, unknown) that are classified as invasive or problematic.*** *Herbivore faecal samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between October 2022 and July 2024; exotic herbivores n = 309; (cattle n = 161 and deer n = 148) and native herbivores n = 360; (eastern grey kangaroo n=21, unknown macropod species n = 190, common wallaroo n = 74, and the common wombat n = 75).*

Dietary overlap

The Levin's niche Breadth (B) was similar between all herbivores, cattle showed the most generalist diet with a B of 13.17, and eastern grey kangaroo had the most specialist diet with a B of 8.72. The niche breadth was highly affected by season; all herbivores exhibited a broader diet breadth in autumn and winter and a far more specialised diet in spring and summer (Figure 6). Schoener's

index showed that all herbivores shared a moderate degree of dietary overlap (Figure 7). The herbivores with the least amount of overlap in their diet were eastern grey kangaroo and cattle (0.497) and eastern grey kangaroo and deer (0.532), with the greatest degree of dietary overlap seen between wallaroo and macropod (0.816), wombat and wallaroo (0.763), and macropod and deer (0.713).

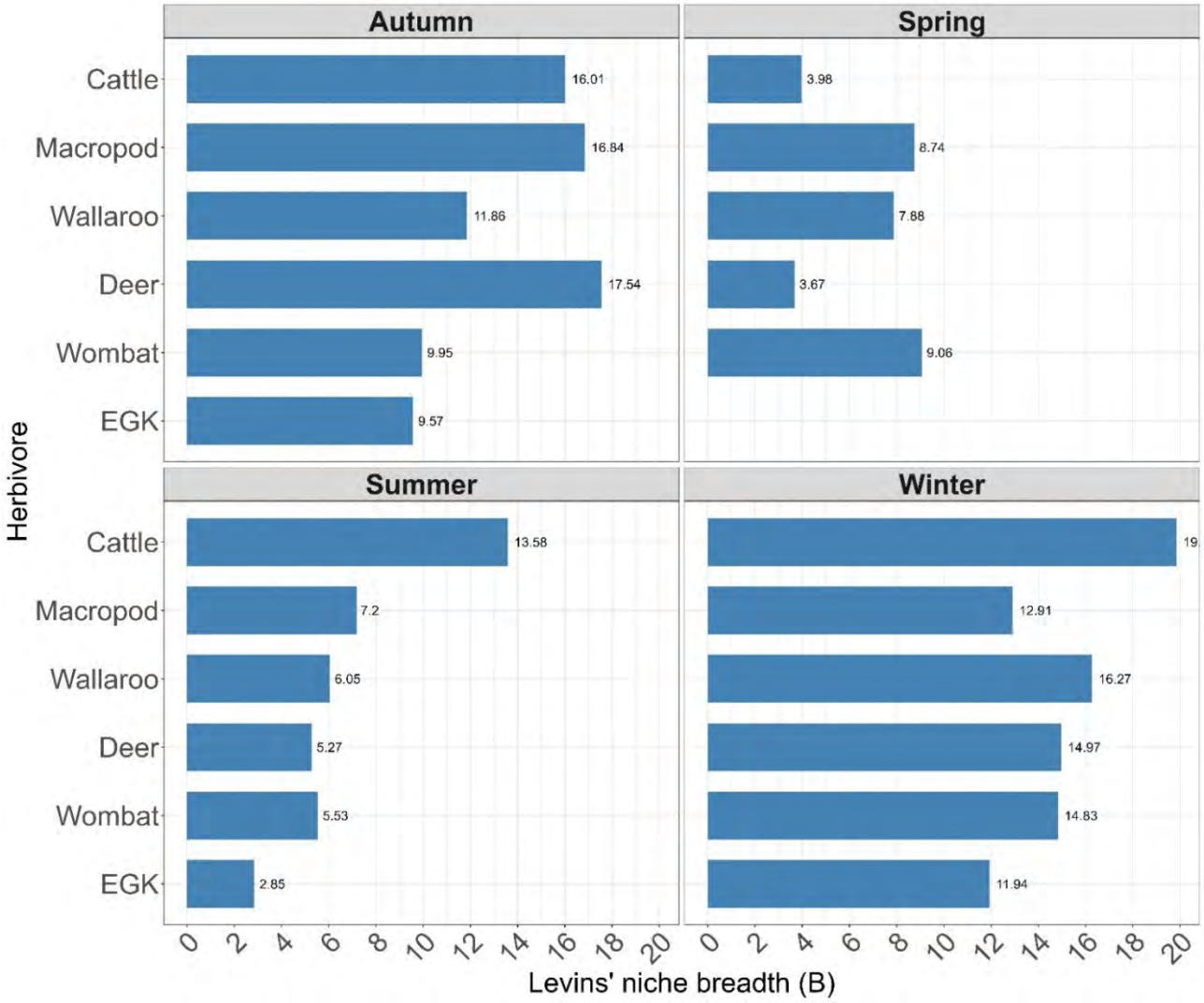


Figure 6. ***Levin's niche breadth (B) based on the diet of herbivores.*** *Smaller Levin's niche breadth (B) signifies a more specialist diet, and larger B signifies a more generalist diet. Herbivore faecal samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between October 2022 and July 2024; exotic herbivores n = 309; (cattle n = 161 and deer n = 148)*

and native herbivores n = 360; (eastern grey kangaroo n=21, unknown macropod species n = 190, common wallaroo n = 74, and the common wombat n = 75).

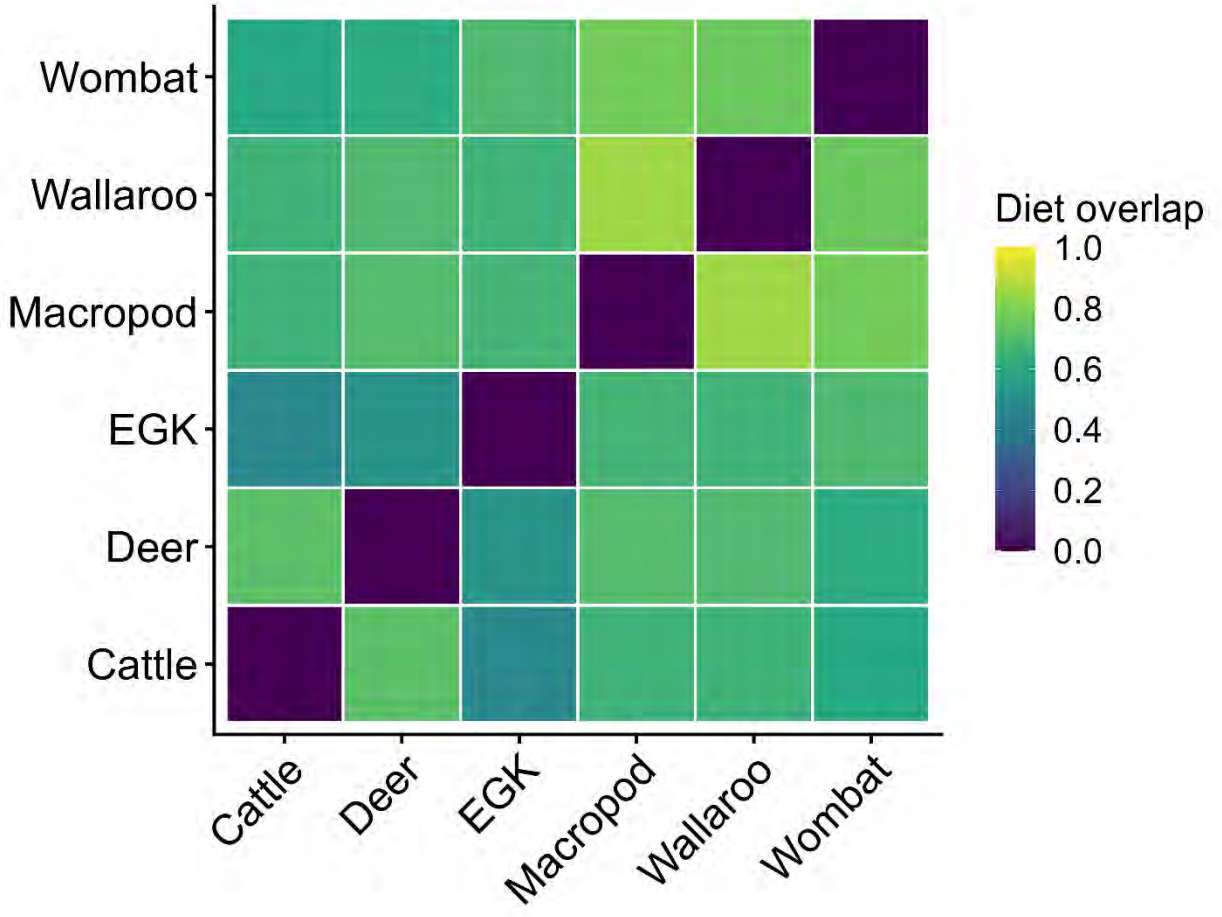


Figure 9. ***Dietary overlap of herbivores based on Schoener's index based on the diet of herbivores.*** *A darker square (1.00) signifies a complete dietary overlap, the lighter the shade of purple, the lesser the dietary overlap. Herbivore faecal samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between October 2022 and July 2024; exotic herbivores n = 309; (cattle n = 161 and deer n = 148) and native herbivores n = 360; (eastern grey kangaroo n=21, unknown macropod species n = 190, common wallaroo n = 74, and the common wombat n = 75).*

Plant Species richness

The plant species richness was analysed using genera level taxonomic assignment. Species richness showed slight seasonal differences, but type II Wald chi-square tests showed no significant differences between the species richness of herbivores, plant nativeness, season, or their two-way interaction (Figure 8). Species richness of native plants was highest for all herbivores in summer, autumn, and winter, but spring species richness was more variable in the composition of plant nativeness across herbivores. The highest species richness was in winter with both unknown macropod and deer each consuming over 50 different native plant genera.

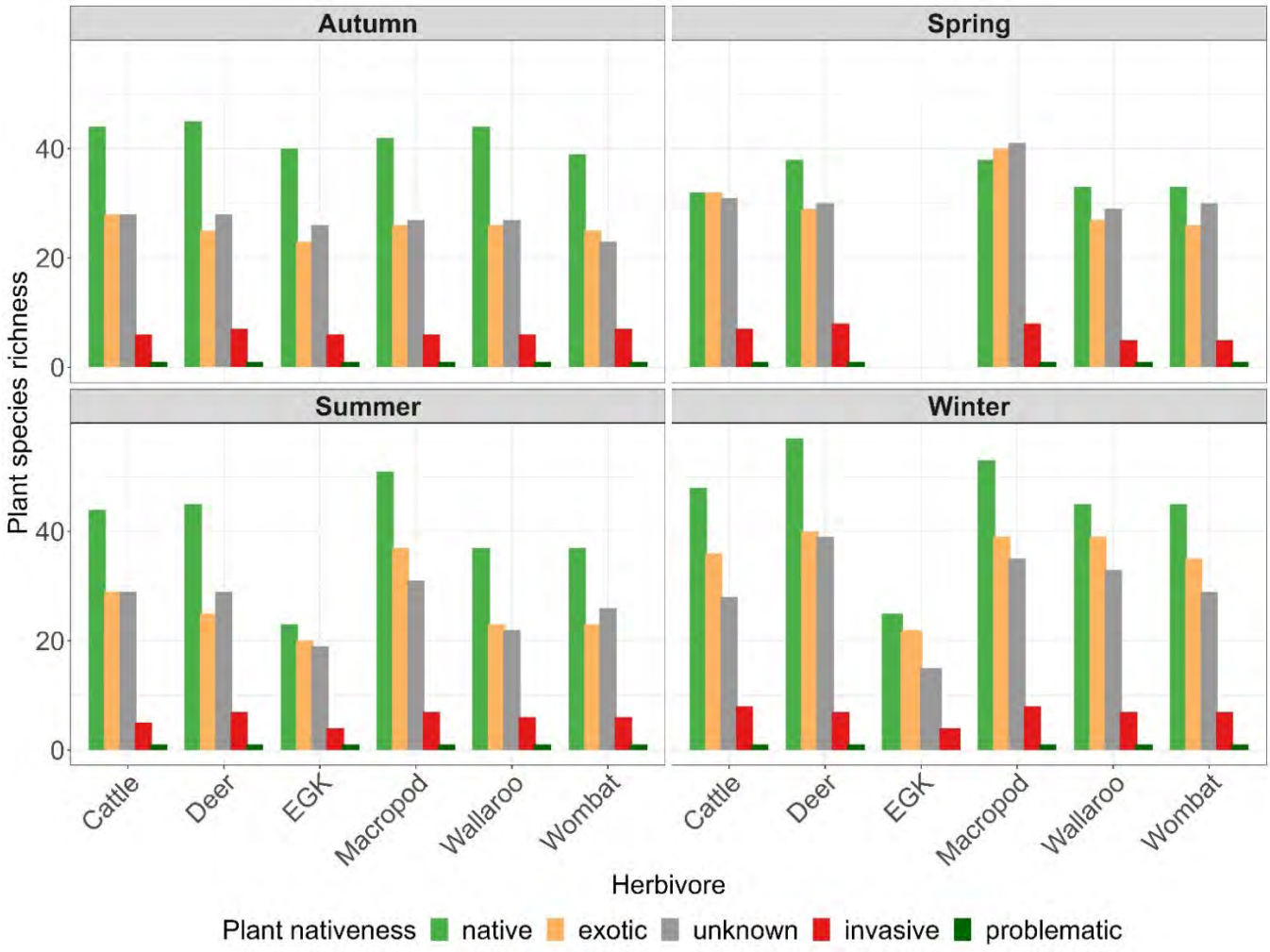


Figure 8. ***Plant species richness based on the seasonal diet of herbivores, using genus instead of species****. Herbivore faecal samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between October 2022 and July 2024; exotic herbivores n = 309; (cattle n = 161 and deer n = 148) and native herbivores n = 360; (eastern grey kangaroo n=21,*

unknown macropod species n = 190, common wallaroo n = 74, and the common wombat n = 75). Plant nativeness pertains to the origin of the plant species (native or exotic) and whether it is classified as invasive or a problematic native, unknown nativeness is due to a taxonomic resolution of family level comprising of genera that could fall into either category.

Model outputs

Binomial models showed the predicted probability of plant nativeness was not different between herbivores, but was significantly different by season, nativeness and their two-way interaction (all $p = < 0.005$), with spring samples predicted to be the most different ($p = < 0.0005$) (Figure 9). The model showed that deer, cattle, and macropod all had a greater likelihood of having exotic plant species in their diets rather than native or unknown species (all $p = < 0.05$). Of the predicted probabilities depicted in Figure 9, I also modelled the probability of plants within each nativeness category (native, exotic, unknown) that were also classified as invasive or problematic (Figure 10). Model outputs showed that plant management status (invasive or problematic native) and season were significantly different (all $p = < 0.0005$), with the greatest seasonal differences having occurred in spring and summer. The paired interaction between plant management status and herbivore species showed no significant difference. Problematic native species showed a higher rate of predicted probability than invasive species for all herbivores across all seasons.

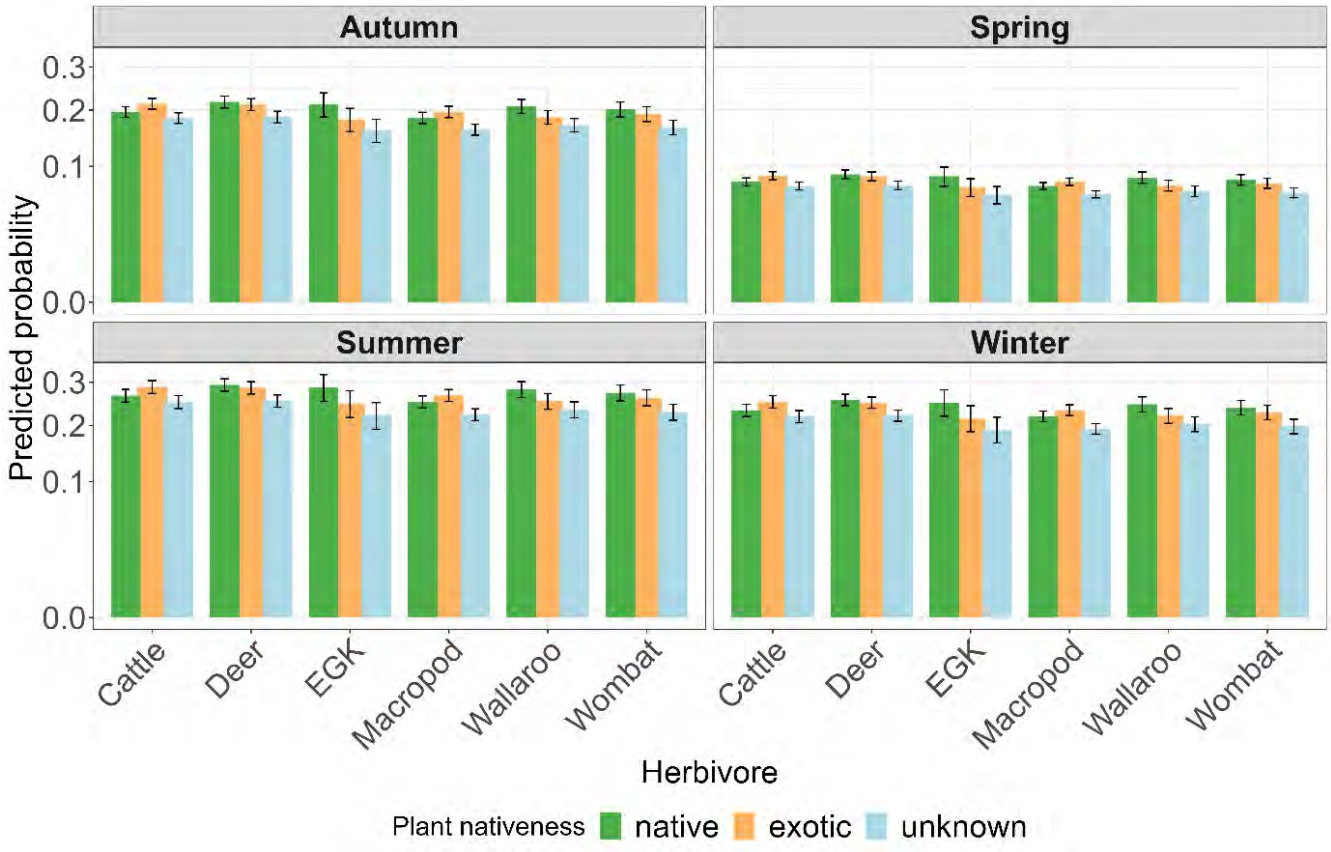


Figure 9. ***Predicted probability of plant nativeness in the diet of herbivores.*** *Graph depicting the predicted probability of an herbivore consuming a plant of native, exotic, or unknown nativeness. Herbivore faecal samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between October 2022 and July 2024; exotic herbivores n = 309; (cattle n = 161 and deer n = 148) and native herbivores n = 360; (eastern grey kangaroo n=21, unknown macropod species n = 190, common wallaroo n = 74, and the common wombat n = 75). Plant nativeness pertains to the origin of the plant species (native or exotic) and whether it is classified as invasive or a problematic native, unknown nativeness is due to a taxonomic resolution of family level comprising of genera that could fall into either category.*

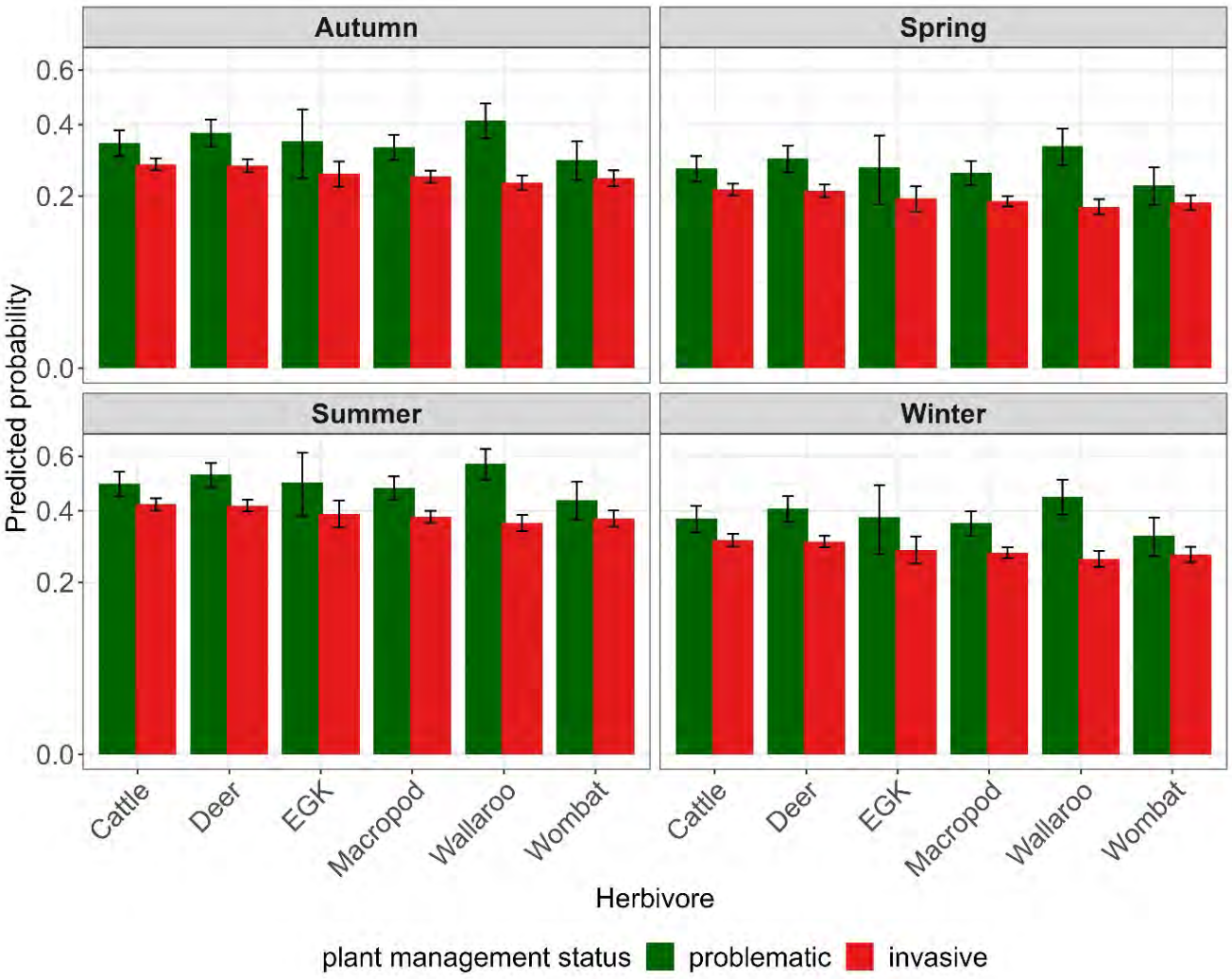


Figure 10. ***Predicted probability of plants within each nativeness category (native, exotic, unknown) that are classified as invasive or problematic.*** *Herbivore faecal samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between October 2022 and July 2024; exotic herbivores n = 309; (cattle n = 161 and deer n = 148) and native herbivores n = 360; (eastern grey kangaroo n=21, unknown macropod species n = 190, common wallaroo n = 74, and the common wombat n = 75). Plant management status pertains to a plant species is classified as invasive or a problematic native.*

Discussion

I expected to see considerable diet separation, as has been reported in similar studies (Mata et al., 2024), based on different gut morphologies, evolutionary history and body size of the different herbivores. However, my results instead suggest an extremely high overlap in the diet of this

mammalian herbivore guild. The highest degree of overlap was seen between the native wallaroo, wombat, and unknown macropod samples. Surprisingly, cattle samples had the greatest dietary overlap with deer, which is unexpected considering the difference in feeding strategies, with cattle being grazers and deer, browsers (Spedener et al., 2024). Furthermore, cattle showed the greatest degree of diet generalisation, suggesting a wide diet breadth which is expected. Deer shared the greatest dietary overlap with unknown macropod samples, suggesting that they both consumed a smaller, yet similar variety of plant genera when compared to cattle which is again expected, considering both species are browsers, likely lead to their differences in resource use to cattle (Gordon, 2003). These results may signify a high degree of competition between macropods and deer. The high overlap between wallaroo and the unknown macropod samples suggests that many of these unknown macropods are in fact wallaroo samples (Figure 7). This is further supported by the Levin's niche breadth (B), whereby wallaroo and unknown macropod samples have similar B values that differ considerably with eastern grey kangaroo samples, except for the samples in Winter which show a greater similarity between eastern grey kangaroo and unknown macropod samples (Figure 6).

Species richness was also similar between all herbivores and seasons, with a p-value of 1, signifying no difference between herbivore and plant nativeness. Species richness is markedly higher for native plants in all seasons apart from spring (Figure 8), which has a high degree of variation compared to other seasons. Furthermore, spring also shows a lower predicted probability for the presence of all plants, which suggests greater resource partitioning and highlights spring as time of high resource availability and low intra specific competition between the herbivores in this guild. This is the only substantial indication of resource partitioning within this guild of herbivores, which contradicts the expectations from classical niche theory, though similar patterns of overlap have been observed in other studies (Dawson and Ellis, 1994), including in an Australian coastal woodland habitat, where a high overlap between exotic and native mammals was reported (Davis et al., 2008).

Niche Partitioning

Niche theory predicts that resource partitioning occurs between species occupying a similar space, and has evolved to reduce competition, allowing for co-existence (Hutchinson, 1953). However, my results signify only weak niche diet differentiation across this herbivore guild. It is likely that rather than just resource partitioning, there are temporal and spatial niche differences present in this system that alleviates direct competition. Temporal partitioning may support co-existence between this herbivore guild, with studies showing that many deer species move into open fields to graze after sunset (Montgomery, 1963, Georgii, 1981, Pagon et al., 2013), whereas both wallaroo and eastern grey kangaroos begin feeding in the late afternoon (Taylor, 1985b, Taylor, 1985a). Similar instances of temporal avoidance have been recorded in many species as a means of coexistence, particularly when there is limited ability for spatial avoidance. The marsh tit (*Poecile palustris*) was recorded visiting free feeding stations early in the day in avoidance of the larger blue tit (*Cyanistes caeruleus*) and great tit (*Parus major*), both of which flocked at feeding stations in the afternoons (Maziarz et al., 2023). Similarly, Williamson's mouse deer (*Tragulus williamsoni*) were shown to share a spatial overlap with their conspecifics, but practiced complete temporal avoidance of the larger ungulate species to alleviate interspecific competition (He et al., 2023). However, due to intrinsic biological constraints, it is important to note that there is little evidence to support a species' ability to completely change their circadian rhythms or temporal activity, but rather shift within their preferred activity phase (Kronfeld-Schor and Dayan, 2003). Furthermore, despite the limited differentiation in the most common resources, there may be a significant difference seen in the diversity of rare taxa consumed (Kartzinel et al., 2015).

The introduction of domestic livestock has been shown to heavily affect the spatial dynamics of native species (Mishra et al., 2002, Masiaine et al., 2021, Lancaster et al., 2022). A study by Madhusudan (2004) analysed the effects of livestock on resource limitation for a native guild across a wildlife reserve in India. They found that population densities of the native gaur (*Bos gaurus*), chital (*Axis axis*), and Asian elephant (*Elephas maximus*) showed a sharp declining

relationship with increasing livestock density. My findings are indicative of a guild that already has strong interspecific competition, it would therefore be expected that in times of resource scarcity that population dynamics would be heavily affected (Dawson and Ellis, 1994). This is further supported by evidence suggesting that wallaroos are negatively correlated with cattle, and practice both diurnal and seasonal separation (Reid et al., 2020). However, my results show wallaroos to have a similarly broad diet to cattle (Figure 6), but only a moderate dietary overlap, which suggests they may also utilise different micro habitats.

Environmental impacts

Diet overlap is complex and dynamic, as evidenced by the fact that a strong dietary overlap can be used to infer a high interspecific competition. This was shown in a study of a cervid guild, whereby the greatest degree of overlap between species was during harsh winters, when there was low resource availability (Jenkins and Wright, 1988). In contrast to this, high dietary overlap may also occur when resources are abundant, as reduced competition allows species to use similar resources. As demonstrated by a study of a sympatric herbivore's guild comprised of wallaroos, goats (*Capra aegagrus hircus*) and sheep (*Ovies aries*), all species showed minimal diet overlap across multiple years, except for the wettest summer, where resources became highly abundant and their diets overlapped by > 80% (Dawson and Ellis, 1994).

Based on these competing interpretations and my results indication of seasonal differences in niche breadth, I posit that the observed patterns in overlap are due to a convergence on limited resource availability. This is supported by my reported smaller niche breadths and obvious changes in species richness during spring, and to a lesser extent in summer, as I would expect these seasons to be a time of abundant resource availability. Australian temperate regions are generally most heavily affected by the El Niño-Southern Oscillation (ENSO), however in support of my theory, a "triple-dip" La Niña, a rare weather event, occurred from 2020-2023 (Jiang et al., 2023). This event led to a prolonged period of higher than average rainfall across Eastern Australia (Huang et al., 2024), likely resulting in seed flushing, a rapid surge of new plant growth in response to dormancy

breaking during spring and summer (Rivera et al., 2002, Wolf and Young, 2016). Sudden growth would have created optimal conditions for herbivore grazers and an abundance of resource availability in Spring, allowing herbivores to be selective and partition resources based on their digestive physiology and preference.

Drought and resource limitation

Despite sampling occurring during a time of higher-than average rainfall, Eastern Australia is predominantly affected by ENSO (Taschetto et al., 2026), which results in periods of extended drought (Nicholls et al., 1996, Lindesay, 2005), creating a scenario of low resource availability. As supported by the high dietary overlap observed in winter and autumn, it would be expected that such events would reduce the available variation in food sources, limiting any opportunities for dietary specialization and increasing interspecific competition.

Many species display behavioural changes such as an increase in aggressive behaviour, in times of food scarcity, forcing young individuals or weaker species into unfavourable habitat (Smythe, 1986). This seems to be almost universal, having been reported across many different communities, guilds and systems (Oksanen, 1987, Kelt et al., 1995, Fedriani et al., 2000, Fritz et al., 2002, Luiselli, 2006, Eurich et al., 2018, Marino and Rodríguez, 2022). For example, high densities of the native Sika deer (*Cervus nippon)* in Japan caused a significant decline in the population size of the much smaller, native Japanese serow (*Capricornis crispus*) (Takada et al., 2025). Because of their smaller body size in comparison to both the exotic herbivores, an increasing feral deer population may result in the smaller native herbivores to become more susceptible to competition during drought and times of low resource availability.

Evolutionary context

The lack of obvious partitioning observed in my results may, in part, be reflective of the historical loss of niche diversity, rather than the present-day ecology. The contemporary native herbivore guild in this system may be functionally incomplete due to the loss of Australian mega-fauna (>100 kg) at least 20’000 years ago (Martin, 1967, Peters, 1986, Roberts et al., 2001, Helgen et al., 2006,

Ripple et al., 2015, Gordon and Prins, 2019). There is some evidence to suggest that many of these extinct species occupied a highly specialised dietary niche, including the giant short-faced kangaroo (*Procoptodon goliah),* the largest recorded species of Kangaroo (Prideaux et al., 2009a, Bowman et al., 2010). Much debate remains over the cause of Australian mega-faunal extinction, with the most probable cause being a combination of human arrival, and a drastic climatic shift (Johnson, 2005, Miller et al., 2005, Murphy et al., 2012, Bird et al., 2013). The remaining native herbivores may have survived in part, due to the adaptability of a broader, more generalised diet. Because of a long evolutionary history, the existing native herbivore guild adapted traits to allow them to coexist with a high dietary overlap in this system, however the introduction of exotic herbivores may be a tipping point.

Large exotic herbivores may partially substitute lost ecological roles; however, they evolved outside of this system and don't conform to the existing niche structure. Due to the lack of dietary specialisation, my results support the idea that they instead contribute to novel interactions rather than restoring historical structure. The more likely consequence of exotic herbivores in this grassland habitat is their facilitation of exotic plant invasions (Braga et al., 2018). Exotic herbivores are more likely to spread exotic seeds (Maron and Vilà, 2001, Best and Arcese, 2009), many of which have traits that facilitate their ability to outcompete native species in a novel environment (Orrock et al., 2008, Schultheis and Macguigan, 2018).

Conclusion

In an ever-changing environment, species must exhibit a degree of trait plasticity to persist (Owen-Smith, 2008; Berg & Ellers, 2010), and accordingly, herbivore foraging behaviour should be viewed as dynamic rather than fixed. Within this context, my results indicate an herbivore guild characterised by a high degree of resource overlap. Over time, such overlap may generate a feedback loop in which herbivores shape plant community composition, and the resulting plant community in turn influences subsequent diet selection. This reciprocal interaction has the potential

to drive landscape homogenisation (Orians & Ward, 2010), further increasing dietary overlap and potentially constraining the long-term coexistence of species within the guild. Consequently, herbivore identity and evolutionary history are critical for understanding patterns of resource use, competitive interactions, and ecosystem trajectories, particularly in the context of grassland restoration.

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Chapter 3

Seeds on the move

Introduction

Herbivores play a vital role in shaping ecosystems and plant communities through selective consumption of plant biomass and mechanical disturbance of vegetation and soil (Schmitz, 2008, Calvino-Cancela, 2011, Pringle et al., 2023). They facilitate plant dispersal and colonisation, acting as long-distance seed dispersers (Iluz, 2010) either by transporting seeds externally on their fur, or by ingesting and depositing viable seed in their faeces (Jaganathan et al., 2016). The latter process of endozoochory can benefit some plants more than others and means, overall, herbivores have a vast potential to (re)shape plant communities. Understanding the consequences of endozoochory in native and exotic herbivores is a critical component of predicting ecosystem change and biodiversity loss.

Many plant species have co-evolved with herbivores or frugivores, and as a result, have developed traits that allow the process of endozoochory to enhance germination success (Rubalcava-Castillo et al., 2025). Many of these traits increase the probability of being eaten and include the development of brightly coloured fruit with high sugar content, making themselves highly visible for dispersers and offering a reward for consumption. Other traits have evolved to allow for increased survival in the gut. These include thicker seed coats, chemical resistance to stomach acids, and the development of dormancy mechanisms that become triggered by scarification (Jones et al., 2025). Plants receive many benefits from this process. Through the evolution of traits that increase the likelihood of being eaten, plants benefit from the dispersal of seeds over larger distances, ability to colonise novel sites, and escape from parent-offspring competition. Further, traits evolved to cope with gut passage, increase germination success through by-passing the need for environmental cues to break dormancy (Miranda et al., 2011), and the benefit of moisture and nutrients provided by faecal material. However, the differences in evolutionary history and herbivore gut morphologies have considerable influence on germination success (Venier et al., 2012). Due to these complex interactions, context is important as some plant species may survive the gut passage of certain herbivores, and not others (Anderson et al., 2014).

Studies have shown a strong link between plant traits and species persistence under grazing pressure, with changes in herbivore assemblages having significant impacts on plant community structures (Clarke, 2003, Dorrough et al., 2004a, Kapás et al., 2020). This can be seen in the expansion and recovery of native vegetation across Australian landscapes after ongoing efforts to reduce European rabbit (*Oryctolagus cuniculus*) populations (Finlayson et al., 2022). By contrast, the reintroduction of the native tule elk (*Cervus elaphus nannodes*) into Californian grasslands resulted in significant changes to invasive exotic grass abundance and an overall increase in both exotic and native biomass (Johnson and Cushman, 2007), suggesting that these herbivores supported the maintenance of open grasslands. Seed dispersal is a major contributing factor of these herbivore-driven changes in plant population persistence, range expansion and community composition (García et al., 2017). The invasion and range expansion of feral exotic and domestic herbivores into novel ecosystems can radically alter plant dispersal networks and have the potential to further the spread of exotic and invasive plants (Holmgren, 2002).

Many studies have quantified diet composition of mammalian herbivores, but very few have looked at the germination success of ingested seeds (Quin et al., 2023a, Yadav et al., 2025), with even fewer studies comparing native and exotic herbivores in the same system. Most comparative endozoochory studies involve only two herbivores (Cosyns et al., 2005a, Mouissie et al., 2005b), or, herbivores of the same gut morphology (Albert et al., 2015, Fuzessy et al., 2016), with ungulates being the most researched group of mammalian herbivores. To my knowledge, there are no endozoochory germination studies comparing a complete mammalian guild made up of exotic (feral and domestic) and multiple native species in a temperate grassland habitat.

Temperate grasslands are found on every continent on earth, except Antarctica (Singh et al., 1983, Henwood, 1998) and represent both biodiversity hotspots (Petermann and Buzhdygan, 2021) and provide critical support for humans . However, temperate grasslands have also been the most heavily affected by anthropogenic influences (White et al., 2000, Stritar et al., 2010, Török et al., 2021), including through the introduction of exotic large herbivores (Mack et al., 2000, Nuñez et

al., 2010, Török et al., 2021). This makes them an important ecosystem for understanding the potential impacts of exotic endozoochory. Australian temperate grasslands provide a unique case study. Until recently, marsupial herbivores dominated and ungulate herbivores were absent (introduced in the last 150 years) but now contain a mixture of feral exotic ungulates and domestic livestock. Cattle are commonly used as biomass managers, and suppressors of dominant exotic plants (Henwood, 2010). Consequently, there are expected to be more drastic differences in seed dispersal between native and exotic plants and herbivores. Such a case study will not only improve my understanding of the role of native, and exotic, both feral and domestic, herbivores in plant recruitment dynamics, but also provide vital information for the restoration and conservation of threatened grassland ecosystems.

The aim of this study was to analyse the interaction of endozoochory by two herbivore groups, native and exotics (one feral and one domestic) on the potential spread of exotic and native plant species. The main objectives were to: (1) evaluate whether there was a difference between native and exotic herbivores, in their potential to transport viable seeds via endozoochory: (2) determine if species richness and abundance of seeds found in faecal matter varied, (3) analyse seasonal differences in the diversity and quantity of viable seeds being dispersed, and (4) test whether exotic herbivores were more likely to disperse exotic seeds. To address these objectives, I conducted a germination study on 591 faecal samples, collected from six herbivore species over a 12-month period. The results from my study provide critical knowledge on herbivore-plant interactions and inform management and restoration of temperate grassland ecosystems globally. I predicted that (1) exotic herbivores would disperse significantly more seeds and greater plant species richness than native herbivores; (2) exotic plant species would predominate in the faeces of all herbivore types, but especially exotic herbivores: (3) seed dispersal would vary seasonally across both herbivore groups: and (4) exotic herbivores would disproportionately disperse exotic relative to native plant seeds.

Methods

Site and study species

The study took place in the Ginninderry Conservation Corridor (GCC) in the Australian Capital Territory (ACT), Australia (35°13’54.8” S, 148°58’35.7” E, Figure 1 (Ginninderry Conservation Trust et al., 2018)). This 580-ha site had a mean elevation of 570m and is bordered by the Murrumbidgee River on one side and urban development on the other (Figure 1). Historically, much of the GCC was used as pasture, but is now comprised of a mosaic of different habitat types, including riparian woodland, open grasslands, woodlands, pasture grass, and remnant patches of critically endangered box-gum grassy woodland (Figure 2). Dominant native herbivore species across the site are all marsupials and include the eastern grey kangaroo (*Macropus giganteus*), common wallaroo (*Osphranter robustus*), red-necked wallaby (*Notamacropus rufogriseus*) and the common wombat (*Vombatus ursinus*), with annual macropod counts averaging at 162 animals. Domestic cattle (*Bos taurus*) herds of 40-80 individuals are rotated across the site throughout the year as a vegetation biomass control measure, and a population of feral fallow (*Dama dama*) and sambar (*Rusa unicolor*) deer exist in large numbers throughout the surrounding Namadgi National Park (Mulvaney et al., 2017, Kennedy, 2025), with significant mobs (herds) regularly using or

passing through the GCC

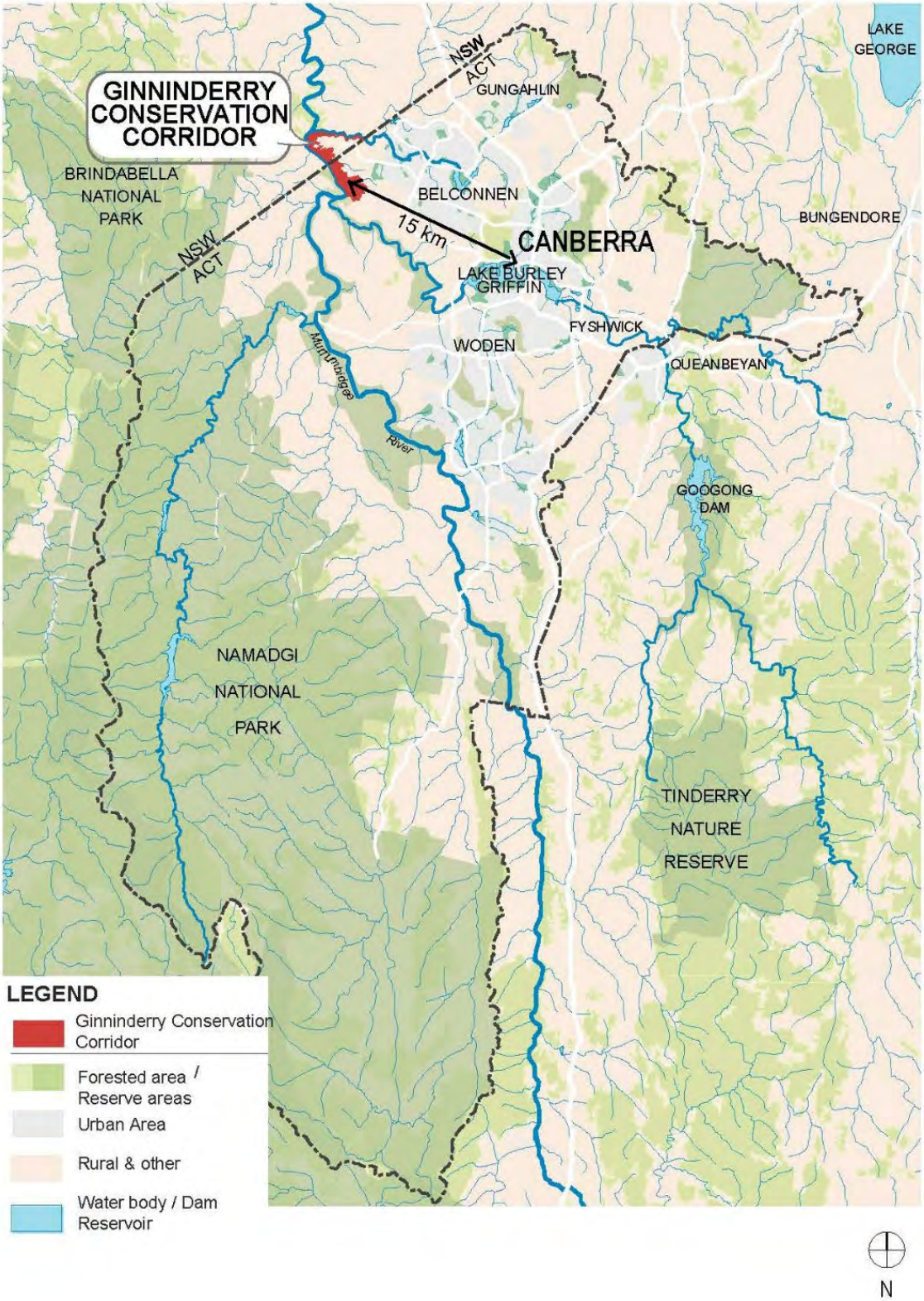


Figure 10. ***Ginninderry Conservation Corridor in the Australian Capital Territory, Australia*** *- (35°13’54.8” S, 148°58’35.7” E) in relation to the ACT (top left) and Australia (top middle). Image*

adapted from Ginninderry Conservation Trust et al. (2018).

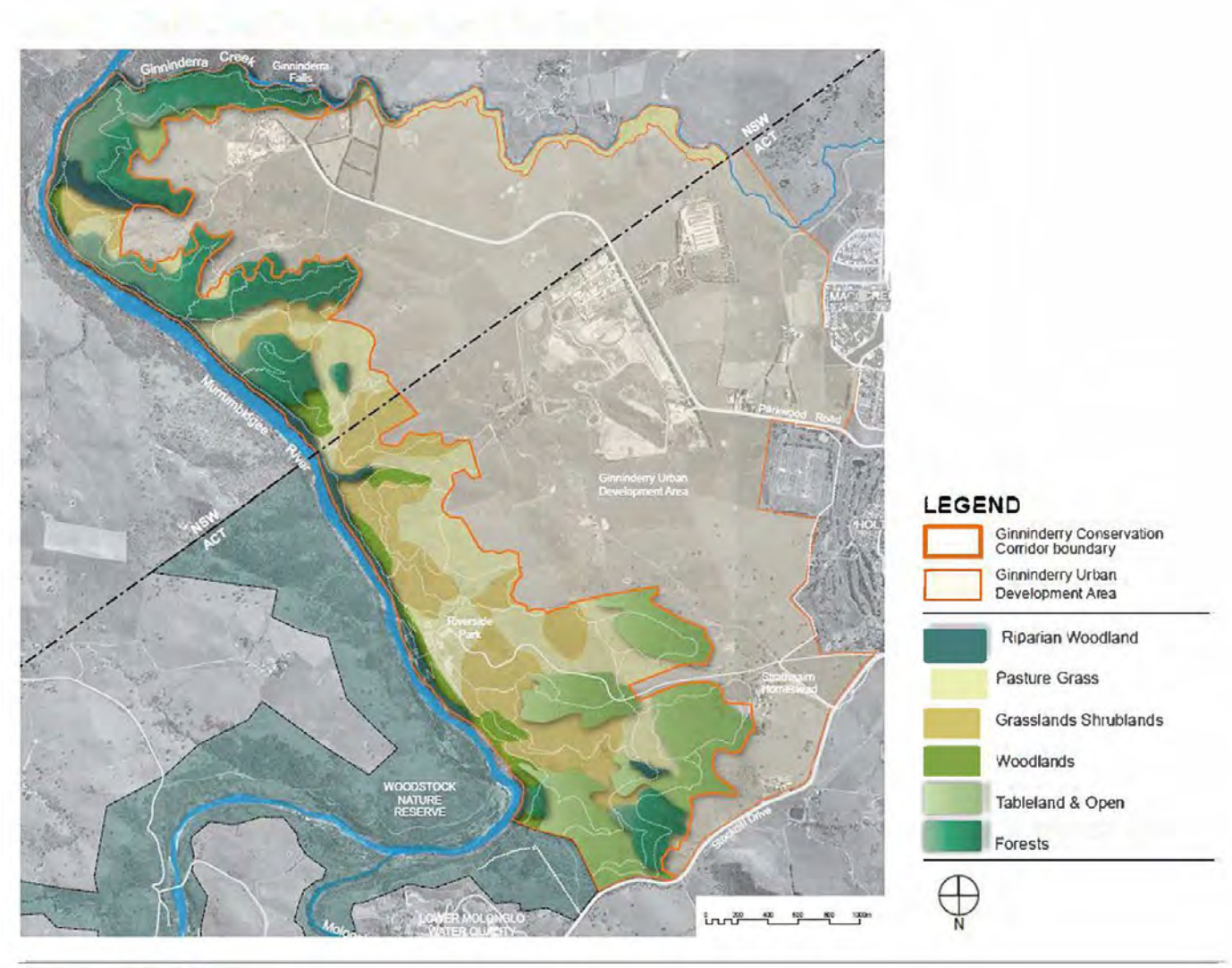


Figure 2. ***Ginninderry Conservation Corridor in the Australian capital Territory, Australia*** *- (35°13'54.8" S, 148°58'35.7" E) with habitat types and borderlines based in a 2015 vegetation survey. Image adapted from Ginninderry Conservation Trust et al. (2018).*

Study design

Sample collection

I selected 12 sites (orbicular shape; 0.12 km²) across the larger area, with all but two sites falling within the GCC area, for random scat collection. The ecosystem was contiguous with no differences in the degree of land management or habitat type during this time across all the sites. Each location was randomly searched for samples by the same individual, with as much of the location covered by foot as possible. All fresh (glossy and wet) faecal samples were collected, given a unique code and

a GPS position was recorded. All faecal samples within 10 cm were collected and treated as a single sample. To ensure the samples were fresh, no collection was performed during or within 24 hours after a rain event. Each location was visited twice per season for 12-months between April 2024 and March 2025 (Autumn; 02–22 April, Winter; 07-13 July, Spring; 18-29 November, Summer; 12 February–04 March). Due to the placement of the cattle herds, there was not enough faecal material in the selected locations during the Winter and Summer sampling periods, so an extra site was added for the collection of cattle samples. All efforts were made to identify the species of origin for faecal samples in the field, which was achievable for all cattle and wombat samples. Macropods were identified to species at the time of collection if a mob was visually present at the time (mixed mobs were not observed). For all macropod samples, where species could not be obtained in the field, one pellet was kept aside and stored at -20°C for later identification of the source herbivore species using DNA analysis. Deer pellets were also impossible to differentiate to species visually and due to their similar use of the landscape and same gut morphology, all deer samples were grouped together.

Sample processing and greenhouse planting

To avoid any freezing injury that may reduce viability, all faecal samples were stored with silica gel beads (Dessiccant, Australia) upon collection and kept in the laboratory, in ambient temperature, to reduce moisture prior to freezing, (Roberts, 2012). Samples were checked daily for up to one week, with saturated silica beads being replaced as needed to dry faecal samples. Faecal samples were then stored at 5°C until the end of the sampling period. A total of 594 faecal samples were collected.

At the end of the two-week sampling period, dry faecal samples were brushed lightly with a small paintbrush in a bio-safety cabinet, to ensure there were no external seeds present from environmental exposure or contamination. Samples collected from the same site that were of the same species of origin, were weighed and combined, except for macropod samples that could not be identified in the field, which were treated as an individual sample and not combined for all the

following steps until data analysis. All samples were placed in a -20° C freezer for 30 days to undergo cold stratification. This treatment is necessary for many seeds, especially those of native plants, perennials, and trees with hard outer coats, to break dormancy and trigger the sprouting process (Baskin and Baskin, 2003, Merritt et al., 2007b).

Following stratification, the faecal samples were broken down by hand to prevent mechanical damage to any seeds. This turned each faecal sample into a dirt like substrate. A 1:1 ratio of faecal sample to sterile potting mix were combined and potted by herbivore species and location collected, in < 2cm depth on top of a layer of sterile river sand. A negative control pot was included in the experiment for every season. Plants were housed in a greenhouse under ideal conditions that were expected to promote germination of most plant species. Temperature was set to 25°C during daytime hours and 18°C during night hours, using natural sunset/sunrise for temperature change over and an average humidity of 59.58% and all pots were watered twice daily. For each season, after a 4-week period of no seedling emergence, gibberellic acid (1g/L GA_3) was added to each pot for seven consecutive days, with this concentration being shown to have a positive effect of dormancy breaking without causing germination suppression (Merritt et al., 2007a). The use of gibberellic acid is well documented for growth experiments as a dormancy breaking hormone. Many plant species require the addition of gibberellic acid in a controlled experiment, because they rely on environmental cues such as fire and light to germinate, this is particularly true of Australian native species (Bell, 1999, Merritt et al., 2007b). Just prior to adding the gibberellic acid, the soil in each pot was turned over with a pair of sterile tweezers, to further replicate disturbance present in the natural environment.

Plant identification

Using the seedling emergence method (Von Oheimb et al., 2005), newly emerged seedlings were removed as soon as identifiable, re-planted in their own pot, given a unique species ID and photographed regularly (Appendix C; Figure 1). As the experiment progressed, emerging seedlings were either matched and recorded according to an existing species ID or given their own. This was

done for each season. A leaf sample of each seedling given a unique ID was collected and stored in silica for genetic identification.

To confirm species identification, I performed DNA-based identification. I extracted the DNA from 146 plant samples, using the DNeasy® Plant Mini Kit (Qiagen, USA) following the manufacturer's instructions. I then amplified a 600 bp region of the Internal Transcribed Spacer (ITS) ribosomal RNA gene using the ITS-3p62plF1 (ACBTRGTGTGAATTCAGRATC) and ITS-4unR1 (TCCTCCGCTTATTATTKATATGC) primers (Kolter and Gemeinholzer, 2021). I performed all polymerase chain reactions (PCR) in a 25µl reaction, using OneTaq® 2X Mastermix (NEB, USA). The PCR reaction conditions were denaturation at 95°C for 5 minutes, followed by 35 cycles of 94°C denaturation for 30s, annealing at 50°C for 30 seconds, extension at 72°c for 60 seconds and a final extension for 8 minutes. Amplicons were then purified using Sera-Mag™ SpeedBeads (Cytiva, USA) and library preparation and sequencing on an AB 3730 capillary sequencer was performed in both forward and reverse directions at the Biomedical Resource Facility, Australian National University.

The forward and reverse sequences were aligned to create contigs for each sample using Benchling (Benchling, 2026), with chromatograms manually checked for errors and misalignment. I then compared the resulting contigs to NCBI Non-Redundant (nr) database (January 2026; (Sayers et al., 2021) using the BLASTn algorithm (Camacho et al., 2009). Top matches were inspected and compared to a local reference database of known species in the area. A species was assigned where similarity was greater than 98% for a single species, and the genus level if multiple species fell within this threshold. If only a single species in the genus was present in area, then I assigned the sample to that species. Finally, I assessed similarity across samples that appeared to be the same species to confirm the variation was within that reported for the species (typically 1-2%) (Ritland et al., 1993).

Plant taxa were assigned to either a native or exotic, with recognition as invasive also noted. Exotic species were those plant species that did not evolve in Australia, with invasive species, all of

which are exotic, assigned according to national weed and invasive species reports where a plant has been officially declared noxious as of 2006 (Wwf, 2006, Csiro and Wild Matters, 2025). Native species can be considered invasive when they expand beyond their recognised distribution or habitat type, however none of the native plant species detected in this study were listed as invasive or environmentally problematic species in Australia.

Herbivore Species Identification

I extracted the DNA from 131 macropod faecal samples that were sub-sampled using the outer surface of the sample, using the QIAamp® Fast DNA stool Mini Kit (Qiagen, USA) following the manufacturer's instructions. Following initial testing, I added a column clean-up using the DNeasy® PowerClean® Clean-up Kit (Qiagen, USA) to further remove inhibitors. Species specific primers were designed to differentiate macropod species, targeting the cytochrome *b* (*cytb*) mitochondrial gene (1146 bp), amplifying a 250b bp section for eastern grey kangaroos, a 150 bp section for wallaroos, a 450 bp section for swamp wallaby, and a 220 bp section for red-necked wallaby (Appendix C; Table 2). I performed all PCRs in a 20µl reaction using Platinum™ Direct PCR Universal Mastermix (Invitrogen™, USA). I performed PCR cycling according to Koehler et al. (2020b), modified to an extension temperature of 68°C. Some problematic samples were applied up to 50 cycles. The amplicons were visualised on 2% agarose gels stained with SYBR Safe (Invitrogen™, USA), using TAE as the buffer and using 50bp DNA ladder (Invitrogen™, USA).

Statistical analyses

Herbivore samples

Herbivores samples were recorded and weighed individually and then combined according to season and site prior to planting, so each sample in the data is comprised of faecal matter from multiple different individuals.

Statistical models

Germination counts were treated as abundance data and analysed using generalised mixed-effects models (GLMMS). Due to the nature of count data exhibiting overdispersion, models were fitted

using a negative binomial error distribution with a log link function (Zuur et al. 2012) rather than a Poisson distribution. The models included herbivore species, plant nativeness, and season, and their two-way interactions were included as fixed effects. Site was included as a random effect to control for spatial clustering among samples collected from the same locations, while sample identity accounted for any variation among individual faecal samples.

To account for variation in faecal sample mass, faecal weight (g) was included in the model as a log-transformed offset. This standardised germination counts by sample mass, such that the model estimates represent the number of seeds germinating per gram of faeces rather than per faecal sample. Model diagnostics were assessed using simulated residuals generated with the DHARMa package (Dormann, 2020). Analysis of variance (ANOVA) were performed on all fitted models, and statistical significance was assessed using TYPE II Wald chi-square tests. Estimated marginal means were calculated using the emmeans package (Searle et al., 1980, Lenth, 2025) and used to visualise model predictions in RStudio (Rstudio, 2023).

Species richness

Species richness was calculated from presence-absence data and computed overall within each season for each herbivore and seed type. I used a negative binomial model to compare average species richness between herbivore, seed type, and the interaction (Zuur et al. 2012). Season was included as a random effect to control for any variation across season. Statistical inference was based on the negative binomial model, with p-values derived from the model outputs. Graphical representations show observed data, rather than model-predicted values. Using the iNEXT package in RStudio (Chao et al., 2016)

(Hurlbert, 1971, Heck Jr. et al., 1975)

Differences in plant taxa detected among herbivore species were visualised using bipartite graphs generated with the bipartite package in R (Dormann et al., 2008), and UpSet plots, generated with the ComplexUpset packages in R (Chen and Boutros, 2011).

Results

Herbivore species identification

Prior to combining samples according to season, site and herbivore species, 300 macropod samples were collected, 213 were successfully identified, 37 as eastern grey kangaroo, and 176 as common wallaroo. Despite best efforts and the amplification of positive controls, I found no positive matches to either red-necked wallaby or swamp wallaby. Both species exist in small, isolated patches across the study site, making it possible that some of my unidentified macropod samples comprise of these species. Therefore, I treated these 87 samples as unknown macropod species. A total of 47 cattle, and 154 deer faecal samples were collected over the course of the experiment (Appendix C; Table 3). Following grouping according to site and season, this equated to 106 native herbivore samples; (10 eastern grey kangaroo, 39 wallaroo, 21 unknown macropods and 36 wombat), and 36 exotic herbivore samples; (6 cattle and 30 deer).

Plant species identification

I identified a total of 4944 germinated seeds found in the faeces of deer, cattle, eastern grey kangaroos, common wallaroos, common wombat, and unknown macropod species to the highest taxonomic level possible (Appendix C; Table 1). A total of 66 plants were identified to species level, and five plants were identified to genus, of which 16 were native, and 50 were exotic (four of which were classified as invasive) (Wwf, 2006, Martín-Forés et al., 2023).

Most common plant species

The top ten most common plant species across all herbivore samples based on germination counts were all exotic or invasive plants (Table 1). Similarly, the top five most common plant species counted in only exotic herbivore samples (Table 2), and in only native herbivores (Table 3), were all exotic and invasive plants. The native herbivore samples had a lower seedling count in their top five most common plants, when compared to the non-native herbivores. Throughout all seasons, no seedlings emerged from any of the negative control pots.

Table 1. ***Top ten plant species that successfully germinated in the faecal samples of native and exotic herbivores.*** *Top ten species are based on the total number of germinated seedlings counted across all samples. Samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between April 2024 and March 2025; exotic herbivores n = 36; (cattle n = 6 and deer n = 30) and native herbivores n = 106; (eastern grey kangaroo n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36). Nativeness pertains to the origin of the plant species and whether it is native, exotic or declared as noxious (invasive). *One deer sample contributed 1172 seed germination counts for fat hen (Chenopodium petiolare).*

Species	Seedling count	Common name	Nativeness	Plant functional group
Chenopodium album	1206	fat hen*	exotic	herb
Trifolium arvense	595	hare's-foot clover	exotic	herb
Verbena incompta	315	purple top	exotic	herb
Digitaria sanguinalis	311	crab grass	exotic	annual C4 grass
Rumex acetosella	193	sheep sorrel	exotic	herb
Eragrostis curvula	189	African lovegrass	exotic - invasive	perennial C4 grass
Cyperus eragrostis	150	umbrella sedge	exotic	sedge
Digitaria ischaemum	120	smooth crabgrass	exotic	annual C4 grass
Verbena officinalus	113	common verbena	exotic	herb
Amaranthus retroflexus	111	redroot amaranth	exotic	herb

Table 2. ***Top five plant species that successfully germinated in the faecal samples of exotic herbivores.*** *Top five species are based on the total number of germinated seedlings counted across all exotic herbivore samples. Samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between April 2024 and March; exotic herbivores n = 36; (cattle n = 6 and deer n = 30) Nativeness pertains to the origin of the plant species and whether it is native, exotic or declared as noxious (invasive). *One deer sample contributed 1172 seed germination counts for fat hen (Chenopodium petiolare).*

Species	Seedling count	Common name	Nativeness	Plant functional group
Chenopodium album	1206	fat hen*	exotic	herb
Trifolium arvense	448	hare's-foot clover	exotic	herb
Verbena incompta	312	purple top	exotic	herb
Rumex acetosella	158	sheep sorrel	exotic	herb
Verbena officinalus	113	common verbena	exotic	herb

Table 3. ***Top five plant species that successfully germinated in the faecal samples of native herbivores.*** *Top five species are based on the total number of germinated seedlings counted across all native herbivore samples. Samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between April 2024 and March 2025; native herbivores n = 106; (eastern grey kangaroo n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36). Nativeness pertains to the origin of the plant species and whether it is native, exotic or declared as noxious (invasive).*

Species	Seedling count	Common name	Nativeness	Plant functional group
Digitaria sanguinalis	258	crab grass	exotic	annual C4 grass
Trifolium arvense	147	hare's-foot clover	exotic	herb
Cyperus eragrostis	142	umbrella sedge	exotic	sedge
Eragrostis curvula	136	African lovegrass	exotic - invasive	perennial C4 grass
Digitaria ischaemum	112	smooth crabgrass	exotic	annual C4 grass

Modelled effects of plant nativeness and season

Negative binomial models showed that overall, germination counts differed significantly by herbivore, plant nativeness, and season (Figure 3) and plant nativeness differed significantly by herbivore and season (all $p = <0.001$). The exotic herbivores, cattle and deer, were not sigificantly different from each other, however they were significantly different from all the native herbivores (all $p = <0.001$). Further, native seeds were less likely to occur than exotic seeds in all seasons, particularly so in spring ($p = < 0.001$), summer ($p = 0.029$), and winter ($p = 0.003$). Expected seed germination counts were reduced in spring and summer, with germination counts in spring significantly lower than both autumn ($p = <0.001$), and winter ($p = 0.027$), and summer lower than autumn ($p = 0.007$) .

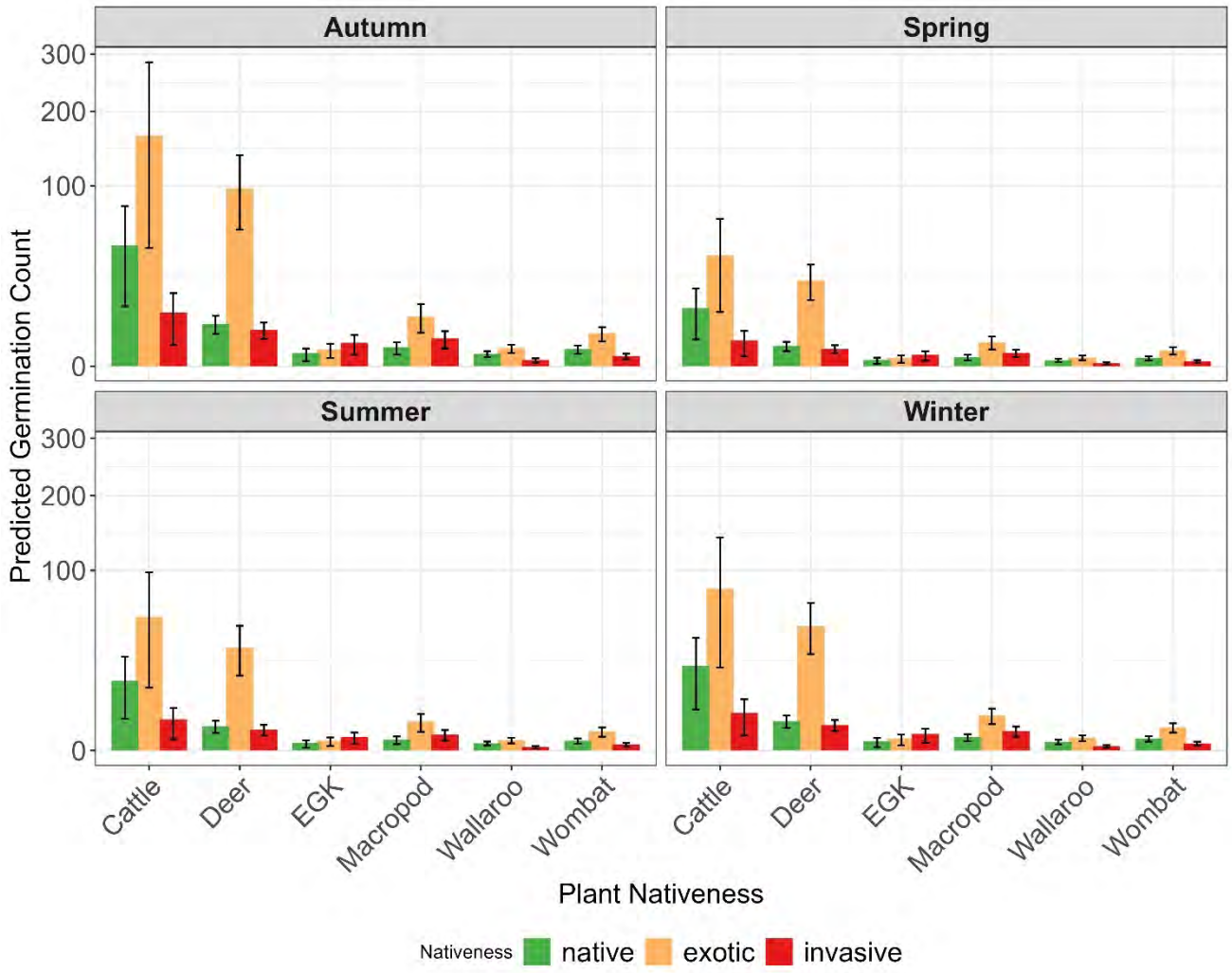


Figure 3. ***Modelled seasonal Effects of Plant Nativeness and Herbivore on Germination****. Negative binomial model showing the seasonal effects of plant nativeness by herbivore. Samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between April 2024 and March 2025; exotic herbivores n = 36; (cattle n = 6 and deer n = 30) and native herbivores n = 106; (eastern grey kangaroo (EGK) n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36). Response signifies the average number of germinated seed in their respective faecal matter according to season. Nativeness pertains to the origin of the plant species and whether it is native, exotic, or declared as noxious (invasive).*

Species richness

Overall, the negative binomial model showed that species richness was not significantly different across seasons or between the two-way interaction of herbivore and plant nativeness. Species

richness varied between seed type ($p = <0.001$) with exotic seeds more prevalent than either native or exotic seeds. Plant species richness varied by herbivore ($p = < 0.001$) with cattle and deer depositing the greater diversity of exotic seed, compared with native herbivores (Figure 4). Despite the negative binomial model showing that species richness did not significantly differ across the seasons, there was considerable variation present (Figure 5), especially in the exotic herbivore samples.

As well as species richness varying by season, and nativeness, by herbivore, there was also a considerable overlap in the plant species that germinated, with deer and cattle sharing the greatest abundance and richness of germinated seed assemblages. The native herbivores did show some overlap in the plant taxa assemblage, however in considerably lower abundances (Figure 6).

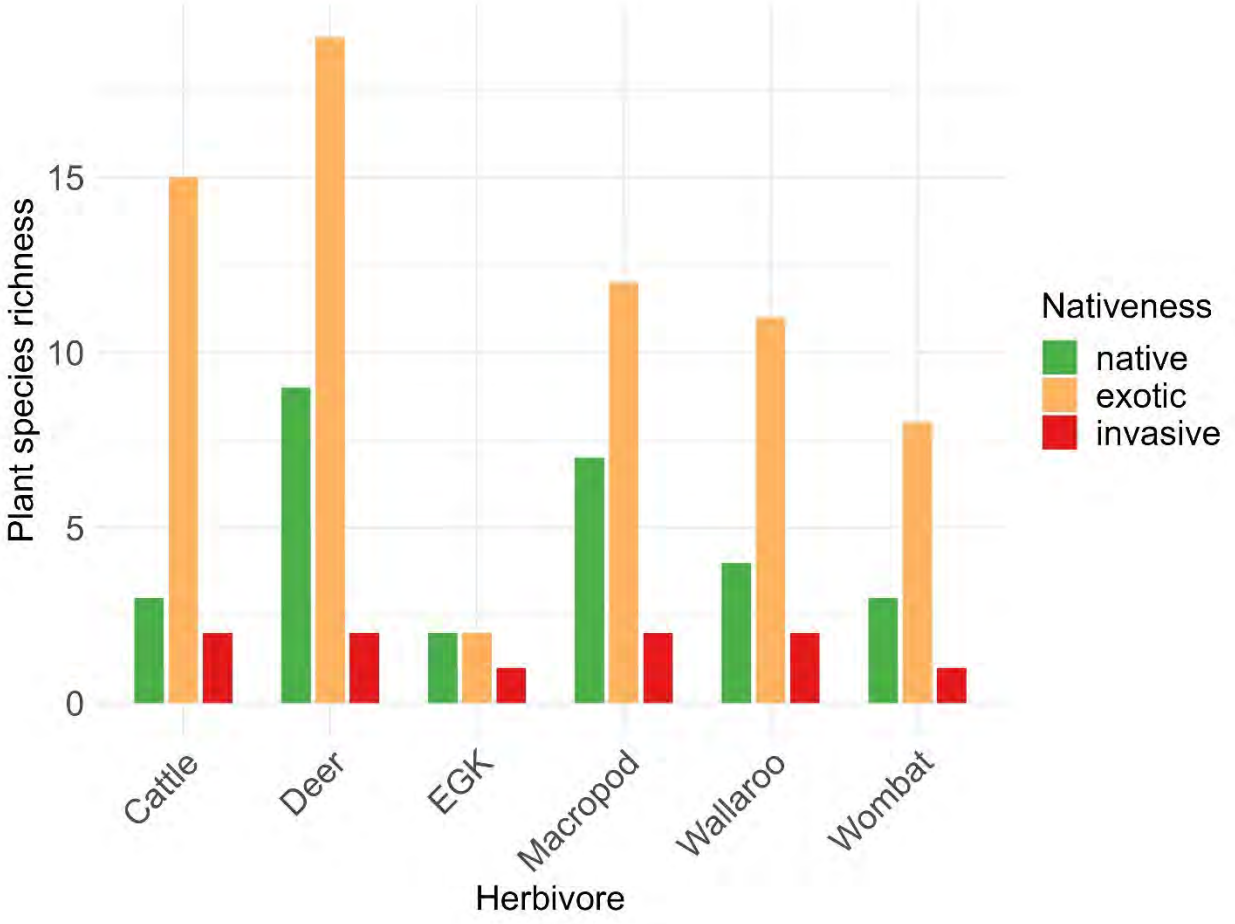


Figure 4. ***Plant species richness by herbivore and plant nativeness****. Graph depicting the plant species richness of germinated seeds found within the faecal samples of herbivores. Samples*

collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between April 2024 and March 2025; exotic herbivores n = 36; (cattle n = 6 and deer n = 30) and native herbivores n = 106; (eastern grey kangaroo (EGK) n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36). Nativeness pertains to the origin of the plant species and whether it is native, exotic or declared as noxious (invasive).

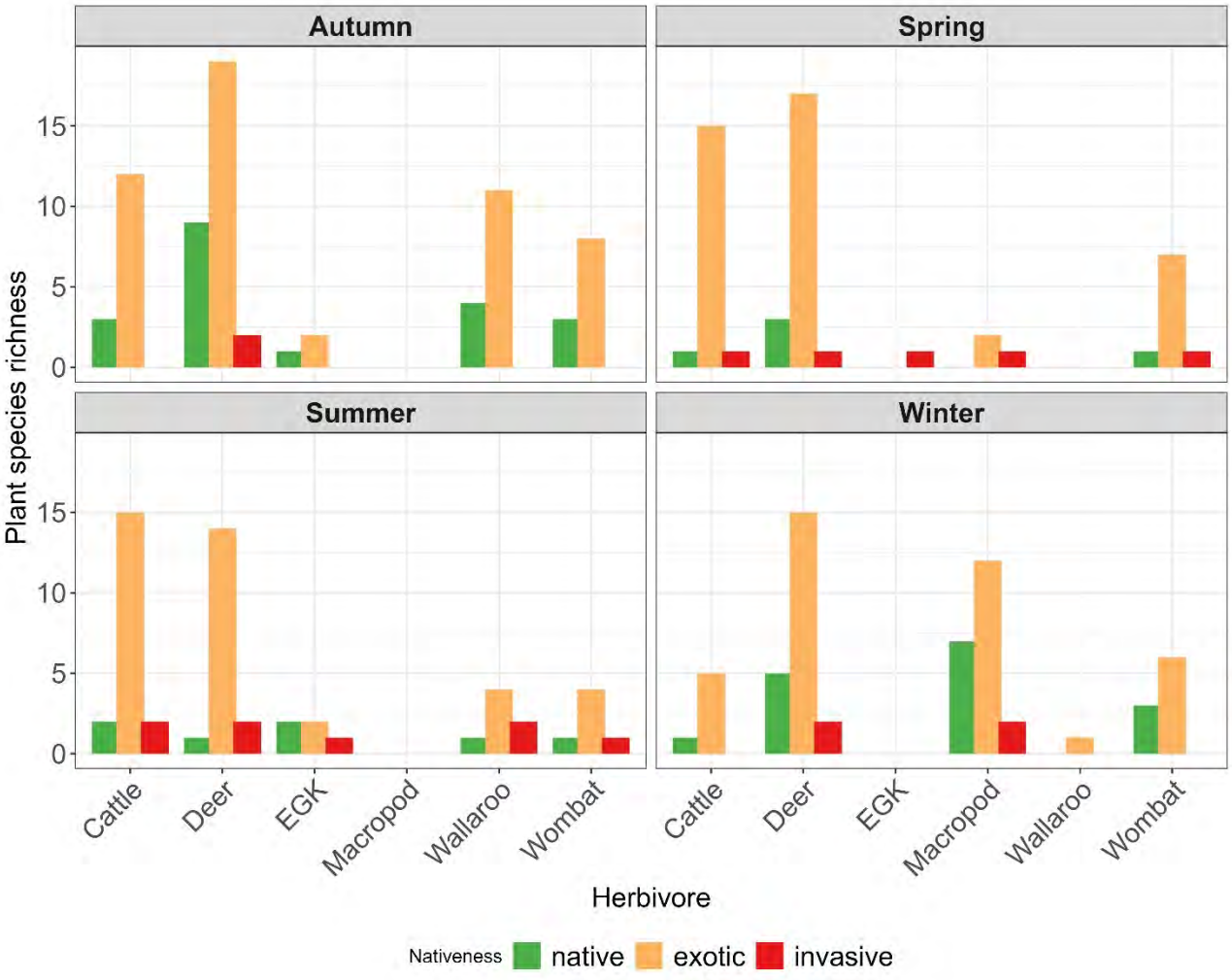


Figure 5. ***Plant species richness by herbivore and season****. Graph depicting the seasonal plant species richness of germinated seeds found within the faecal samples of herbivores. Samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between April 2024 and March 2025; exotic herbivores n = 36; (cattle n = 6 and deer n = 30) and native herbivores n = 106; (eastern grey kangaroo (EGK) n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36).*

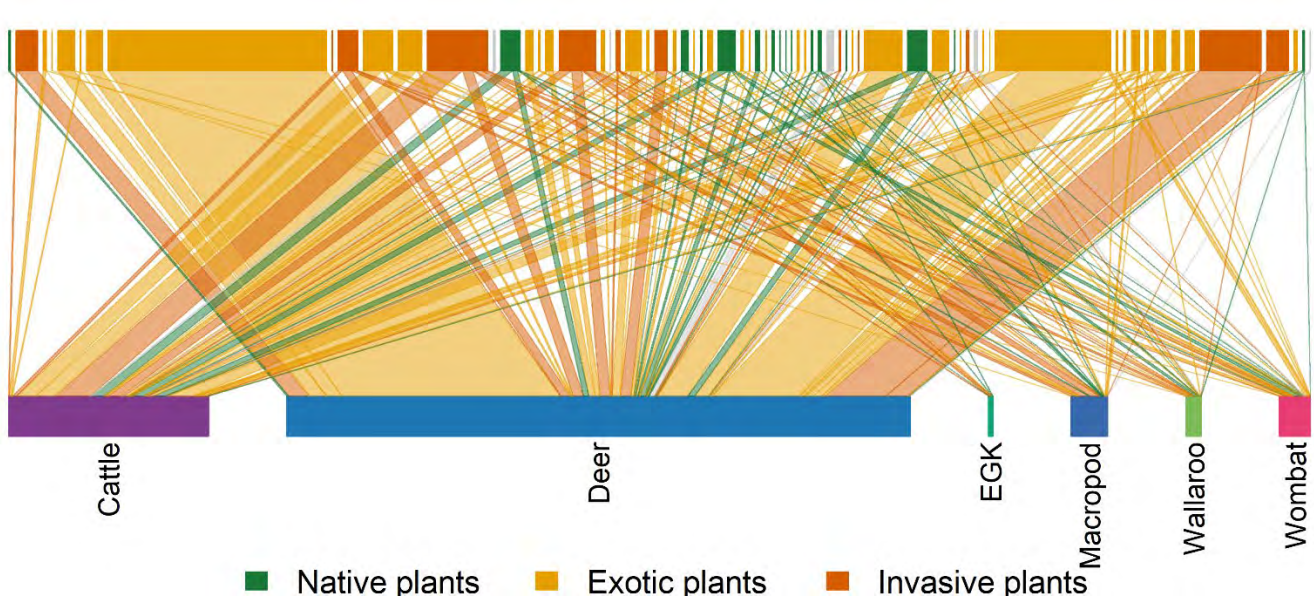


Figure 6. ***Bipartite network illustrating dietary interactions between six mammalian herbivore groups and plant taxa, classified by plant nativeness.*** *The lower bars represent herbivore groups (cattle, deer, eastern grey kangaroo (EGK), macropod, wallaroo, and wombat, while the upper bars represent individual plant taxa, coloured according to their classification as native, exotic or invasive. Connecting bands represent endozoochoric interactions between the herbivores and plant taxa, with band widths proportional to their relative abundance of plant taxa successfully germinated from faecal samples. Samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between April 2024 and March 2025; exotic herbivores n = 36; (cattle n = 6 and deer) n = 30) and native herbivores n = 106; (eastern grey kangaroo (EGK) n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36).*

Seed Density

Log-transformed offset negative binomial models showed that overall, estimated seed density (g^{-1}) differed significantly by season, herbivore, plant nativeness and the two-way interaction of herbivore and plant nativeness (all $p = <0.001$) (Figure 7). The negative binomial model showed that deer had less native ($p = 0.065$) germinated seeds per g^{-1} of faecal matter than exotic, as did cattle ($p = 0.045$). The estimated seed densities were low (0.03 – 0.41 seeds g^{-1}) for all herbivore

species, except for deer and cattle (Figure 7). Cattle samples had a low estimated seed density for native plants, but higher estimated concentrations for exotic (0.97 seeds g^{-1}) plant species. Deer samples had a distinctly higher exotic estimated seed density (3.76 seeds g^{-1}), with estimated values approximately four times higher than cattle, and ranging from nine to 125 times more exotic seeds per gram of faecal material than native herbivores.

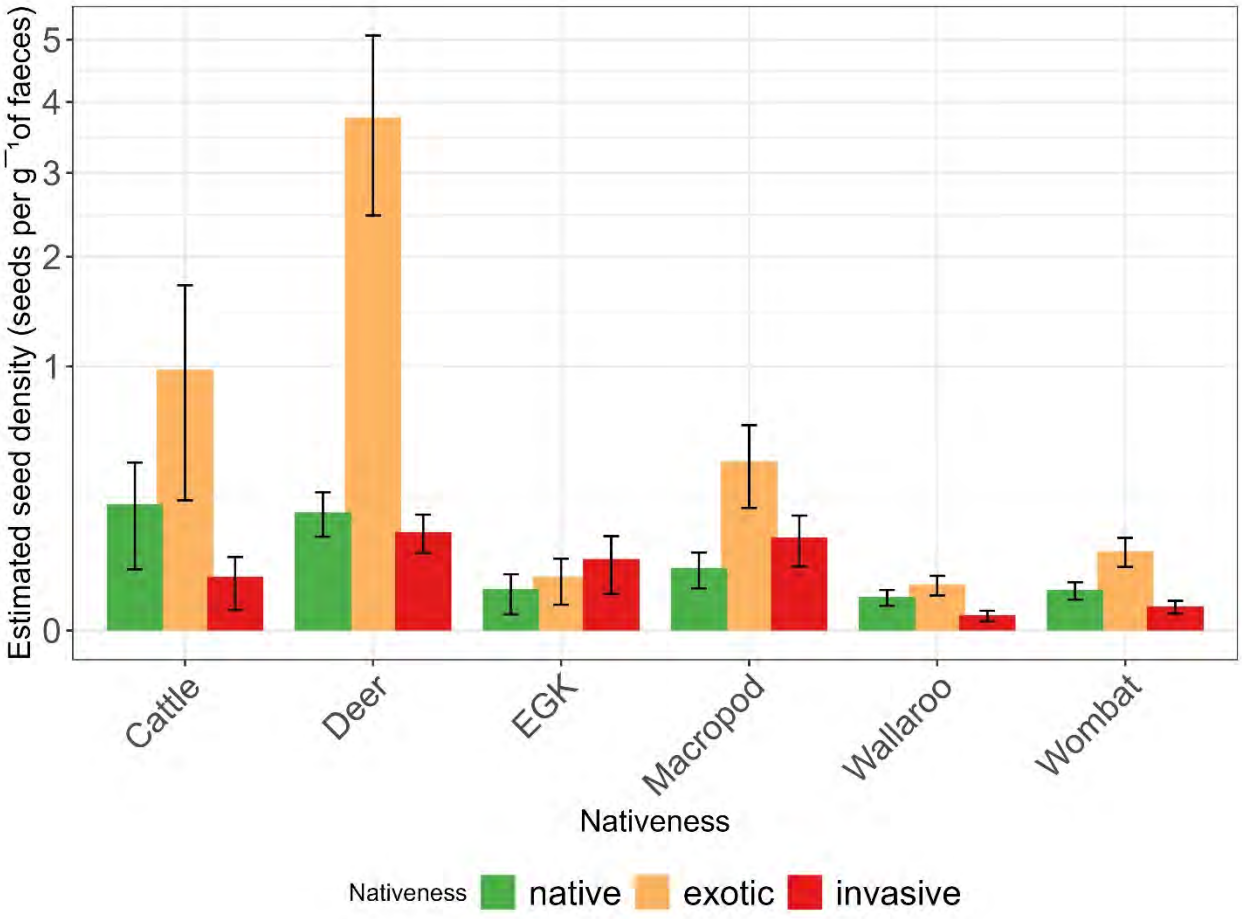


Figure 7. ***Seed density per gram (g^{-1}) of faeces by herbivore species.*** *Graph depicting the average number of germinated seeds per gram (seeds g^{-1}) of herbivore faecal matter using a log transformed offset. Samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between April 2024 and March 2025; exotic herbivores n = 36; (cattle n = 6 and deer) n = 30) and native herbivores n = 106; (eastern grey kangaroo (EGK) n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36). Nativeness pertains to the origin of the plant species and whether it is native, exotic, or declared as noxious (invasive).*

Rarefaction curves

Rarefaction curves signify the diversity of herbivore assemblage at equal sampling intensity. The deer rarefaction curve was the highest overall and still increasing, whereas the cattle rarefaction curve began to plateau around 40 species (Figure 8). Wallaroo and wombat curves rose and plateaued quickly and showed a lower species richness. Eastern grey kangaroo and unknown macropod sample curves showed low species richness but also high uncertainty. Their extrapolation curves supported the high degree of uncertainty of these samples. Furthermore, the extrapolation curves showed that if more seeds were sampled, there would be an expected increase in species richness for deer and to a much lesser extent, cattle. Extrapolation curves for wallaroo and wombats showed that species richness had been captured.

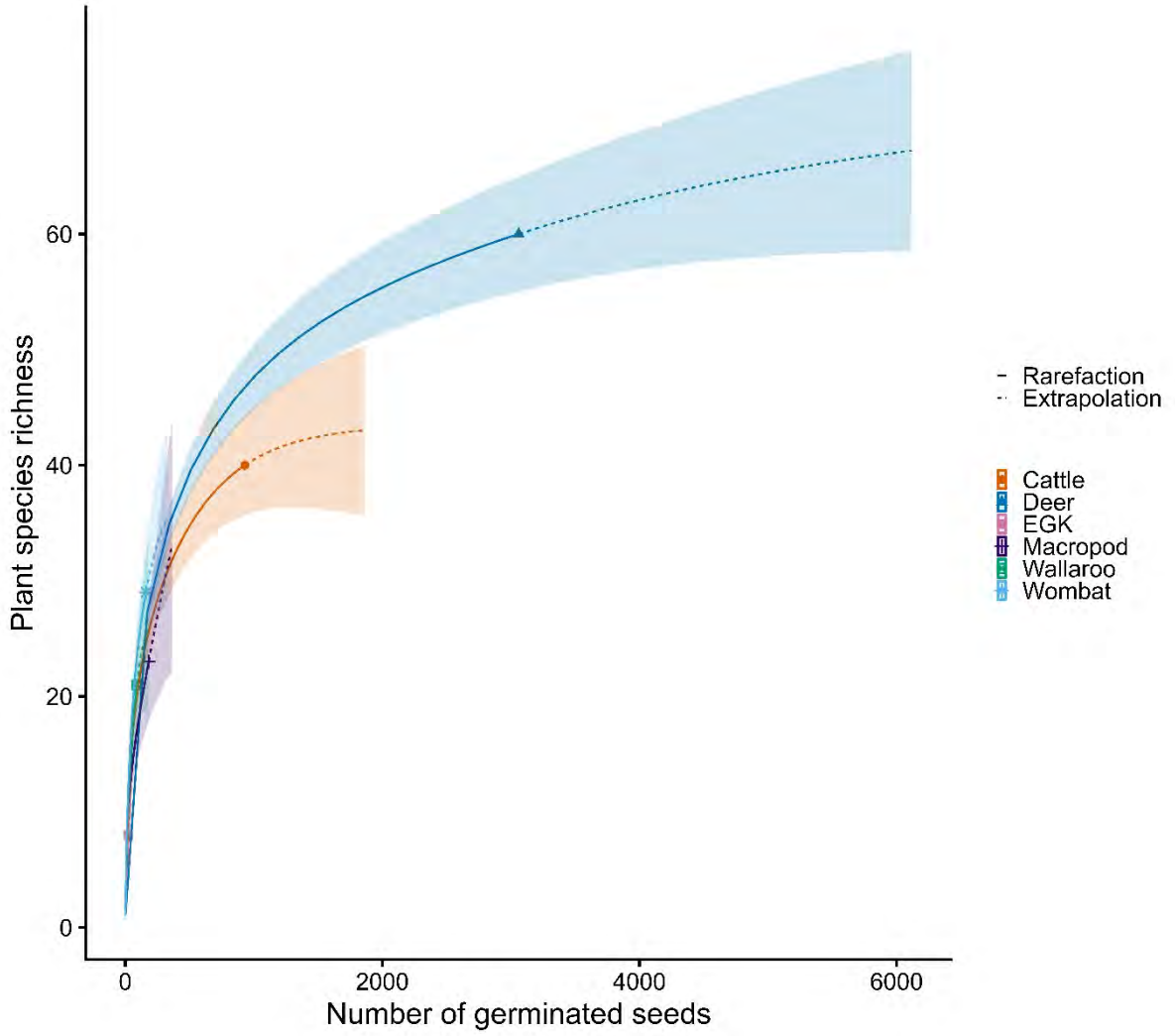


Figure 8. Individual-based rarefaction curves for germinated seed assemblages across herbivores. Richness was standardised by the number of germinated seeds to account for unequal sampling effort between herbivores. Solid lines indicate observed richness, dashed lines indicate extrapolated richness, and shaded regions represent 95% confidence intervals. Samples collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between April 2024 and March 2025; exotic herbivores n = 36; (cattle n = 6 and deer) n = 30) and native herbivores n = 106; (eastern grey kangaroo (EGK) n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36).

Discussion

I expected to see a similarity across the native herbivores in the breadth and number of viable seeds found in their faeces, predominantly due to previous studies showing similar diets (Evans et al., 2006) and their shared feeding strategies. However, my results showed that apart from winter, eastern grey kangaroos and unknown macropods showed little, to no species richness. Further, wombat faeces shared more plant species with the ungulate herbivores than with macropods (Figure 6, 7). This may be explained by a difference in major gut biome (Hume, 1982a), and contrasting digestive strategies. Macropods are foregut fermenters, whereas wombats are hindgut fermenters (Harrop and Hume, 1980, Barboza and Hume, 1992), resulting in longer retention times and dry faceal matter, which is probably more favourable conditions for some seeds (Petre et al., 2015, Soltani et al., 2018).

Overall, negative binomial models predicted that native herbivores have a lower germination count of native and exotic plant seeds than exotic herbivores, particularly in spring and summer (Figure 3). Autumn shows the highest germination count in exotic plants in the exotic herbivore samples. In the context of ecosystem impact, the exotic herbivores have a high species richness of both exotic plants in comparison to the native herbivores (Figure 4, 5), and noticeably more exotic seeds per gram of faecal matter, markedly so in deer samples, and to a lesser extent in cattle (Figure 7). Rarefaction curves support the species richness results, with extrapolation curves suggesting that sampling is likely cloe to complete sampling across th eherbivores except for deer and unknown macropod samples. Extrapolation curves for deer suggest that additional sampling would likely increase the species richness detected, whereas the high degree of uncertainty for unknown macropod samples is likely due to the fact that it is comprised of multiple different species.

It is important to note that raw greenhouse germination counts do not fully capture dispersal effectiveness but rather germination potential (Pakeman and Small, 2009) and it is likely that some plant species were present in the faecal samples but remianed dormant. Furthermore, some species may have increased success rates in greenhouse conditions as evidenced through the single deer

sample that germinated over 1000 *Chenopodium petiolare* seedlings, which may not be representative of the number of seeds germinated in the environment, but nontheless my results highlight the potenital for exotic herbivores to move large numbers of viable seed across the landscape

Not all herbivores are equal.

Herbivores act as ecosystem engineers, through their grazing activity (Bauer and Hoye, 2014, Ross et al., 2020), transportation of nutrients (Augustine et al., 2003, Chang et al., 2018) and seed dispersal (Giombini et al., 2024). However, their engineering roles are not ecologically equivalent. The high propagule loads observed in cattle and deer samples, suggests that the exotic herbivores in this system can exert a disproportionate influence on plant community composition relative to their density, exhibiting keystone species-like effects.

Different plant species exhibit different functional traits, from seed coat and size to dormancy and germination strategies to improve establishment after germination (Boesewinkel and Bouman, 1984, Karaguzel et al., 2004, Escobar et al., 2021). Certain traits are then selected for, based on environmental filters such as the soil moisture, chemical content, competition and disturbance levels (Vandelook et al., 2008, Fraaije et al., 2015). The process of endozoochory may be considered another form of environmental filter, because traits are selected for in the same manner. This is supported by studies that link particular seed traits such as the lack of an appendage, size (Pakeman et al., 2002) and mass of seeds (Couvreur et al., 2005) to enhanced germination success from endozoochory (Picard et al., 2016). For example small seeds have been shown to survive better likely due to limited damage inflicted by chewing (Mouissie et al., 2005a). These traits may be more common in exotic species allowing them to be more successfully germinated. The greater species richness and predicted germination count of both deer and cattle likely reflect this, with their particular gut morphologies better supporting exotic species. Alternatively, it is possible that exotic herbivores preferentially consume exotic plants, or are forced to do so because they are more abundant in the ladnscape.

Fossil evidence shows that open savannah grasses from Eurasia, South America and Africa have co-evolved with primitive mammalian ungulates during the Eocene epoch (33.9 million years ago), at which time many functional traits would have started to emerge. It would thus be expected that ungulate herbivores would be more adept at facilitating the dispersal of American and Eurasian plants (Janzen, 1984). The importance of evolutionary context from a restoration perspective is highlighted by the example of stipoid grasses, a genus of perrenial grasses that comprises over 140 species, that have been evolutionarily linked to modern day ungulates: horses (*Equus spp*.) and pronghorns (*Antilocapra spp.*) (Stebbins, 1981). Currently, at least ten species of South American stipoid grasses are considered highly invasive across the south-east of Australia, with a high liklehood that similar exotic ungulate herbivores share adapted traits that may help faciilitate such invasions. Further studies have shown that in sites with multiple ungulate herbivores present, there is often a large overlap in the plants they disperse via endozoochory, with some plants able to rely on co-occuring ungulates, whereas others are solely dispersed by a single vector (Baltzinger et al., 2019). This supports the idea that both shared evolutionary history and present day functional traits of both plants and herbivores play an important role in germination success.

I acknowledge that greenhouse germination counts represent potential dispersal vectors rather than confirmed field recruitment, but I posit that having multiple exotic herbivores in a system and a more diverse assemblage of germinating seeds, increases the likelihood that at least one species matches the environmental conditions. A study by Kirmer et al. (2012), supports this idea, reporting an increase in biomass production, biodiversity and development through the sowing of high diversity seed mixtures, whereas low-diversity mixtures delayed successional progress in grassland restoration. High diversity seed mixes have also shown to provide compensation for the failure of some species (Lepŝ et al., 2007, Bischoff et al., 2010). In contrast, native herbivores exhibited lower levels of both species richness and abundance of seeds in their faecal deposition, suggesting they are less likely to reinforce invasive plant dominance. In the Australian grassland context, both native herbivores and plants evolved in fire-driven systems (Miller and Murphy,

2017) with a lack of hoofed ungulates (Milewski and Diamond, 2000b). Plant dispersal adaptations are consequently more aligned with fire cues to break dormancy (Williams et al., 2003, Rawson et al., 2013, Hodges et al., 2019), insect pollination (Brundrett et al., 2024) and the gut morphology of small-bodied mammals, predominanlty hind-gut fermenters (Hume, 1982b). Conversly, the scale and composition of ungulate endozoochory is a novel dispersal mechanism in the Australian grassland system.

Exotic herbivores reinforce exotic plant communities.

My results indicate that exotic herbivores support and reinforce exotic plant dominance and create biotic homogenization, replacing native biodiversty with invasive exotic plants (Olden et al., 2004). This is supported by the theory of invasional meltdown, whereby exotic species facilitate and reinforce each others invasion success, and in many cases, increase the overall magnitude of their impact (Howarth, 1985, Simberloff and Von Holle, 1999, Simberloff, 2006).

My findings demonstrate that deer, and to a lesser extent cattle, disperse a high species richness and abundance of seeds through their faecal deposition in comparison to native herbivores, consisting predominantly of exotic and invasive species. Fallow deer move across large spatial scales, with daily home ranges varying from 0.5 km^2 to 9.75 km^2, depending on season and sex (Borkowski and Pudełko, 2007, Morse et al., 2009, Comte et al., 2025). Within their native range, fallow deer often use woodland-forest ecotones, though have demonstrated an increasing preference for cleared and native grassland areas in the east Australian alps (Mccarthy et al., 2025) with populations expanding (Burgin et al., 2015, Potts et al., 2015). Increasing numbers paired with the use of these novel ecosystems, and the long distance movement between them, may further the spatial footprint of invasive plants, by linking grassland patches via long-distance dispersal (Bartuszevige and Endress, 2008).

Domestic ungulate herbivores such as cattle, are used pastorally in grassland biomes aross the world (Lyons et al., 2023, Millett et al., 2025) in staggering numbers, there is an estimated one domesticated herbivore for every two people on earth (Mottet et al., 2018). Most studies analysing

the impacts of ungulate grazing however, were based in North America, Europe and Asia, where native bovine species occur (Gao and Carmel, 2020), while very few occur in ecosystems that naturally lack ungulates, such as Australian grassland systems (Pykälä, 2003, Eldridge and Delgado-Baquerizo, 2017, Bussan, 2022).

My findings suggest that, in the Australian grassland system, ruminants, both domestic and exotic, have introduced a novel gut morphology, where it was previously dominated by marsupial foregut fermenters (Hume, 1982b). The fundamental differences in these gut morphologies play a huge role in seed survival due to differences in seed retention time and associated chemical processes (Lowry, 1996), a critical consideration that is under-studied and underappreciated. My results further suggest that ruminant herbivores represent significant vectors of weed invasion in temperate grasslands propose the need to re-evaluate the impact of domestic grazing animals in native ecosystems and to assess potential negative impacts through endozoochory.

Reinstating native grazing systems

Grassland restoration efforts most often focus on fire, weed spraying, mowing and re-planting of native species. However, if the vectors of exotic plant invasion through endozoochory remain prevalent, restoration interventions risk becoming cyclical and resource intensive which are likely to limit long-term success. The replacement of domestic livestock, with native animals, such as kangaroos, as a sustainable meat alternative has been suggested by Wilson & Edwards (2008). The results of my study add evidence to the case for the benefits of this alternative approach to land management because the number and variety of seeds moved is lower than for exotic herbivores.

Kangaroo populations across much of Australia are in high abundance (Croft and Witte, 2021), and often treated as a pest species or culled to reduce population size (Cowan and Tyndale-Biscoe, 1997, Descovich et al., 2016). Despite this idea requiring a complex social transformation, the replacement of cattle production for iconic native species has been successfully expanded around the world, including the bison (*Bison bison*) in the USA, the red deer (*Cervus elephus*) in Scotland and the springbok (*Antidorcas marsupialis*) in South Africa (Wilson and Edwards, 2008).

The endozoochory impact of kangaroos and wallabies is lower than exotic feral and domestic herbivores, strenghtening the case for this a sustainable solution for the restoration of Australian grasslands.

Conclusion

The result of my study indicates that the ecological impact of endozoochory on temperate grasslands is potentially highly influenced by the abundance and evolutionary history of different herbivores and plant functional traits. Evidence further suggests that the abundance of exotic herbivore species is a key driver of ecological impact (Collins et al., 2020). While domestic herbivores may have a role in biomass management, their potential role in reinforcing exotic plant invasion dynamics requires further consideration. Despite the limitations of greenhouse studies, my complete guild comparison- in a system that had no ungulates until 150 years ago- is rare in the literature and adds to our understanding of the impacts and interactions of both exotic plants and herbivores. Furthering this knowledge is a vital component of grassland conservation, with the active and concurrent management of both necessary for grassland restoration.

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Chapter 4

What goes in doesn’t always come out

Introduction

Global extinctions and the consequential loss of biodiversity is occurring at such an alarming rate that many consider us to be on the brink of the earth's sixth mass extinction event (Ceballos et al., 2015). The continued loss of native species is a major driver of change (Barnosky et al., 2011) and has profound impacts on ecosystem functions (Cardinale et al., 2012, Hooper et al., 2012). Invasive species are one of the major threatening processes behind reduced biodiversity and native species declines, accounting for roughly 20% of all animal extinctions (Clavero and García-Berthou, 2005, Dueñas et al., 2021).

Plant invaders alter landscapes through modifying fire regimes, nutrient cycling and other ecosystem processes that reduce the abundance of native species (Mack et al., 2000, Hejda et al., 2009). As demonstrated by the common ragweed (*Ambrosia artemisiifolia*), a highly invasive and noxious plant common in regions of China. Studies have shown ragweed to be an incredibly fast spreading weed that suppresses native plants and causes habitat homogenization, with densities recorded up to 7000 individuals per square metre (Wan et al., 2005, Huang et al., 2009).

Zoochory is an important ecological process, by which plants have adapted highly specific traits to utilize animals to disperse their seeds (Howe and Smallwood, 1982, Fedriani et al., 2024), with these specific traits often referred to as seed dispersal syndrome (Valenta and Nevo, 2020, Vargas et al., 2023). Long distance dispersal away from the parent plant is advantageous as it reduces the competition with offspring and allows for the potential colonization of new areas (Gelmi-Candusso et al., 2017). Specific mechanisms of endozoochory include epizoochory, the passive attachment to animal fur or feathers (Sorensen, 1986), myrmechory, a specific food body attachment (elaiosome) to seeds to attract and reward ants (Karnish, 2024) and endozoochory, whereby seeds are accidently or deliberately ingested by an animal, survive the gut passage and are deposited in faecal material (Iluz, 2011).

Plant traits such as brightly colored or sugar dense fruit, have evolved to attract vertebrate dispersal vectors and to enhance their endozoochory potential (Gautier-Hion et al., 1985, Razanamandranto et al., 2004, Lepková and Mašková, 2024). This symbiotic relationship between native plants and herbivores is undoubtably a key process in maintaining the succession of native plant species across many habitats. For instance, Anderson et al (2014) showed many native Serengeti plants have specialized traits that enhance their dispersal success via endozoochory, specifically associated with grazing history (Anderson et al., 2014).

However, endozoochory by large grazing mammalian herbivores aiding in the facilitation and spread of exotic plant species is likely an important but often overlooked pathway affecting invasion dynamics and (Panter and Dolman, 2012, Baltzinger et al., 2020, Lozada-Gobilard et al., 2021, Karremans et al., 2023). The omission is likely due to most grassland plants lacking fruiting bodies or obvious traits that could be linked to endozoochory. Though some studies support grazing animals as exotic and invasive plant dispersal vectors, such as domestic cattle in Californian prairies (Chuong et al., 2016) and Pampas grasslands in Argentina (Vignolio and Fernández, 2010).

The association between typical gravity or wind dispersal plants and endozoochory success by grazing animals may be explained by Janzen's proposed theory, foliage is the fruit (Janzen, 1984). The theory posits that the accidental ingestion of herbaceous plant seeds by large grazing mammals over millions of years resulted in the selection of traits that both enhance the propagule load and the edibility of foliage at the time of seeding to act as bait for grazing animals. This hypothesis is rarely mentioned or tested, however it may help to explain why some traits associated with plant invasiveness such as high propagule load, disturbance tolerance and rapid germination (Vavra et al., 2007) may be linked to enhanced dispersal by endozoochory. Although direct evidence of co-evolution is difficult to demonstrate, both extant and extinct megaherbivores are thought to have exerted strong selective pressures on plant dispersal strategies (Janzen and Martin, 1982, Søndergaard et al., 2025).

Temperate grasslands are found on every continent on earth except for Antarctica and are of great importance to human life (Singh et al., 1983, Scholtz and Twidwell, 2022), yet they are considered a globally endangered terrestrial habitat type (White et al., 2000, Török et al., 2021). Grasslands have been used for pastoralism, grazing domestic animals and have undergone extensive land use changes. Furthermore, European colonization and globalization facilitated the widespread global movement and introduction of these practices, making temperate grasslands highly susceptible to the invasion of exotic species, due to their intrinsic link to pastoralism and plant cultivation (Macdougall et al., 2018).

The geographic isolation of the Australian continent led to the evolution of unique mammalian herbivores, soft-footed marsupials, resulted in unique responses to disturbance by native grassland plants (Mcintyre and Lavorel, 1994a, Dawson, 2006). Furthermore, the historical use of fire by the indigenous peoples of Australia means that many native grasslands plant species may have specialized traits associated with fire regimes, rather than heavy grazing (Gill, 1975, Bradstock et al., 2002, Lamont and Downes, 2011).

A study by Kimball and Schiffman (2003) showed that native perennial grasses declined in both abundance and growth following cattle grazing, whereas European exotic grasses were unaffected. It may, therefore, be reasonable to assume that exotic plants which have co-evolved with continuous ungulate grazing pressure, maintain grazing-tolerant traits which may afford them an advantage in Australian grassland systems.

The lack of sweet, fleshy fruiting bodies found in plants such as grasses (Gibson, 2009), which are typically associated with herbivore grazers, may have caused an oversight in the role that endozoochory plays in influencing the dispersal of exotic and invasive species. This is particularly relevant in the management of Australian grasslands, where exotic grazing mammals are in high abundance (Freeland, 1990a, Hartley et al., 2022). The effective management of invasive plant

species requires understanding of the mechanisms driving their spread and continued persistence in the landscape.

For this study I hypothesized that the co-evolutionary history between ungulate herbivores and exotic plant species will be a determinant of endozoochorous germination success (Holmgren, 2002), with the expectation that exotic herbivores will be more adept at spreading viable exotic seeds than native herbivores.

To my knowledge no other study has looked at the comparative analysis of germinated seed assemblages and diet analysis of a mammalian guild in this way. To test my hypothesis I asked: (1) if exotic plant species disproportionately represent germinated assemblages compared to diet composition? (2) if certain plant functional groups are more adept at dispersal by endozoochory than others, relative to consumption? (3) Is there evidence to suggest that we can predict risk factors associated with highly invasive plant species being spread via endozoochory?

Methods:

Site and study species

The study took place in the Ginninderry Conservation Corridor (GCC) in the Australian Capital Territory (ACT), Australia (35°13’54.8” S, 148°58’35.7” E (Ginninderry Conservation Trust et al., 2018)). GCC is a 580-ha site, bordered by the Murrumbidgee River on one side and urban development on the other. Historically, much of the GCC was used as pasture, but is now comprised of a mosaic of different habitat types, including remnant patches of critically endangered box-gum grassy woodland. Dominant native herbivore species across the site are all marsupials and include the eastern grey kangaroo (*Macropus giganteus*), common wallaroo (*Osphranter robustus*) and the common wombat (*Vombatus ursinus*), with annual macropod counts averaging 162 animals. A domestic cattle (*Bos taurus*) herd of 40-80 individuals is rotated across the site throughout the year as a vegetation biomass control measure, and a population of feral fallow (*Dama dama*), and to a lesser extent sambar (*Rusa unicolor*) deer, exist in large numbers throughout the surrounding

Namadgi National Park (Kennedy, 2025), with significant herds regularly using or passing through the GCC

Data collection

Diet dataset

Fresh faecal samples were collected from 10 zones across the GCC between October 2022 and July 2024 (Spring; 18 October - 17 November, Summer; 22 January –16 February, Autumn; 10 – 24 May, Winter; 4 – 22 September ’23 & 25 June – 16 July ‘24). A total of 309 exotic herbivores samples; (cattle n = 161 and deer n = 148) and 360 native herbivore samples; (eastern grey kangaroo n=21, unknown macropod species n = 190, common wallaroo n = 74, and the common wombat n = 75) were collected. DNA extraction and metabarcoding was performed to determine the diet composition but see Chapter 2 for a complete description of the methods and analysis for this dataset.

Germinated seed dataset

Fresh faecal samples were collected from 12 sites across the GCC April 2024 and March 2025 (Autumn; 02–22 April, Winter; 07-13 July, Spring; 18-29 November, Summer; 12 February–04 March). After grouping the samples according to site, and season, a total of 106 native herbivore samples; (10 eastern grey kangaroo, 39 wallaroo, 21 unknown macropods and 36 wombat), and 36 exotic herbivore samples; (6 cattle and 30 deer) were recorded. The complete methods are described in Chapter 3 but briefly; samples were air-dried, brushed, and polished, to remove any seeds picked up from the environment, and then underwent stratification and were grown in a greenhouse. Emerged seedlings were given a unique identification code and grown as reference for emerging seedlings as the experiment progressed. DNA-based identification was performed to confirm plant species identification.

Dominance index

A dominance index was calculated for the germinated seed assemblage and diet, the seed dominance index was assigned to hexagonal bins on the spatial map, and the diet dominance index

was plotted as a box plot. Dominance index was calculated as the difference between native and exotic plant genera divided by the total to standardise the index, using the following formula;

$$dominance\ index = \frac{native\ plant\ genera\ occurence - exotic\ plant\ genera\ occurence}{total\ occurences}$$

Where values of 1 indicate entirely native plant taxa, values of zero indicate equal occurrence of both native and exotic plant taxa, and -1 values indicate entirely exotic plant taxa.

Germination persistence

To quantify the relative persistence to germination of the plant genera through the endozoochory process, I compared the log-transformed germination persistence index by comparing the frequency of occurrence of genera found in both the diet analysis and seed germination assemblage. This method was based on log response ratios and binomial responses in Hedges et al. (1999), however I used occurrence frequencies rather than treatment means, used base-2 logarithms instead of the standard log response and added a pseudo count (+1) to account for the zero-inflated data (Anscombe, 1956, Haldane, 1956). I used a base-2 logarithm because it provides a more intuitive interpretation of persistence where each unit increase represents a doubling in relative occurrence. Log_2 persistence was calculated using the following formula;

$$Log_2 germination\ index = log_2\left(\frac{(seed\ occurence + 1)}{(diet\ occurence + 1)}\right)$$

Where positive values indicate the genera to be more common in germinated seed assemblages and negative values indicate the genera are more common in the diet analysis.

Mapping and statistical analysis

All mapping and statistical analysis was conducted and visualised using the tidyr and dplyr packages (Wickham, 2016) in R studio (Rstudio, 2023). All maps were generated using GPS locations of herbivore faecal samples with hexagonal bins used to aggregate samples into equal-area cells to account for samples being pooled for germination study, using the sf and tmap packages

(Pebesma, 2018, Tennekes, 2018). For all satellite imagery and national vegetation index satellite imagery (NVIS) I used the terra package (Hijmans, 2020).

All statistical models used occurrence data for analysis. Linear models were used to analyse persistence values and included season, plant nativeness, plant functional group, herbivore nativeness (exotic or native), and herbivore species, as well as their pair-wise interactions. Reported p-values were generated using Type II ANOVAs (Fox and Weisberg, 2018). Since persistence violated normal distribution, I compared variable responses using Tukey adjusted pairwise comparisons and estimated the marginal means of model outputs using the emmeans package (Lenth et al., 2019, Lenth, 2025).

For plant nativeness proportional data, I fitted beta regression negative binomial generalized linear mixed models (glm) using the glmmTMB packages (Brooks et al., 2017). Reported p-values were generated using Type III Wald X tests (Fox and Weisberg, 2018).

Results

I found an overall pattern of both exotic and invasive plant taxa having over-representation in the germinated seed assemblage relative to the taxa found in the diet, with grasses, herbs and sedges representing the plant functional groups of which most of the germinated seeds belonged to.

Spatial patterns

A total of 4944 germinated seeds were recorded in the greenhouse experiment and based on my spatial mapping of GPS locations of faecal samples collected, seedlings would have potentially germinated across the site with no obvious pattern in deposition location but rather a random distribution. I did, however, find that of all germinated seed assemblages, exotic plant species contributed between 50 -100% of all but one hexagon, which was native dominated (Figure 1; left). The overall mean number of seeds per deposition was 0.97 seeds, with a minimum value of zero and the maximum mean number of 391 seeds per deposition (Figure 1; right). No obvious pattern in number of seeds per deposition was detected.

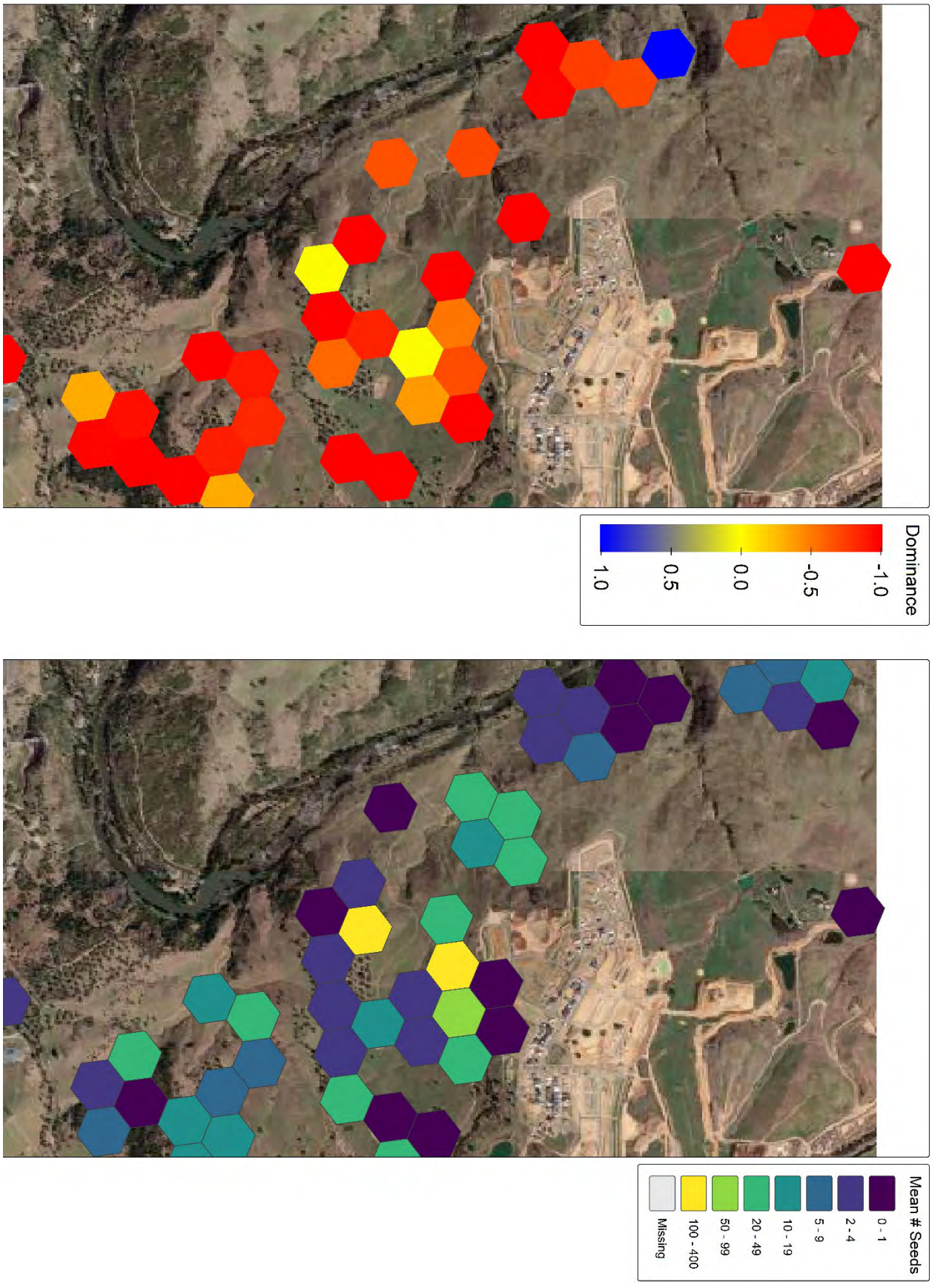


Figure 1. (Left): Hexagonal bin map depicting spatial variation in germinated seed nativeness dominance. *GPS locations of herbivore faecal samples were aggregated into equal-area hexagonal*

cells based on sampling locations. Hexagons are coloured according to dominance which was calculated as the relative dominance of native and exotic taxa, with positive values (red) indicating an exotic-dominated seed assemblage, and negative values (blue) indicating a native-dominated seed assemblage. Values of zero (yellow) indicate equal representation of both native and exotic taxa. Satellite imagery of the study site is shown as the basemap. ***(Right): Hexagonal bin map depicting spatial variation in germinated seed dispersal efficiency.*** *GPS locations of herbivore faecal samples were aggregated into equal-area hexagonal cells based on sampling locations. Hexagons are coloured according to the mean number of germinated seeds per faecal sample recorded within that cell. Higher values indicate areas where herbivores deposited a greater number of viable seeds per faecal sample. Satellite imagery of the study site is shown as the basemap. Herbivore samples were collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between April 2024 and March 2025. The study comprises of exotic herbivores n = 36; (cattle n = 6 and deer n = 30) and native herbivores n = 106; (eastern grey kangaroo (EGK) n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36).*

Exotic species proportions

Based on Beta regression negative binomial generalized linear models, the proportion of exotic plant species differed significantly by dataset (Type III Wald chi-square tests; *p = 0.0008*) and herbivore (Type III Wald chi-square tests; *p =0.0007*), as did their pairwise interaction (Type III Wald chi-square tests; *p =0.0443*). Deer (*Tukey-adjusted p = 0.032*) and cattle (*Tukey-adjusted p = 0.038*) samples both had a significantly higher proportion of exotic plants in the germinated seed dataset when compared to the diet, as did wallaroo samples, but to a lesser extent (*Tukey-adjusted p = 0.45*). Wombat, eastern grey kangaroos, and macropod samples showed similar proportions of exotic plants in both germinated seed assemblages and taxa recorded on their diet (Figure 2). DHARMa residual diagnostic tests showed no evidence of over or under dispersion in the data and detected no evidence of extreme outliers. The Kolmogorov–Smirnov (KS) test did however find

significant deviation from the expected distribution; however, this was the best fit model with the large number of zeros in the data driven by native genera.

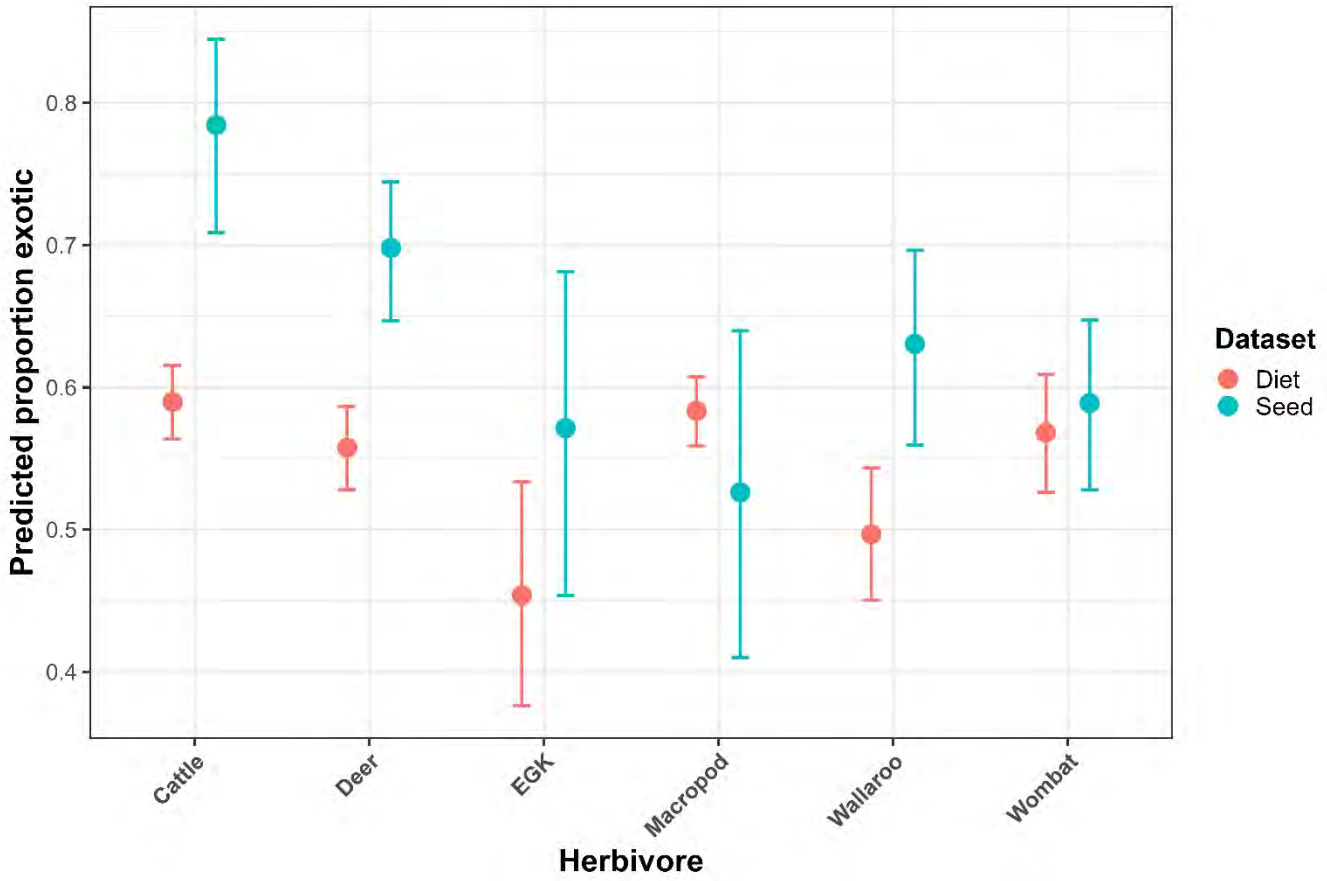


Figure 2. ***Proportion on exotic plants found germinated and consumed by an herbivore guild.*** *Graph depicting the beta regression negative binomial generalized linear model mean responses of the exotic proportion of taxa found in the different datasets; Diet (diet analysis) and Seed (seeds germinated), both from herbivore faecal material). Herbivore samples were collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between October 2022 and July 2024 for the diet analysis and between April 2024 and March 2025 for the germination study. The diet analysis comprises of exotic herbivores n = 309; (cattle n = 161 and deer n = 148) and native herbivores n = 360; (eastern grey kangaroo n=21, unknown macropod species n = 190, common wallaroo n = 74, and the common wombat n = 75). The seed germination study comprises of exotic herbivores n = 36; (cattle n = 6 and deer n = 30) and native herbivores n = 106; (eastern grey*

kangaroo (EGK) n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36).

Germination persistence

In total, 95 genera were present only in the diet analysis and 19 only in germinated seed assemblage. Four invasive species were detected in both the germinated seed assemblage and the diet analysis. The 12 plant genera that represented the greatest divergence from equal representation in both diet taxa and germinated seed assemblages were comprised of exotic species (Figure 3). The eight genera with positive log germination persistence values all represent at least a 1.5 order of magnitude over-representation in the germinated seed assemblage when compared to the diet analysis. Winter and summer samples showed the greatest persistence of germinated seeds, however the invasive *Eragrostis curvula* was only disproportionately represented in the seed assemblage during spring and summer.

The three genera with negative values, *Medicago spp*., *Eleocharis spp*., and *Acaena spp.* represent absence in the germinated seed assemblage dataset, but exceedingly high occurrences in the diet.

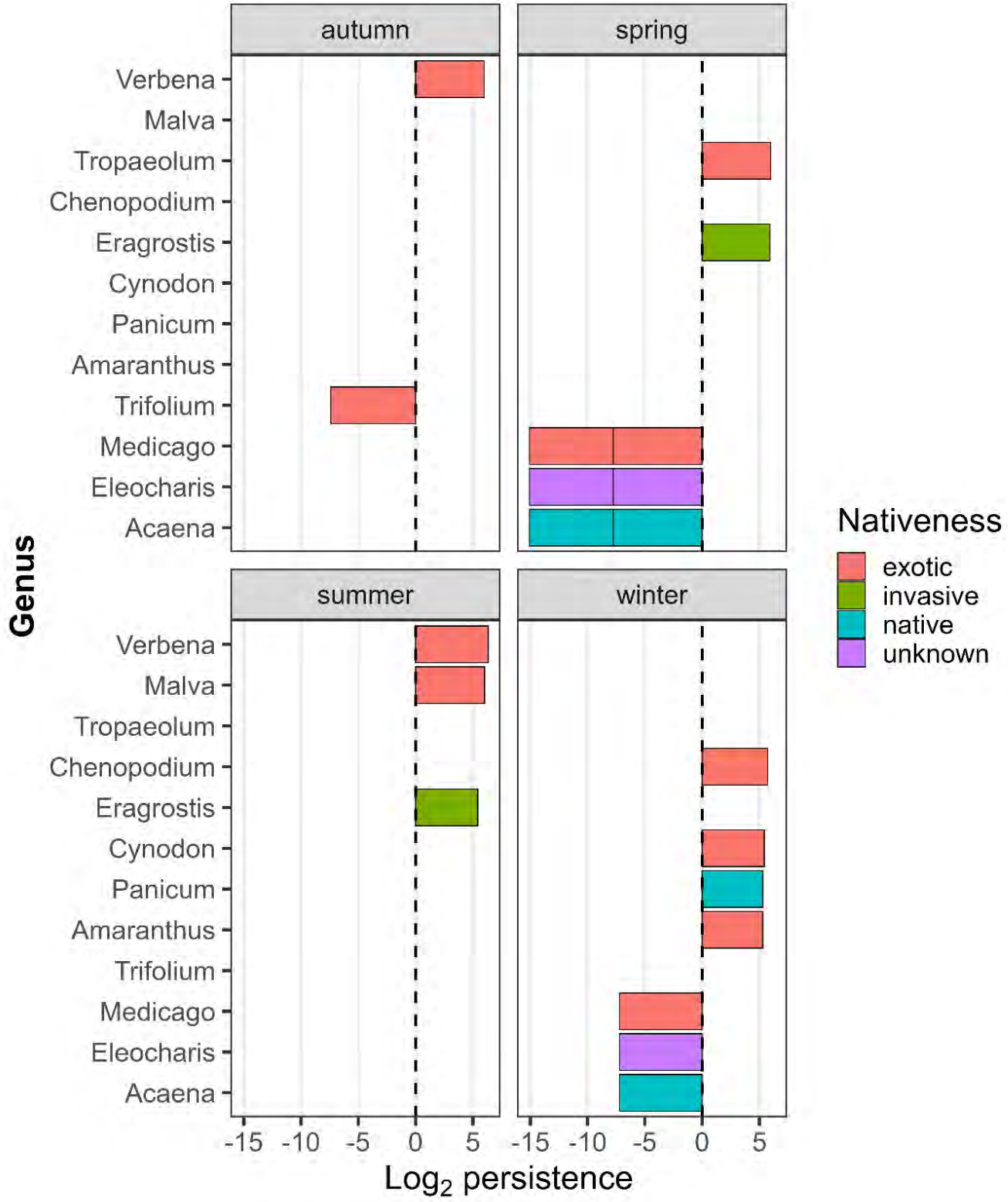


Figure 3. ***Top 12 genera which showed the greatest divergence from equal representation in the diet and germinated seed assemblages, both from herbivore faecal material.*** *Log_2 persistence represents germination persistence, that is, the degree to which genera were over- or under-represented in seed assemblages relative to its abundance in the diet. Positive germination*

persistence values of five represent 1.5 orders of magnitude more represented in seed assemblage, and negative germination persistence of five represents 1.5 orders of magnitude more represented in the diet assemblage. Germination persistence values ±15 represent a genus that are not only absent from one assemblage relative to the other but are found in exceedingly high occurrences in their respective dataset. Herbivore samples were collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between October 2022 and July 2024 for the diet analysis and between April 2024 and March 2025 for the germination study. The diet analysis comprises of exotic herbivores n = 309; (cattle n = 161 and deer n = 148) and native herbivores n = 360; (eastern grey kangaroo n=21, unknown macropod species n = 190, common wallaroo n = 74, and the common wombat n = 75). The seed germination study comprises of exotic herbivores n = 36; (cattle n = 6 and deer n = 30) and native herbivores n = 106; (eastern grey kangaroo (EGK) n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36). Plant nativeness pertains to the origin of the plant species (native, exotic or unknown nativeness), unknown nativeness is due to a taxonomic resolution of family level comprising of genera that could fall into either category.

Plant nativeness

Based on linear models, the log germination persistence values by plant nativeness differed significantly by herbivore, nativeness, and season (*all $p < 0.0001$*), as did the two-way interaction between herbivore and season ($p < 0.0001$) (Figure 4), with invasive plants being significantly different in persistence in both winter ($p = 0.0101$) and summer samples ($p = 0.0189$). Deer samples showed invasive seed germination persistence values in all seasons and were the only herbivore to have any positive germination persistence values in autumn. Eastern grey kangaroo samples showed positive germination persistence of all plants regardless of nativeness since there were no samples represented in the diet dataset in spring. Eastern grey kangaroo samples also had the smallest negative germination persistence values across all seasons except for autumn, which indicated a similar occurrence of plant genera in both the diet and seed datasets. Apart from spring,

cattle samples showed the greatest number of negative germination persistence values indicating high occurrences of some plant genera in the diet that were absent from the germinated seed assemblage.

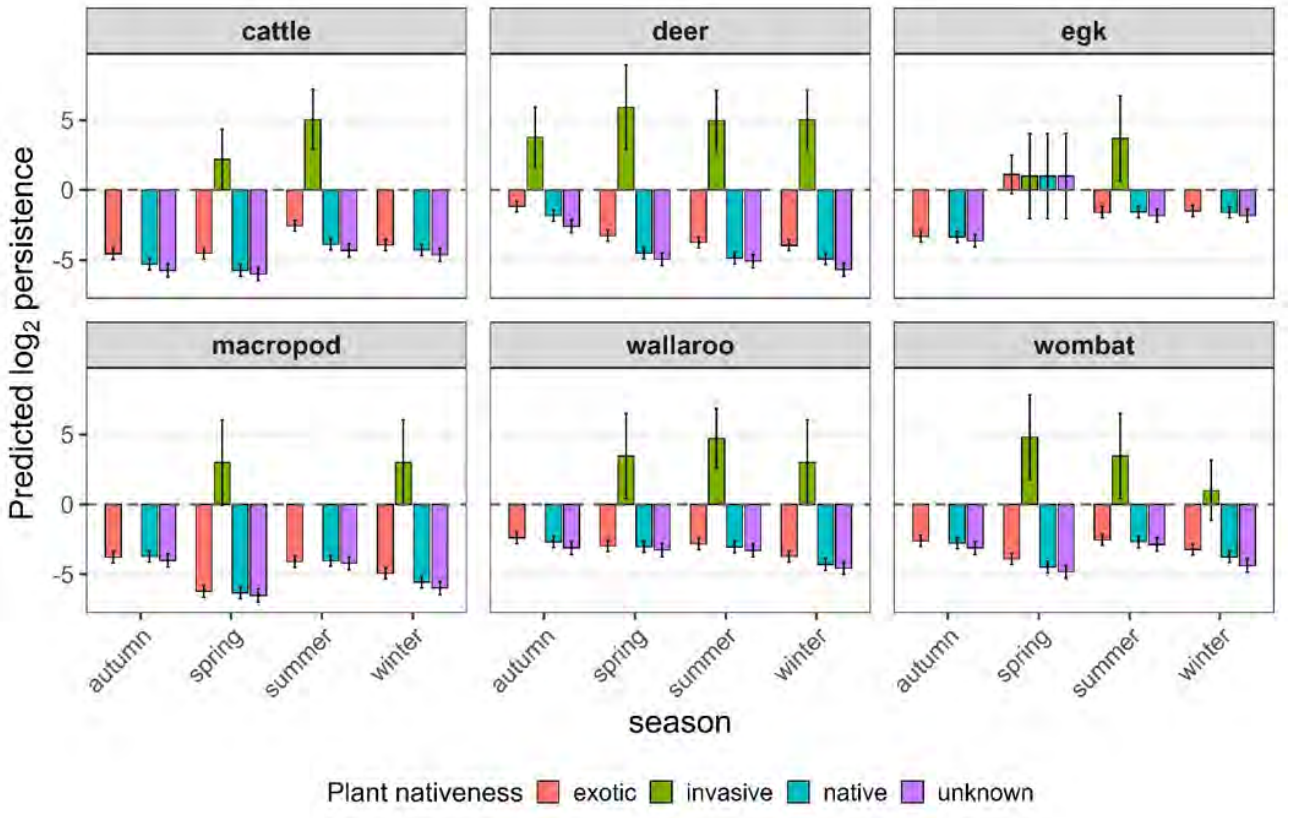


Figure 4. ***Boxplot depicting the predicted mean germination persistence values by plant nativeness across seasons and by herbivore.*** *Log_2 persistence represents germination persistence, that is, the degree to which genera were over- or under-represented in seed assemblages relative to its abundance in the diet. Positive germination persistence values of five represent 1.5 orders of magnitude more represented in seed assemblage, and negative germination persistence values of five represents 1.5 orders of magnitude more represented in the diet assemblage. Herbivore samples were collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between October 2022 and July 2024 for the diet analysis and between April 2024 and March 2025 for the germination study. The diet analysis comprises of exotic herbivores n = 309; (cattle n = 161 and deer n = 148) and native herbivores n = 360; (eastern grey kangaroo n=21, unknown macropod species n = 190, common wallaroo n = 74, and the common wombat n = 75). The seed germination*

*study comprises of exotic herbivores n = 36; (cattle n = 6 and deer n = 30) and native herbivores n = 106; (eastern grey kangaroo (EGK) n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36). Note** There were no eastern grey kangaroo samples present in the diet dataset in spring.*

Plant functional groups

Based on linear models, the log germination persistence values by plant functional group were significantly different by herbivore, season, plant nativeness and functional group (*all; $p < 0.0001$*), as was the pairwise interaction between herbivore and plant nativeness and herbivore and season (all; *$p = 0.0001$*). The combined effect of plant nativeness, functional group and season also showed significant differences *($p = 0.002$*). Overall, all plant functional groups occurred more in the diet assemblage than in the germinated seed assemblage, however, the models indicated that invasive grasses, shrubs and herbs all exhibited significantly greater persistence than did other functional groups (all; Tukey *adj. $p < 0.001$*, Figure 5). The invasive species driving the positive persistence values by functional group were, shrub: European blackberry (*Rubus fruticosus),* herb: St John's wort *(Hypericum perforatum*) and poison hemlock *(Conium maculatum),* and grass: African lovegrass (*Eragrostis curvula*).

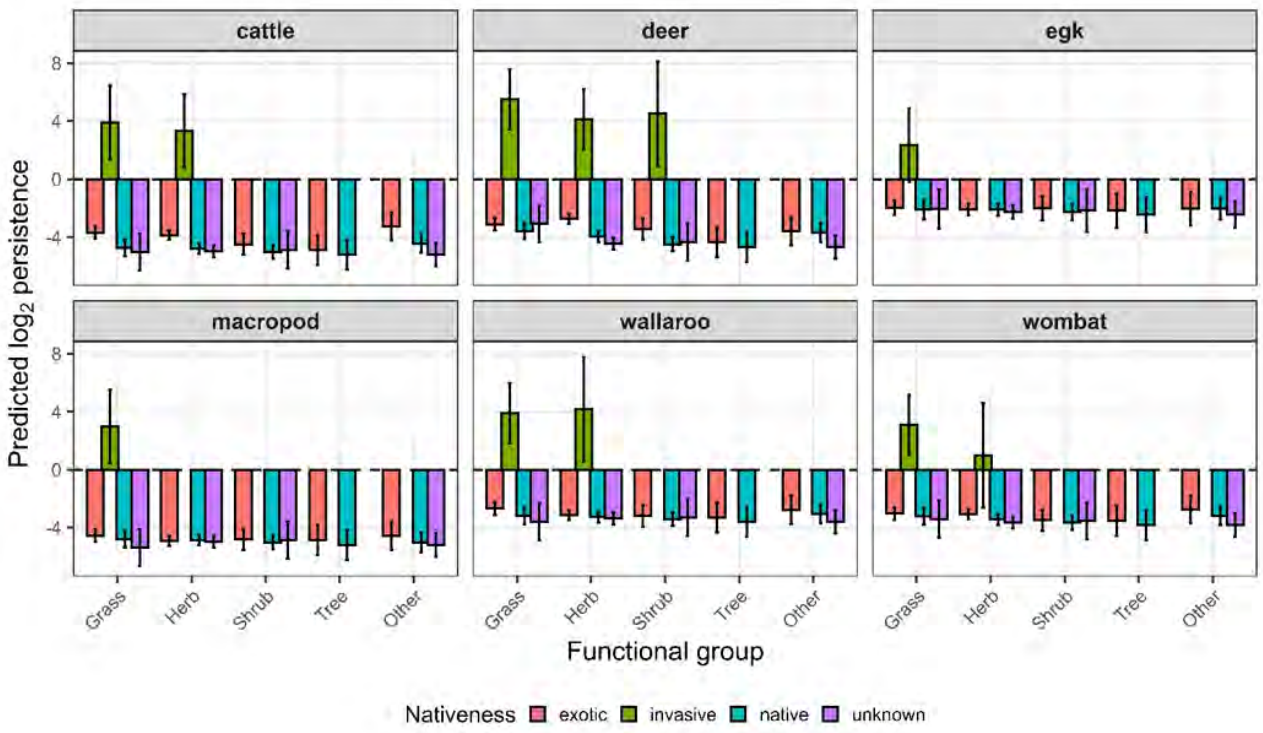


Figure 5. ***Boxplot depicting the predicted spread of germination persistence values by plant functional group in the diet and germinated seed assemblages, both from herbivore faecal material.*** *Estimated Log₂ persistence values represent germination persistence and are based on linear model represents the degree to which genera were over- or under-represented in seed assemblages relative to its abundance in the diet. Positive germination persistence values of five represent 1.5 orders of magnitude more represented in seed assemblage, and negative germination persistence values of five represents 1.5 orders of magnitude more represented in the diet assemblage. Herbivore samples were collected across the Ginninderry Conservation Corridor, Australian Capital Territory, between October 2022 and July 2024 for the diet analysis and between April 2024 and March 2025 for the germination study. The diet analysis comprises of exotic herbivores n = 309; (cattle n = 161 and deer n = 148) and native herbivores n = 360; (eastern grey kangaroo n=21, unknown macropod species n = 190, common wallaroo n = 74, and the common wombat n = 75). The seed germination study comprises of exotic herbivores n = 36; (cattle n = 6 and deer n = 30) and native herbivores n = 106; (eastern grey kangaroo n=20, unknown macropod species n = 21, common wallaroo n = 39, and the common wombat n = 36). Plant nativeness*

pertains to the origin of the plant species (native, exotic or unknown nativeness), unknown nativeness is due to a taxonomic resolution of family level comprising of genera that could fall into either category.

Discussion

Dietary composition only partially reflected germination success, indicating that consumption alone is a poor predictor of endozoochory potential as most genera detected in the diet did not germinate over the course of the greenhouse experiment. Conversely, a few taxa were disproportionately represented in the germination samples, indicating a high propensity for endozoochory as a dispersal mechanism for these species.

The only native plant species to show germination persistence in the seed assemblage was hairy panic grass (*Panicum effusum*), which occurred in winter. A study in the south-eastern Australia showed that *Panicum effusum* seeds required smoke as a dormancy breaker (Read and Bellairs, 1999), however, a study in Iran demonstrated this species persisted in the seed bank producing low abundances of germinated seedlings without a dormancy breaker (Alijani et al., 2023). The addition of gibberellic acid in the germination study may have aided germination success, however, under the right conditions this species could naturally germinate, with other species within the genera able to persist in seed banks for up to 7-years (Brock, 2011).

The remaining species that persisted in the germinated seed assemblage were all exotic or invasive plant species. Of the genera indicated as having the greatest persistence in the seed assemblage, six were herbaceous and three were grasses. When all plants were combined by functional groups, linear models predicted invasive grasses to be the most likely to persist in the seed assemblage, followed by invasive herbs. This trend was driven by the high abundance of African lovegrass (*Eragrostis curvula*) propagules across all herbivore samples, and the combined abundance of St John's wort (*Hypericum perforatum)* and poison hemlock (*Conium maculatum*) in cattle, deer and wallaroo samples. However, endozoochory success is likely driven by species

specific traits not completely captured by functional group classifications. The seasonal persistence of different plant species may indicate that particular risk factors could be avoided. For example, only one genus persisted in the seed assemblage in autumn, implying the use of cattle grazing for biomass reduction of some invasive species may be most effective during this time. However, a study by Gioria and Pyšek (2016) indicated that invasive species dominated the seed bank of invaded sites in Europe, as supported by other studies (Krinke et al., 2005, Gioria and Osborne, 2010). The preservation of viable but dormant exotic seeds in the seedbank, further illustrates the long-term consequences of exotic and invasive seed dispersal across fragmented Australian temperate grasslands.

Surprisingly, several genera of fern were found in germinated seed assemblages, but no detections of fern were present in the diet of any herbivore. It is unlikely that this is due to contamination as faecal material was brushed thoroughly prior to any further processing. This is very likely a detection problem as although *trn*L primers were designed for broad plant detection, they are known to perform poorly at amplifying pteridophytes, leading to under-representation (Taberlet et al., 2007). However, ferns produce over 2.2 million spores which are distributed across a single frond, making their accidental consumption highly likely (Rose and Dassler, 2017, Brock, 2025). Previous research supports fern species to have successfully dispersed by endozoochory through other mammalian species (Boch et al., 2016, Brock and Collier, 2020, Pauly et al., 2025). I was surprised to see little seasonal differences in functional groups; however, the considerable diversity and number of species within each functional group must be emphasized as contributing to this result.

Invasion meltdown and homogenization

Contrary to expectations, I found no evidence of spatial use or propagule pressure hotspots based on the deposition of fecal material across the study site. Instead, I discovered that herbivore activity, based on faecal material, was widespread across the landscape, likely resulting in broadly distributed propagules. This is suggestive of a landscape scale dispersal of seeds through

endozoochory, rather than localized invasion hotspots. The widespread dispersal of exotic propagules, particularly by deer and cattle, supports the idea that exotic herbivores in this system have the potential to facilitate invasion meltdown, whereby exotic species facilitate and reinforce each others invasion success, potentially increasing the overall magnitude of their impact (Howarth, 1985, Simberloff and Von Holle, 1999, Simberloff, 2006). Apart from the highly invasive plant species which persist regardless of the herbivore species, the high proportion of exotic species persisting in the seed assemblage occurred in deer and cattle samples.

Aside from simply depositing high loads of exotic seeds, fallow deer have been shown to travel at least 2km daily, with home ranges over 600 ha across Eastern Australia (Comte et al., 2025). The large spatial movements of deer allow them to act as mobile links for propagules, connecting invaded and less invaded habitats. Furthermore, ungulate herbivores create far more disturbance of the soil (Evans, 1997) due to their hard-hooved feet and grazing behaviors, which creates gaps in the vegetations and allows for the succession of new propagules to germinate (Belsky, 1986, Barney et al., 2016). As my results show, the concurrent disturbance events and deposition of upwards of 400 seeds dominated by exotic species, could allow these exotic species a further competitive advantage (Lockwood et al., 2005). Further evidence has suggested that ongoing propagule pressure further aids in invasion by introducing genetic variation which allows for adaptation to new environments (Simberloff, 2009). It would be reasonable to expect that the repeated dispersal of the same suite of exotic and invasive species may promote biotic homogenization and reduce spatial variation in plant communities.

My findings support this hypothesis with the persistence of a few exotic and invasive plant species that had high occurrences in the germinated seed assemblage compared to diet composition. Similar patterns have been observed in other invaded systems, where a few highly abundant exotic herbivores have a disproportionate effect on exotic plant success. One such example is the invasion of two succulents, *Carpobrotus edulis* and *Carpobrotus acinaciformis* across an island archipelago off the siliceous coast, south of France. The two exotic mammals found across the islands, the

European rat (*Rattus rattus*) and European rabbit (*Oryctolagus cuniculus*) acted as the primary seed dispersers with enhanced germination success recorded through endozoochory (Bourgeois et al., 2005).

Furthermore, cattle have been shown to enhance the spread of some plant species across fragmented grasslands in Sweden, with habitat specialists being the most likely to face local extinction (Plue and Cousins, 2018). I posit that this South-East Australian grassland system is likely already experiencing a degree of homogenization, as evidenced by the dominance of exotic biomass consumed paired with the greater germination potential of exotic and invasive plant seeds being deposited into the system. These findings are alarming as remnant temperate grasslands communities are already fragmented and highly susceptible to exotic invasion (Prober and Thiele, 2005, Williams and Morgan, 2015).

Plant traits linked to invasion success

Many plant species increase their investment into dispersal appendages such as hooks and barbs which act as specialized adaptations for dispersion mechanisms such as wind, water or animal dispersion (Leslie et al., 2017, Ansong, 2024, Gould and Valdez, 2024). However, my findings suggest that in the context of non-fruiting grassland species, it may be seeds without specialized traits and appendages to attract herbivores that are more likely to have success as invasive species. Some of these plant traits are thought to play a role in the shift from naturalized exotic to invasive species and include high seed production, persistence in seed banks and rapid establishment (Murray and Phillips, 2010). These plant traits overlap with those proposed in Janzen's (1984?) foliage as fruit theory. The theory posits that the accidental ingestion of seeds over time resulted in small seed size, large numbers and resistant seed coats, all traits that evolved to enhance both the overall survivability in the landscape, and the journey through a grazing animal's gut (Janzen, 1984).

Although I did not empirically test this theory, there are many studies that have shown small, round seeds to be the most likely to germinate through mammalian endozoochory (Mouissie

et al., 2005b, Henrik Bruun and Poschlod, 2006, Kuiters and Huiskes, 2010, Thomson et al., 2010, Iravani et al., 2011). Un-specialized seeds (without specialized appendages) were also found to form the bulk of species germinating from sheep and rabbit dung in Scotland (Pakeman et al., 2002). Furthermore, similar patterns were recorded in a forest ecosystem in Britain comparing endozoochory with six large herbivores. They found only 7% of all seeds recorded had endozoochory specific traits (flesh, nut or specialized appendages), whereas 36% of seeds were without specific dispersal mechanisms, instead comprised of small and highly abundant seeds (Eycott et al., 2007). It has also been shown that in Australian grasslands, macropods deliberately consume seedheads when available, consequently dispersing some plant species that are not specially adapted to endozoochory (Jarman, 1994).

This evidence is in partial favor of Janzen's theory; however, he also posits that the foliage itself should adopt traits that make them more desirable for the herbivores (Janzen, 1984). This is likely true for some grassland plant species, however, as an example, African lovegrass (*Eragrostis curvula*), which I found to represent the species with the greatest persistence in the germinated seed assemblage, only partially supports this theory. African lovegrass, classified as invasive across many continents including Australia (Csurhes et al., 2016) and the USA (Firn et al., 2018), was only found in very few occurrences in the diet dataset. This is likely driven by the fact that as adult plants, they are generally considered undesirable, and only moderately palatable by grazing animals (Leigh, 1961, Roberts et al., 2021). This directly opposes Janzen's idea that to increase endozoochory success, foliage should be more palatable. However, their small seeds are stored in highly condensed panicles, with one panicle able to produce up to 1000 seeds at a time (Johnston and Cregan, 1980). Furthermore, the seeds have a high survivability rate that favors endozoochory and long persistence in the seed bank, which is evidenced in the output of seeds germinated which may correlate to invasion success (Rejmánek, 1999, Hutang et al., 2023, Price et al., 2023).

This further supports the idea that unspecialized seeds, that is; small, round, and not intrinsically linked to a specific dispersal mechanism, is an adaptive strategy by plants to increase

their persistence in a landscape under fluctuating environmental conditions. It is likely that these traits have an evolutionary link to large herbivore grazing pressure and are concurrent to the invasive nature of many grassland plant species.

Grazing in grasslands

Endozoochory is not an entirely novel ecological processes in Australia, there are many endemic plants species that have evolved fleshy fruiting bodies that facilitate seed dispersal by vertebrates, with birds and frugivorous mammals representing the predominant dispersal vectors for many native woody taxa (Wenny, 2001, Dennis et al., 2005, Calvino-Cancela, 2011, Groom and Lamont, 2015, Blanco et al., 2020). In contrast, the majority of Australian grassy and herbaceous species exhibit dispersal syndromes associated with gravity, wind, fire and ants (myrmecochory), rather than adaptations for dispersal by large mammalian herbivores (Braithwaite, 1990, Hobbs and Yates, 2003, Hill, 2004, Standish et al., 2007, Warren and Giladi, 2014, Miller and Murphy, 2017, Bryceson et al., 2023).

Although endozoochory undoubtedly occurred in Australia's history, the expansion of C4 dominated grasslands occurred later in Australia than on other continents, during the Miocene ~3.5 million years ago (Andrae et al., 2018, Tyler Karp et al., 2021). C4 grasses dispersed eastward following a period of warmer and dryer conditions, and relied primarily on wind dispersal (Osborne, 2008, Bryceson et al., 2023). This shift and increase in grass abundance likely stimulated the evolutionary switch from browsing to grazing in the modern kangaroos (Bryceson et al., 2023). However contemporary Australian herbivores such as wombats and kangaroos did not spread from Northern Australia (Queensland) until the Early Pleistocene (Strömberg, 2011). Some Australian herbaceous genera, including *Solanum*, appear to have evolved traits such as prickles and spines in response to an increase in marsupial herbivory, making them particularly well adapted for epizoochory rather than endozoochory (Milton et al., 1990)

Nevertheless, as previously mentioned, seeds possessing traits such as small, rounded propagules, seem to frequently survive gut passage (Pakeman et al., 2002, Henrik Bruun and Poschlod, 2006,

Lovas-Kiss et al., 2020), suggesting that successful endozoochory in Australian grasslands may often involve opportunistic dispersal rather than specialized evolutionary adaptions. Differences in digestive physiology between marsupial herbivores and ungulates is also likely to influence endozoochory success and likely works as an environmental filter, due to variation in gut retention times and digestive processing (Clauss et al., 2003, Cosyns et al., 2005b, Van Weyenberg et al., 2006). It is probable that this is the main difference contributing to the contrasting patterns of seed germination persistence observed among herbivore species.

Similar patterns to my findings have been reported in Western Australia, where the western grey kangaroo (*Macropus fuliginosus*) dispersed fewer seeds than introduced rabbits, and less than 25% of those germinated seedlings were native species. In contrast, emus (*Dromais novaehollandiae*) dispersed substantially higher numbers of native plants, supporting the idea that many Australian plant taxa may possess dispersal traits more closely aligned with native avian dispersers than mammalian herbivores (Calvino-Cancela, 2011).

Native plant species evolved in the absence of large grazing ungulates with no close historical analogue (Keast, 1968, Milewski and Diamond, 2000a, Arman and Prideaux, 2015), and subsequently, were not exposed to the associated selective and heavy grazing pressure. Consequently, many Australian grassland species are likely to be particularly vulnerable to the novel combination of heavy ungulate grazing and endozoochory seed dispersal, introduced since European settlement. Studies support some ungulate herbivores, particularly deer, as better dispersers than others (Heinken et al., 2002, Myers et al., 2004, Jaroszewicz et al., 2013, Karimi et al., 2018) and it is reasonable to expect that the opportunity for exotic establishment is further supported where native recruitment has been suppressed by grazing.

The association between exotic herbivores and degradation of Australian grasslands is well established, with studies reporting reduced native vegetation height, density and occurrence, and increased soil compaction and exotic plant richness linked to both intensity and historic exotic

grazing increases(Eldridge and Delgado-Baquerizo, 2017, Beever et al., 2018, Travers et al., 2018, Hartley et al., 2022). Moreover, native perennial grassland species, which are important in reducing land degradation and erosion by maintaining ground cover due to their deep root systems, are more heavily affected by exotic grazing herbivores resulting in their replacement by exotic annual species (Mcintyre and Lavorel, 2001, Dorrough et al., 2004a, Prober and Thiele, 2005, Snyman et al., 2013).

My findings suggest that the threat to native grasslands is unlikely due to enhanced endozoochory alone but rather, the collective interaction between enhanced exotic seed dispersal, reduced native plant recruitment, and sustained heavy grazing pressure. This is supported by a significant increase in the invasion success of Buffel grass (*Cenchrus ciliaris)* across Queensland savannah ecosystems under the combined influence of cattle grazing and propagule load (Fensham et al., 2013).

In contrast to Australian grassland systems, ecosystems across other continents such as Europe and North America may benefit from large ungulates in their dispersal capabilities of native plants. In the right context, herbivore mediated seed dispersal plays an important ecological role by maintaining connectivity among fragmented plant populations, facilitating recolonization and promoting the persistence of native plant communities (Taylor et al., 1993, Vellend et al., 2003, Myers et al., 2004, Auffret et al., 2012). In these systems where native herbivores have been lost, endozoochory may represent an important missing ecosystem process, particularly in forested habitats. As evidenced by the fact that neotropical dry forests (Ávila et al., 2015) comprise of many fruiting plants with white-tailed deer (*Odocoileus virginianus*) representing one of its last extant mega-herbivores (Ficcarelli et al., 2003). A study across an Ecuadorian neotropical forest, supported the idea that white-tailed deer are crucial vectors for the dispersal of many endemic plant species (Buitrón-Jurado and Ramírez, 2014, Jara-Guerrero et al., 2018). The ecological consequences of endozoochory therefore depend strongly on the evolutionary history of plant-herbivore interactions, habitat type and of the species being dispersed.

Management implications

My results signify that exotic propagules were widespread, therefore, management focused solely on plant invasion fronts may be insufficient as herbivore mediated dispersal suggests that invasive species will be continually (re)introduced into managed areas. Heavily reducing source populations of invasive plants, via slashing and mowing prior to seeding, may be more effective than targeting individual locations or hotspots to reduce the invasive species re-entering the seed bank. Management actions should concurrently prioritize the removal or active management of deer to reduce propagule pressure and movement of exotic and invasive plant species across the broader landscape.

The seasonal management of grazing cattle may also be used strategically to manage invasive species biomass. My results showed that no genera persisted in autumn or winter months for cattle samples, indicating seasonal use of cattle grazing may be more effective than continuous grazing. This strategy may provide a two-fold benefit in also reducing the grazing pressure enforced on palatable native species (Zhang et al., 2018).

Topsoil removal and re-seeding may also be a strategy in areas of complete exotic domination. A Californian grassland study showed this tactic to reduce exotic vegetation through reduced competition (Buisson et al., 2008). This strategy may also be required to reduce the persistence of exotic and invasive species in the seed bank. A study in Portugal showed that plant removal is insufficient because in invaded grasslands, the same exotic and invasive species dominated the seed bank (Marchante et al., 2011)

My findings highlight the complex interaction between herbivore identity, plant traits and life history and habitat type. It is therefore expected that long-term, continuous management incorporating a combination of tactics, will be required to restore Australian native-dominated temperate grasslands.

Future directions and limitations

While the presented findings substantially improve our understanding of herbivore mediated seed dispersal several limitations should be acknowledged and play an important role in identifying areas for future research.

Firstly, I potted all potential seeds directly with faecal material, and although this has been done in previous studies (Cosyns et al., 2005a, Tomowski et al., 2025) it limited my ability to make connections between seed traits and germination success. Removing and identifying the seeds manually prior to potting would have overcome this limitation whilst simultaneously allowing the direct comparison of the number of seeds consumed with the number successfully germinated. Unfortunately, the manual sorting of seeds was not a viable option for this study given the direct germination method was a far cheaper and less time-consuming option but future endozoochory studies across Australian grasslands that utilize this method would greatly increase our knowledge.

Secondly, the indirect comparison of seed germination potential and consumption through diet analysis was another limitation. Although I believe that by sampling every site twice per sampling season increased my chances to capture variation in both endozoochory potential and diet of all the herbivores across the site, the two analyses were conducted on different faecal samples. The diet samples were collected 12 months prior to the seed germination samples, and this was done to maximize the number and quantity of samples used in each study. To further reduce any sampling biases, all faecal material used for the diet analysis was completely homogenized prior to DNA extraction. This process would have undoubtably damaged any seeds contained within, rendering them unviable. If sampling power was doubled and had taken place concurrently, the same limitation would remain, where the input and output are not directly comparable. However, I believe that by using occurrence data and many samples, my results are an accurate indication of the broad patterns of seed dispersal based on consumption.

Conclusions

Herbivore diets do not necessarily predict dispersal outcomes, as endozoochory acts as a selective filter, influencing which plant species remain viable after gut passage. By integrating dietary, germination and spatial analyses, my study demonstrates that introduced herbivores may contribute to landscape redistribution of exotic propagules, particularly species like deer, that have large home-ranges. The movement of viable exotic seeds has the potential to reinforce invasion, increase connectivity between native and exotic dominated sites and ultimately promote homogenization of plant communities.

My findings highlight the broader importance of considering herbivores not only as consumers of vegetation and biomass, but also as vectors of seed dispersal which is essential in better understanding how exotic herbivores are shaping Australian grasslands. Furthermore, a holistic understanding of these interacting ecological processes is essential for developing more effective management strategies that concurrently reduce the spread of invasive species and further promote native species recovery.

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Chapter 5

How similar is similar enough?

Introduction

Large Herbivores have big impacts on biomes and contribute to many ecosystem functions, consequently shaping plant community structure (Trepel et al., 2024). These include selective browsing, heavy grazing pressure, digging and wallowing behaviors, preventing woody encroachment, and seed dispersal (Owen-Smith, 1988, Beguin et al., 2011, Bakker et al., 2016, Gonzalez and Ghermandi, 2021, Mahmoudi et al., 2021, Allbee et al., 2023, Campbell et al., 2025). However, a mass extinction event at the end of the Pleistocene resulted in the global loss of many megafaunal species (> 44kg) with losses dominated by herbaceous mammals (Martin, 1973, Stuart, 1991, Roberts et al., 2001, Elias and Schreve, 2007, Faith and Surovell, 2009, Villavicencio et al., 2016, Moleon et al., 2020). Examples include the South American giant ground sloth (*Megatherium americanum*), the North American mammoth (*Mammuthus columbi*), the Eurasian woolly rhinoceros (*Coelodonta antiquitatis*), and the Australian *Diprotodon optatum* (Tonni et al., 2003, Stuart and Lister, 2012, Muhs et al., 2015, Price et al., 2021, Pires, 2024).

The loss of mega herbivores has exponentially increased under anthropogenic influence (Alroy, 2001, Koch and Barnosky, 2006, Ripple et al., 2015), and their global disappearance has resulted in the accompanying loss of the ecosystem functions that they provide (Guimarães Jr et al., 2008, Dirzo et al., 2014, Bakker et al., 2016, Guyton et al., 2020). Furthermore, the potential for cascading effects following these lost functions is evidenced by the long-term exclusion of mega herbivores in Kenya, which resulted in the reduced recruitment and survival of *Acacia* seedlings, and a significant shift in the abundance of small mammals and venomous snakes (Keesing and Young, 2014).

In a bid to restore these ecosystem functions, there has been an increase in the interest and use of rewilding as a conservation tool (Malhi et al., 2016, Gordon et al., 2021d, Schowanek et al., 2021). In this context, rewilding involves the (re)introduction of locally extinct species, or the use of proxies thought to perform the same ecological roles (Soulé and Noss, 1998, Svenning et al., 2016, Svenning, 2020, Svenning et al., 2024). The earliest and most controversial example of

experimental rewilding is the large-scale nature development, the Oostvaardersplassen, an artificially created reserve in the Netherlands that saw the introduction of species such as Konik ponies (*Equus ferus caballus*) and heck cattle (*Bos taurus*) as functional equivalents of extinct herbivores (Cornelissen and Vulink, 1996, Lorimer and Driessen, 2014, Gordon et al., 2021a). Although the study reported some positive results in response to large herbivore grazing, such as increased species richness (Ejrnæs et al., 2024), this experiment was not without its problems. The philosophy of the Oostvaardersplassen was to avoid human intervention to allow natural processes to occur such as die off during harsh winters (Schwartz, 2019). This tactic was highly controversial and culminated in a mandated change in management regime (Van Geel et al., 2018) in response to public outrage, when 60% of the herbivore population experienced die off during a particularly harsh winter (Vera, 2009, Theunissen, 2019, Gordon et al., 2021a).

Nevertheless, an increasing interest in rewilding has led to publications and essays in several high-profile journals supporting the idea of Pleistocene rewilding, focusing on the use of mega herbivores to restore ecological functions lost some 13’000 years ago at the end of the Pleistocene (Owen-Smith, 1987, Donlan, 2005, Zimov, 2005, Seddon et al., 2014a, Smith et al., 2022, Lundgren et al., 2024). This has ignited the collective imagination of scholars and the public worldwide, with suggestions ranging from the use of genetic technology to de-extinct species such as the woolly mammoth (*Mammuthus primigenius*) (Seddon et al., 2014b), or to introduce African bush elephants (*Loxodonta Africana*) into Australian savannah ecosystems (Bowman, 2012).

However, the question remains, do we understand how (re)introduced herbivores influence plant community structure and ecosystem function? Over 75% of the earth’s terrestrial surface has evidence of human-induced modification (Ellis and Ramankutty, 2008), shifting ecosystems away from their historical states. These changes have formed ecosystems that either retain characteristics of their historical condition while exhibiting altered species composition and ecosystem functions (hybrid ecosystems) or have undergone irreversible change into novel ecosystems with no historical analogue (Hobbs et al., 2009, Ellis, 2011, Hobbs et al., 2014). This reality is insufficiently explored

yet highly relevant given that, contemporary ecosystems have been so profoundly altered that even herbivores returning to their historical ranges may perform ecological roles that differ from those they once fulfilled (Hobbs et al., 2006, Williams and Jackson, 2007, Seastedt et al., 2008, Schowanek et al., 2025).

This is the nexus where my thesis sits, with a particular focus on understanding the trophic interactions between herbivores and plants in modified ecosystems. The broad aim was to investigate the impacts of native and exotic herbivores on grassland ecosystems, focusing on Australian temperate grasslands as a case study. I further aimed to better understand how these ecosystem functions may be altered or driven by exotic and native herbivores. Each chapter was written as a stand-alone piece which contained its own discussion and interpretation of the results. This final chapter aims to integrate the findings of these chapters with broader ecological and management implications, while also addressing the major limitations and future directions of this research.

Are all herbivores ecologically equal?

Functional equivalence argues that species occupying similar ecological niches perform similar ecological functions (Shmida and Ellner, 1984, Hubbell, 2001, Hubbell, 2005, Zhou and Zhang, 2008). The question of whether ecological equivalence is applicable for mega herbivore species remains highly contentious, however the idea that functional role is a more accurate determinant of ecosystem impact than species level is growing in popularity (Blackburn et al., 2014, Sagoff, 2020). Multiple studies show evidence to support this idea (Deraison et al., 2015, Liu and Li, 2026), including a meta-analysis by Lundgren et al. (2024) which presented evidence to suggest that functional traits are more important than herbivore nativeness in determining plant responses to herbivory.

This idea is connected to functional overlap or functional redundancy, whereby multiple species within a particular niche contribute the same ecosystem functions and can therefore “fill the gap” if one species is lost (Rosenfeld, 2002). Functional redundancy in an ecosystem has been

linked to species richness and diversity, with studies showing high biodiversity regions, such as the tropics, to have the highest species richness and, therefore, the greatest degree of redundancy (Walker, 1992, Safi et al., 2011, Cooke et al., 2019).

Potential functional overlaps in temperate grasslands were highlighted in my thesis, in which I illustrated the considerable overlap in the diet and endozoochory potential of all herbivores in this guild, regardless of whether they were native or exotic (including domestic cattle, which were managed exotic species). Further evidenced by the idea that overlapping ecosystem functions are provided by all mammalian herbivores to some extent and include: reduction of biomass (Borer et al., 2020), encroachment mitigation (Gordon et al., 2017, Opedal et al., 2021), nutrient cycling (Mckendrigk et al., 1980, Delsuc et al., 2014, Lemoine and Smith, 2019) and seed dispersal (Ripple et al., 2015, Manning et al., 2024). There is also evidence that links herbivore body size to ecological function and the subsequent plant responses of herbivory (Owen-Smith, 1988, Olofsson et al., 2004, Denyer et al., 2010, Pringle et al., 2023). This evidence collectively supports the idea that overlapping functional traits and size similarities between two herbivore species provides the ecological justification for the use of species proxies.

However, demonstrating that herbivores provide similar ecosystem functions does not necessarily mean they produce the same ecological outcomes. For example, multiple species may consume the same plants but use the resource differently, altering the vegetation response. This is evidenced by a study in a coastal dune reserve in the Netherlands, which showed that cattle (*Bos taurus*) and European bison (*Bison bonasus*) had spatial overlap and both consumed a high proportion of the same woody plants, however bison sought bark, actively debarking trees, whereas cattle only browsed on twigs (Cromsigt et al., 2018). Chapter 3 of my thesis further highlights this idea, in that although all studied herbivores dispersed seeds across the landscape, the quantity of propagules and the plant species being dispersed were not evenly distributed across all the herbivores.

A study by Bescond-Michel et al. (2025) analyzed 303 reports employing the International Union for Conservation of Nature's (IUCN) Environmental Impact Classification for Alien Taxa (EICAT) framework to assess the impact of introduced large herbivores. The analysis found 3.7 times more negative than positive ecosystem impacts and highlighted that some species such as the American bison (Bison bison) showed exclusively negative impacts in their alien ranges. Further evidenced in Chapter 1 of my thesis, which showed that many studies focused on functional traits or ecological effects of a single herbivore species, particularly domestic livestock (Filazzola et al., 2020). Consequently, this narrow perspective may fail to capture the dynamics of an intact herbivore guild, where species may exhibit complementary rather than redundant functions, and, where ecological impacts attributed to a focal species may instead reflect interactions among multiple herbivores. For example, assemblages with guilds comprising of small and large herbivores have been shown to have more positive effects on plant species richness than one without the other, with similar patterns observed across North America, Europe and Africa (Bakker et al., 2006, Burkepile et al., 2017). I also presented a similar pattern in Chapter 1, where mixed guilds with domestic and exotic herbivores had smaller negative effect sizes on plant species richness if a native herbivore species persisted in the guild, compared to those that did not. Ecosystem functioning and redundancy are likely far more complex than simple functional trait overlaps, and we risk overlooking these nuanced effects in single species studies. Although evidence does support that many herbivore species demonstrate a strong overlap in some of their functions (Pringle et al., 2014), I argue that relying on functional traits alone is not a strong enough determinant of ecosystem impact and vegetation response and by doing so we run the risk of over simplifying a highly complex system (Gravel et al., 2016).

Domestic herbivores

The problem remains that many ecosystems have lost ecological functions which have led to further degradation and reduction in biodiversity (Dobson et al., 2006, Oliver et al., 2015, Valiente-Banuet et al., 2015), yet we are unable to reintroduce species that are globally extinct. However, the

necessity of large grazers in ecosystems is evidenced by a study showing that in grasslands affected by fertilizers, biomass production outpaced herbivory which had significant implications for biodiversity (Borer et al., 2020). So, in many instances, the question becomes, how similar is similar enough, in the context of using species proxies based on their functional traits to replace lost ecosystem functions?

The wilderness continuum concept proposed that ecosystems exist along a spectrum of human influence, suggesting that conservation and restoration can occur across varying degrees rather than only pristine wilderness (Lesslie and Taylor, 1985). The idea of 'rewilding lite' is the notion that large domestic herbivores may be an alternate solution to reinstating historical herbivory and disturbance regimes, particularly in areas of high human density and agriculture settings, as it retains the option for management interventions (Gordon et al., 2021c)

In the Australian context, cattle grazing is used quite frequently in temperate grasslands as a conservation tool to reduce the biomass of dominant exotic plant species because there are no analogous native large grazers (Fraser and Chisholm, 2000, Dorrough et al., 2004b, Lunt et al., 2007, Lebbink et al., 2021). The dominant native herbivores in this system, particularly eastern grey kangaroos (*Macropus giganteus*), do reach very high population densities and could potentially be used more efficiently for biomass reduction (Snape et al., 2021). However, there is a strong divide in this thinking, with farmers often viewing kangaroos as competition to livestock grazing, often leading to active management of populations by farm and property owners (Croft and Witte, 2021). Furthermore, in times of resource abundance, kangaroo populations can explode leading to severe grazing pressures and high mortality rates in drought seasons, raising ethical concerns (Caughley et al., 1985, Wilson and Edwards, 2019, Snape et al., 2021, Wilson and Coulson, 2021). This dichotomy has likely driven the acceptance of cattle grazing for conservation purposes in Australia because they are easily controlled in highly urbanized and semi-pastoral environments. Rewilding lite is, therefore, attractive because it still allows for active management (Gordon et al., 2021d). Similar conflicts exist across the globe, for example in Chile, the native guanaco (*Lama guanicoe*)

has a strong diet and niche overlap with domestic grazing animals leading to heavy grazing pressures and the persecution of guanacos (Pozo et al., 2021). The value of active herbivore management is further demonstrated by the Oostvaardersplassen rewilding experiment, where severe winters led to a crash in the unmanaged herbivore populations, with public outcry resulting in termination of the project (Theunissen, 2019). This followed proposed management interventions that were not implemented and included culling or removal of animals to simulate natural predation in the absence of natural top-down processes such as large predators (Duncan, 2006, Van Geel et al., 2018, Gordon et al., 2021b)

Despite the potential value of rewilding lite, studies presenting positive results and increased biodiversity caused by livestock grazing only represent a fraction of the literature, with many studies highlighting unpredictable and variable responses of livestock grazing with the likelihood that a trade-off of some kind will occur (Van Klink et al., 2016, Pakeman et al., 2019, Filazzola et al., 2020, Copeland et al., 2023, Evans et al., 2023). For instance, the use of cattle to manage invasive Buffel grass (*Cenchrus ciliaris)* across conservation sites in Queensland, Australia resulted in the desired reduction in biomass. However, this also led to the secondary invasion of Indian couch grass (*Bothriochloa pertusa*) into the region. This is further evidenced by Chapter 1 of my thesis, which highlighted the high variability of livestock effects on plant communities and pointed to the fact that grazing responses are site and species specific.

In a novel ecosystem, exotic plants may escape or attract herbivory, both of which allow for the potential of exotic herbivores to facilitate or suppress invasions (Cappuccino and Carpenter, 2005, Inderjit, 2012). Non-native herbivores may preferentially consume exotic or native plants depending on the system and, therefore, the effects will be varied. For instance, the co-evolution of many forest plants and the African bush elephant has led to multiple plant strategies including repellence by the Indian elm (*Holoptelea grandis*) which omits a pungent smell when damaged and is, therefore, avoided; or the Sabara tree (*Leptonychia usambarensis)* which is a fast-growing tree

that benefits from heavy elephant browsing resulting in coppice and a constant successional state (Sheil, 2020).

My Chapter 1 results are supported by other studies, which are more suggestive of exotic herbivores causing mixed or positive effects on exotic plant richness and abundance (Parker et al., 2006, Johnson and Cushman, 2007, Nuñez et al., 2010). In instances such as Australia, where exotic herbivores are not acting as effective exotic plant control, the question must be asked, are they at least restoring lost ecosystem functions to justify their use?

The Pleistocene is an epoch that started 1.8 million years ago ended roughly 10’000 years ago, and was as time of climactic fluctuations, including a glacial maximum, where sea levels were up to 120 meters lower than present day (Hays et al., 1976) (Lister and Sher, 1995) (Hofreiter and Stewart, 2009). During the late Pleistocene, a global mass extinction event occurred, with considerable debate as to the cause but commonly attributed to a combination of climate change and the arrival of modern-day humans (Martin, 1973, Barnosky et al., 2004, Martin and Klein, 2022).

Throughout the Pleistocene, the Australian continent supported a far more diverse assemblage of megafaunal marsupials than today (Johnson, 2006, Prideaux et al., 2010), including the largest ever marsupial, the giant wombat (*Diprotodon optatum*) which weighed over 2,700kg (Price and Piper, 2009, Price et al., 2021), Sthenurine kangaroos such as the giant short-faced kangaroo (*Procoptodon goliah*) which weighed up to 240kg (Janis et al., 2014), and the ‘marsupial tapir’ (*Palorchestes azeal*) which weighed over 500kg (Mackness, 2009, Richards et al., 2019), all filling various habitat niches. However, contemporary Australia has not had any native mega browsers for over 40,000 years (Dawson, 2006, Prideaux et al., 2007, Murray and Nevard, 2024). The largest extant native herbivore is the red kangaroo (*Macropus rufus*), a grazing marsupial with maximum adult body size reaching 89kg in males and 36kg in females (Moss and Croft, 1999). We therefore lack a solid reference as to exactly what ecosystem functions were lost with the extinction of Australian megafauna. Many researchers, however, speculate that since the loss of mega

herbivores, climate, soil, and anthropogenic fire regimes had a greater role in shaping current Australian grassland assemblages (Bird et al., 2013, Cook et al., 2019).

Furthermore, the loss of ecosystem functions in contemporary Australian grasslands and woodlands have been driven by the more recent and rapid decline of digging mammals rather than mega-herbivore extinctions (Martin, 2003, Davidson et al., 2012, Fleming et al., 2014). Australian soils are nutrient poor and the role that digging mammals play in bioturbation, water infiltration and plant recruitment represents a critical process that is not being replaced by exotic mega-herbivores (Garkaklis et al., 1998, Newell, 2008, Fleming et al., 2014, Munro et al., 2019, Ross et al., 2020).

Additionally, the top-down control exerted by large predators across Australia is another missing ecological process that has no analogous replacement in the current ecosystem. Historically, large marsupial carnivores acted as top-down control, with the largest, the marsupial lion (*Thylacoleo carnifex*) weighing up to 150kg going extinct during the Pleistocene (Wroe et al., 1999). However in the more recent history of mainland Australia, the thylacine (*Thylacinus cynocephalus*), the dingo (*Canis familiaris dingo*), and the Tasmanian devil (*Sarcophilus harrisii*) were the predominate predators (Johnson, 2014). The thylacine became extinct on the mainland in the 1930's, likely persisting in Tasmania until the 1980s (Brook et al., 2023). Similarly, the largest extant marsupial predator, the Tasmanian devil has been extinct from mainland Australia for ~3000 years, with populations restricted to Tasmania (Brüniche–Olsen et al., 2018) but facing significant declines (Hollings et al., 2014, Fancourt et al., 2015).

The importance of large predators is evidenced by a study showing that in areas where the Dingo are functionally extinct, researchers saw a 99% greater abundance of kangaroo density, and an equivalent reduction in native pasture biomass and grass seed heads (Letnic et al., 2012, Rees et al., 2017). This highlights the enormous potential for ecosystem alteration by large exotic ungulate grazers in the Australian system which in most habitats have no natural predators (Freeland, 1990a, Tanentzap et al., 2012). Further emphasizing the likelihood that exotic mega herbivores are more

likely to create novel ecosystem processes in Australian grassland systems rather than restoring any that have been lost.

Pathway to invasion meltdown

Environmental filtering, whereby particular environmental factors select for or against certain species, therefore playing a role in shaping community structures, has long been hypothesized as being an important ecological process (Keddy, 1992, Davis et al., 2000, Grime, 2006). This hypothesis has been shown to be true of endozoochory, where only the seeds able to survive the gut passage of an animal are successfully dispersed (Pakeman et al., 2002, Myers and Harms, 2009, Panter and Dolman, 2012, Albert et al., 2015, Lepková and Mašková, 2022), and was further discussed in both Chapters 3 and 4 of this thesis.

The same can be said of herbivore diet, through which seeds are ingested, yes, but additionally, plant traits such as anti-herbivory defenses, herbivore preference and resource availability all act as ecological filters (Geho et al., 2007, Walker et al., 2023). Preference and resource availability acting as ecological filters is supported by the theory of optimal foraging, whereby species select specific food resources to maximize their energetic benefits (Macarthur and Pianka, 1966, Pyke et al., 1977, Pyke, 1984, Stephens and Krebs, 1986). Further, Chapter 2 of my thesis implied that the overall abundance of plant taxa found in the diet of the mammalian herbivore guild was likely driven by availability, with similar patterns observed using simulation data, where the encounter rates of particular plant species drove herbivore diet selection (Newman et al., 1995). Additionally, a study in Europe found that exotic plants that successfully germinated had a greater number and diversity of anti-herbivory chemical metabolites than their native counterparts, increasing their invasion potential (Macel et al., 2014).

As a key finding of my thesis, I therefore posit that both endozoochory and diet act together as an ecological filtering mechanism (Figure 1). Collectively acting as a cyclical process, this filtering mechanism may be an over-looked driver of ‘invasion meltdown’ in the Australian temperate grassland system (Daly et al., 2023). This is the hypothesis that mutualistic interactions

between exotic species facilitate their establishment and enhance invasion success leading to increased ecosystem impacts (Simberloff and Von Holle, 1999, Green et al., 2011). Many studies support this hypothesis, as evidenced by a grazing exclosure experiment in British Columbia which showed that grazing by non-native geese (*Branta canadensis*) produced a positive feedback cycle whereby a greater preference for native grasses indirectly benefited grazing-tolerant exotic plants, increasing their abundance over time. Furthermore, these geese were shown to successfully disperse seeds through endozoochory, with 80% of seeds germinated being exotic plant species (Best and Arcese, 2009). Further demonstrated by the exotic bluegill sunfish (*Lepomis macrochirus*) increasing the invasion success of the bullfrog (*Rana catesbeiana*) across the USA (Werner and Mcpeek, 1994, Adams et al., 2003).

In Chapter 3 and 4, I highlighted that in Australian grassland ecosystems, most of the seeds germinating following endozoochory via mammalian vectors were exotic or invasive species. It is therefore reasonable to assume that repeated dispersal of the same suite of exotic and invasive plant species over time could impact plant community structure, leading to an increase in exotic plant availability. I hypothesis that this cyclic process may consequently lead to biotic homogenization, whereby ecosystems lose spatial variation and suffer increasing loss of biodiversity (Olden et al., 2004, Seabloom et al., 2006, Holl et al., 2022).

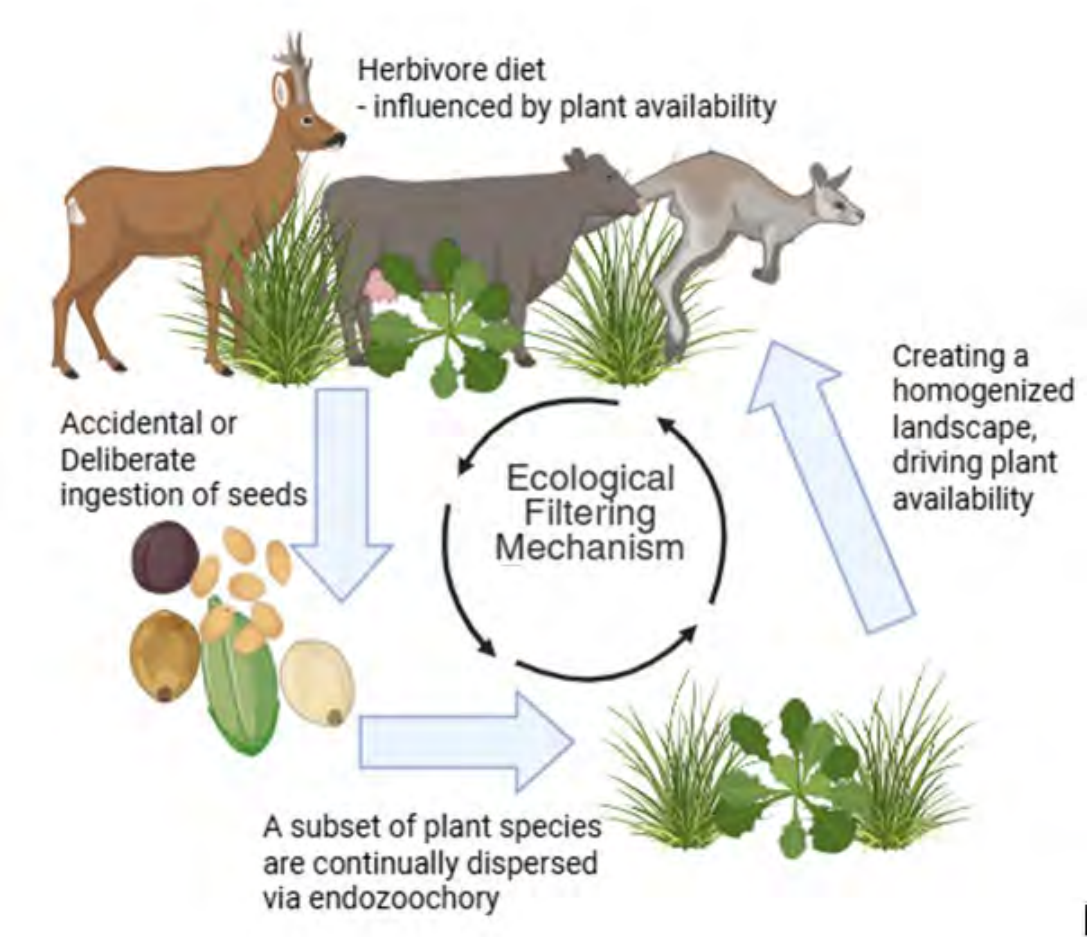


Figure 11. Ecological Filtering Mechanism in explaining potential invasion meltdown and habitat homogenisation in degraded Australian grassland systems. Endozoochory seed dispersal and diet acting together as an ecological filtering mechanism. The repeated, successful dispersal of a suite of exotic plants through endozoochory favors this subset of plants to outcompete native plants. Over time, this may create a homogenized landscape, shaping plant availability for large herbivore grazers which are then driven to consume a greater abundance of seeds, reinforcing the cycle. Created in BioRender.com

Climate change

Throughout my thesis, I have shown that exotic herbivores act as highly proficient seed dispersers of exotic seeds in south-east Australian grasslands, with climate change likely to facilitate an increase in the ecosystem impacts. Climate change is a growing concern globally, not just in Australia, and will undoubtably have considerable global impacts, likely increasing the distribution

and impact of range exotic species (Walther et al., 2009, Dehnen-Schmutz et al., 2018, Biancolini et al., 2024). It has been predicted that the climatic suitability for some invasive plant species across south-eastern Australia will increase over the coming three decades (O'donnell et al., 2012), with further evidence suggesting that exotic plant species have far greater plasticity in their tolerance of changing climatic niches (Gallagher et al., 2010). Ungulate herbivores like deer have also been shown to exhibit niche shifts, with evidence suggesting they have already expanded outside of modelled ideal habitats across much of Australia (Kelly et al., 2023). Shifting assemblages due to climate change will bring its own challenges, and the potential for exotic herbivores to have increasingly disproportionate ecosystem impacts as warming continues. Additionally, extreme global weather events are likely to increase in occurrence and duration with an increasing frequency of severe droughts across south-east Australia predicted (Hope et al., 2010, Herold et al., 2021). Extreme drought events are likely to increase competition between herbivore species, and although the ecological winners and losers are unknown (Prugh et al., 2018), increased resource overlap will likely result in consequences such as a fitness cost to native herbivores (Ruprecht et al., 2026). A study by Ritchie et al. (2009), using model data, showed that both eastern grey kangaroos and wallaroo (*Macropus robustus*) may limit each other's abundance under certain circumstances, with environmental factors being the greatest determinant. Their model also suggested that eastern grey kangaroos are more abundant alongside cattle, suggesting cattle may provide beneficial habitat modifications. However, Chapter 2 of my thesis has shown that there is a considerable overlap in the diet composition and niche breadth between all the herbivores in this system, so the ability for competitive exclusion in times of scarcity likely comes down to diet plasticity and range size. For example, in times of drought, African savannah herbivores have been shown to react in different ways, dependent on their feeding strategy. Grazing ruminant animals such as buffalo (*Syncerus caffer*) and wildebeest (*Connochaetes taurinus*) migrated to drought refugia, whereas smaller browsers such as kudu (*Tragelaphus strepsiceros*) and duiker (*Sylvicapra grimmia*) altered their landscape use by incorporating more browse in their diet (Abraham et al., 2019). Other studies have

looked at guild level changes to drought and warming (Ogutu et al., 2008, Belovsky and Slade, 2024) but the interaction between exotic, domestic and native herbivores is so complex, and site specific, that although resource limitation will likely be a driver of population regulation, which species decline and increase remains unknown.

The exotic predators occurring across south-east Australian grasslands are the European red fox (*Vulpes vulpes*), the feral cat (*Felis catus*), and the dingo which became naturalized in Australia soon after their arrival over 3000 years ago (Fleming et al., 2012). Dingoes are found in high abundances across many parts of Australia and have been shown to predate on large mammals including red kangaroos, feral goats (*Capra hircus*) and young sambar (Cervus unicolor) deer (Dickman, 1996, Allen et al., 2013, Forsyth et al., 2018), however due to major conflict with sheep famers, they are less common in modified habitats across south-east Australia (Allen and West, 2013). Both foxes and cats do predate on small joeys, impacting on population recruitment (Dickman, 1996, Banks et al., 2000) however, in the absence of dingoes, there are no natural predators large enough to challenge deer, cattle or adult wombats or macropods in the South-East Australian grassland system (Freeland, 1990b). Therefore, resource availability is the primary regulator of herbivore population size within this ecosystem, with my thesis demonstrating the potential functional redundancy and considerable resource overlap between exotic and native herbivores, which may be an underestimated mechanism further regulating species abundance in Australian grasslands.

Is evidence biased or limited?

Despite growing interest in the use of species proxies and domestic grazing animals for conservation outcomes (Richmond et al., 2010, Svenning et al., 2016, Perino et al., 2019, Gordon et al., 2021c), I posit that the supporting evidence is heavily biased and reveals a lack of knowledge of many ecosystems, particularly Australasian ecosystems. As revealed by my meta-analysis (Chapter 1) and supported by other studies, most experiments examining plant responses to large herbivores occur across Europe and North America (Schieltz and Rubenstein, 2016, Hyvarinen et al., 2021). As

discussed throughout my thesis, Sahul, the combined continent of Australia and New Guinea was geographically isolated for millions of years (Braithwaite, 1990, Long, 2017), resulting in a high diversity of endemic species, with terrestrial mammal diversity dominated by soft-footed marsupials, and a lack of any ungulate herbivores (Johnson, 2006).

I argue that the cost of Australia's evolutionary isolation has been an exceptional vulnerability to novel species introductions and altered disturbance regimes. This is reflected in the loss of more than 10% all Australia's endemic terrestrial mammals since European invasion less than 200 years ago (Macintyre, 2004), whereas Continental North America has lost only a single native terrestrial mammal species over a comparable period (Butchart et al., 2010, Woinarski et al., 2015a, Woinarski et al., 2015b). There is, therefore, a dire need to increase our knowledge base, especially considering the vast variability in large herbivore effects reported, even in the well-studied ecosystems.

Limitations in germination studies

The use of a greenhouse to conduct endozoochory studies has been undertaken in many similar studies (Cosyns et al., 2005a, Stroh et al., 2012, Karimi et al., 2020, Jones et al., 2025), however, the gap between germination potential and successful recruitment in the natural environment still exists and was not able to be addressed in my thesis. Furthermore, studies have looked at the species- specific trait data of invasive Australian grassland plant seeds (Murray and Phillips, 2010), and endozoochory success of exotic plants lacking conventional traits such as fruiting bodies (Davis et al., 2010), however to my knowledge, there are no Australian temperate grasslands studies linking this data.

Removing the seeds prior to planting in endozoochory experiments is a beneficial method in that one can obtain seed trait data (Picard et al., 2016) and quantify seeds consumed against seeds germinated (Orłowski et al., 2016). However, in Chapter 3 of my thesis, I made the decision to retain the seeds and the faecal material together for the endozoochory study due to many studies implying that faecal matter likely plays a role in germination success and survival (Bazely and

Jefferies, 1985, Traveset et al., 2001, Jaroszewicz and Pirożnikow, 2011). For example, toad rush *(Juncus bufonius*) seeds extracted from the soil seed bank from wetlands in Hungary, were shown to have increased germination success when potted with mallard (*Anas platyrhynchos*) faeces, whereas spike rush (*Eleocharis palustris)* germination was reduced (Jiménez-Martín et al., 2025). Similarly, a study by Ramos et al. (2024) revealed that the species-specific, micro-climatic conditions of faecal material can determine germination success, with cattle dung having a greater impact on the germination and survival success of mesquite (*Neltuma flexuosa*) seedlings when compared to domestic horse dung. They further showed that the manure of the native mara (*Dolichotis patagonum*) reduced germination success. The ability to grow in dense nutrient environments such as faecal material may be another trait that allows some plants to become invasive, particularly in low nutrient Australian ecosystems. Therefore, the source faecal material is clearly an important factor in endozoochory success that may be overlooked in studies that remove the seeds prior to planting. Although I did not empirically test this in my thesis, the retention of seeds and faecal material in my study provided an important contribution to existing knowledge, though many gaps remain. The combined interaction between plants traits, herbivory, and environmental conditions plays an enormous role in plant community structure and persistence in the landscape (Takatsuki et al., 2025) and further supports the need to focus on these combined effects plus propagule pressure in the dung, and their combined influence on actual plant recruitment in the field.

Management implications

There is no single solution or action to prevent the herbivore mediated spread of exotic and invasive plants. As highlighted throughout this thesis, both the impacts of large herbivores and consequential invasion process is complex.

Management strategies need to implement a multi-pronged approach by reducing the propagule pressure, which is the number of exotic seeds released into the environment, while simultaneously improving the resilience of native plant populations. This was proposed by Baughman et al. (2022), which called for a renewed effort in re-seeding native species to restore

degraded habitats. They suggested that previous failures may be overcome by recognizing local adaptations in other source populations and harnessing this genetic variation when selecting plant species and source populations used for re-seeding

Define the objective

Effective management requires a clearly defined goal prior to intervention. This will be site specific and may include different priorities such as the reduction of invasive species spread, diversity restoration or the balance between production and biodiversity in agricultural settings. Defining these priorities is essential because different objectives will result in different trade-offs. Previous chapters in my thesis demonstrated that herbivore impacts vary by species and season, highlighting management actions are unlikely to have universally positive outcomes. The fine balance between herbivore-mediated ecological functions and the potential adverse effects needs to be considered (Cordero et al., 2023). For example, the use of exotic herbivore grazers may suppress some invasive species, while simultaneously dispersing or facilitating others (Ward et al., 2017).

Strategic management

Based on my findings, I advise that in instances where domestic grazing is required, the use of strategic rather than general grazing would be more beneficial. Chapters 2, 3 and 4 of my theses showed that grazing effects are seasonal, particularly in the context of endozoochory potential in deer and cattle. By timing grazing practices to heavily target specific, invasive plant species' biomass reduction, and subsequently remove grazing during peak seeding events, there may be a reduction in dispersal via endozoochory. However, adaptive rather than continuous grazing management requires active vegetation monitoring.

Frequent vegetation surveys are needed to detect rapid changes in plant communities before, during and after invasions to understand how these changes are influencing ecosystem processes (Blossey, 1999), and to better understand the long-term changes (Webster and Halpern, 2010). Furthermore, surveys should track not only vegetation composition, but herbivore land use and management effectiveness. The ability to respond quickly based on regular monitoring feedback

will be more efficient than short-term or sporadic surveying efforts. Based on my research, there is now a baseline of plant consumption and seed dispersal across the Ginninderry Conservation Corridor (GCC). This offers a benchmark against which regular plant surveys in the future, could follow ecosystem trajectories, and their facilitation by both native and exotic herbivores.

Integrated management

Herbivore management plans need to be combined with other control measures to be effective (Mohler et al., 2021, Zimdahl and Basinger, 2024). This may include not only the active control of herbivores but the strategic timing of weed control, such as spraying well before seeding events to reduce propagule sources. The use of computational models has been suggested to better predict the most efficient weed management strategy (Doyle, 1991, Marschner et al., 2024, Singh et al., 2025). Two previous weed management models based on Australian grassland habitats, proved successful in the use of target species' dynamics and ecosystem parameters to predict the most effective biocontrol treatments, and significantly reduced the need for field trials (Buckley et al., 2004, Shea et al., 2006). However, highly modified and invaded systems must also overcome missing native plants in the seed bank (Bossuyt and Honnay, 2008) and highly enriched soil nutrients due to fertiliser use (Marrs et al., 1998), both of which affect recovery of native grasslands. A multi-factorial study by Resch et al. (2022) revealed that mowing multiple times are year to remove plant biomass was inadequate in reducing soil nutrients and improving native plant biodiversity when compared to topsoil removal and native re-seeding.

More intensive restoration efforts such as topsoil removal and reseeding are most common in North Europe (Geissen et al., 2013), with increasing global interest suggesting this may be a promising restoration management tool. Multiple different methods have been used in top-soil removal and long-term re-seeding projects across Australian grasslands (Cuneo et al., 2018, Gibson-Roy, 2023); with those reporting positive results including the transfer of topsoil with its seedbank from previously cleared native vegetation in Western Australia (Waryszak et al., 2021) and herbicide treatments to remove weed biomass, followed by topsoil removal and re-seeding in

south-eastern Australia (Williams et al., 2015). Other studies in North American and European grasslands have shown that the combination of topsoil removal, exotic neighbour removal, and the transplanting of native seeds in hay had the greatest positive outcomes in restoring native biodiversity (Buisson et al., 2006, Kiehl and Pfadenhauer, 2007). However a long term study by Resch et al. (2022) emphasized that success using this method requires several decades of restoration monitoring and active management to achieve the target plant community and prevent re-invasion. Furthermore, as the demand for native seeds increases, there is a need for improvement of native seed harvest and production in Australia to ensure ongoing sustainability of wild source populations (Merritt and Dixon, 2011, Nevill et al., 2018), and to maintain the genetic diversity of restoration sites (Brown et al., 1995, Management, 2012, Kramer et al., 2018, Pedrini et al., 2020).

The effective management and restoration of degraded grasslands will therefore require an ongoing and adaptive, evidence-based approach. Single intervention methods are not likely to succeed in isolation, and long-term outcomes will depend on combining herbivore management, invasive plant control, active restoration, and ongoing monitoring with a clearly defined management framework.

Conclusions

By integrating diet and endozoochory of a novel herbivore guild, my thesis demonstrates the complex roles of exotic and native herbivores in shaping plant community structure. Large herbivores can act as ecological filters, with non-native herbivores playing a key role in shaping contemporary Australian grassland plant communities, through consumption and seed dispersal, potentially leading to landscape scale redistribution of invasive and exotic plants. My findings improve the understanding of Australian herbivore ecology and provide a solid foundation for future research on the impact of native and exotic large herbivores.

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Appendix A – Chapter One

Table 1. List of studies included in the meta-analysis. Study is listed by first author and year, as can be found in the chapter one reference list. Country pertains to the study location, herbivore type is the nativeness of any herbivores mentioned as being excluded in each study, ecosystem pertains to the study location, effect size is the number of data points contributed to the meta-analysis for that study.

Study	**Country**	**Herbivore type**	**Ecosystem**	**Effect size**
Alejandro, Loydi, Roberto A. Distel, and Sergio M. Zalba. (2010)	Argentina	domestic	Montane grassland	4
Bakker, Elisabeth S., et al. (2006)	USA	all	sage brush steppe	7
Baur, Lauren E., et al. (2017)	USA	exotic	mountain grassland & mixed grass prairie	12
Beck, Jared J., et al. (2015)	USA	domestic	serpentine grassland	20
Briggs, Sue V., et al. (2008)	Australia	domestic	grassy woodland	1
Chamane, Sindiso, et al. (2017)	South Africa	domestic	mesic grassland	3
Cushman, J. Hall, Laura E. Saunders, and Tyler K. Refsland. (2020)	USA	domestic & native	savannah grassland	2
de Villalobos, Ana E., and Leonela Schwerdt. (2018)	Argentina	exotic	Pampas mountain grassland	6
Debeko, Denbeshu, et al. (2024)	Ethiopia	domestic	mountain grassland	3
DiTommaso, Antonio, et al. (2014)	USA	native	pasture grassland	6
Dvorský, Miroslav, et al. (2022)	Czech Republic	exotic	natural temperate grassland	8
Elson, Anna, and David C. Hartnett. (2017)	USA	native	prairie	1
Farmilo, Brad, et al. (2023)	Australia	domestic	natural temperate grassland	8
Fensham, Rod J., Jennifer L. Silcock, and John M. Dwyer. (2011)	Australia	all	grassy woodland	3
Garrido, Pablo, et al. (2019)	Sweden	exotic & native	grassland	3
Gates, Emily A., et al (2017)	USA	domestic	mixed-grass prairie	3
Griggs, Jennifer A., et al. (2006)	USA	native	mountain grassland & forest ecotone	6
Habtemicael, Mezgebe, Tesfay Yayneshet, and Anna C. Treydte. (2015)	Ethiopia	domestic	semi-arid highland	2
Hayes, Grey F., and Karen D. Holl. (2003)	USA	domestic	mesic grassland	1
Isbell, Forest I., and Brian J. Wilsey. (2011)	USA	domestic	mixed-grass prairie	10
Johnson, Brent E., and J. Hall Cushman. (2007)	USA	native	grassland	7

Joubert, Lize, James S. Pryke, and Michael J. Samways. (2017)	South Africa	all	moist grassland	2
Keeley, Jon E., Daniel Lubin, and C. J. Fotheringham. (2003)	USA	domestic	blue oak savannah	2
Kilheffer, Chellby R., et al. (2019)	USA	native	high dune grassland	1
Kiss, Réka, et al. (2021)	Hungary	domestic	grassland	1
Kouba, Yacine, et al.(2021)	Algeria	domestic	arid steppe	3
Kusakabe, Ryota, et al. (2018)	Mongolia	domestic	mountain grassland & desert steppe	6
Labadessa, Rocco, Balázs Deák, and Orsolya Valkó. (2020)	Italy	domestic	mediterranean grassland	6
Lesage, Josephine C., Grey F. Hayes, and Karen D. Holl. (2022)	USA	domestic	coastal prairie grassland	4
Loydi, Alejandro. (2019)	Argentina	exotic	Pampas mountain grassland	8
Mancilla-Leytón, et al. (2013)	Spain	domestic	mediterranean forest-grassland ecotone	1
Manrique, Rosa, et al. (2007)	Chile	all	semi-arid grassland	7
Mavromihalis, J. A., et al. (2013)	Australia	domestic	temperate grassland	3
Mekuria, Wolde, and Edzo Veldkamp. (2012)	Ethiopia	domestic	savannah woodland	8
Meyers, Lindsey M., Edward S. DeKeyser, and Jack E. Norland. (2014)	USA	domestic	continental grassland	6
Michels, Guilherme Heck, et al. (2012)	Brazil	feral	sub-tropical grassland	2
Moinardeau, Cannelle, et al. (2020)	France	exotic	grassland	25
Mugica, Leire, et al. (2021)	Spain	domestic	grassland	63
Paneru, Prativa, et al. (2023)	Nepal	domestic	sub-tropical grassland	3
Pettit, N. E., and R. H. Froend. (2001)	Australia	domestic	grassy woodland	12
Porensky, Lauren M., Rachel McGee, and David W. Pellatz. (2020)	USA	domestic & native	mixed-grass prairie	3
Price, Jodi N., Nathan K. Wong, and John W. Morgan. (2010)	Australia	domestic & native	grassy woodland	5
Relva, María Andrea, Martin A. Nunez, and Daniel Simberloff. (2010)	Argentina	exotic	forest ecotone	2
Rutherford, M. C., and L. W. Powrie. (2013)	South Africa	domestic	arid savannah grassland	5
Sato, Chloe F., Daniel Florance, and David B. Lindenmayer. (2019)	Australia	domestic	remnant grassy woodland	2
Scott-Shaw, Rob, and Craig D. Morris. (2015)	South Africa	domestic & native	mesic grassland	4
Seabloom, Eric W., et al. (2009)	USA	exotic & native	savannah grassland	4
Sigcha, F., et al. (2018)	Spain	domestic & native	grassland	5
Skaer, Meghan J., Dawn J. Graydon, and J. Hall Cushman. (2013)	USA	domestic	coastal grassland	7

Sottile, Gonzalo David, et al. (2015)	Argentina	domestic & exotic	forest-steppe ecotone	1
Souther, Sara, et al (2019)	USA	domestic & native	semi-arid grassland	2
Souther, Sara, et al. (2020)	USA	domestic	semi-arid grassland	6
Tanentzap, Andrew J., et al. (2009)	New Zealand	exotic	alpine grassland	4
Thomas, T. W., et al. (2022)	USA	domestic	sagebrush steppe	6
Tulloch, Ayesha IT, et al. (2023)	Australia	all	arid grassland	1
Ward, Lena K., and R. D. Jennings. (1990)	England	domestic & exotic	chalk grassland	1
Ware, Ian M., Pat Terletzky, and Peter B. Adler. (2014)	USA	domestic	grassy-shrubland	6
Watson, Brogan L., et al. (2021)	USA	domestic	bunchgrass prairie	2
Webster, Christopher R., et al. (2008)	USA	native	mosaic of fields and woodlots	10
Whitehead, Amy L., et al. (2014)	New Zealand	domestic	dry grassland	9
Wilsey, Brian J., and Leanne M. Martin. (2015)	USA	native	prairie grassland	8
Zhang, Minna, et al. (2022)	Mongolia	domestic	meadow steppe	6

Appendix B – Chapter Two

Appendix B Table 1. Complete list of plant species identified in the diet analysis. Samples collected across the Ginninderry Conservation Corridor, ACT, between April 2024 and March 2025.

PlantID	Family	Genus	Species
Acacia11	Fabaceae	Acacia	spp
Acaena43	Rosaceae	Acaena	novae-zelandiae
Acaena157	Rosaceae	Acaena	ovina
Acaena42	Rosaceae	Acaena	spp
Alternanthera48	Amaranthaceae	Alternanthera	spp
Amyema25	Loranthaceae	Amyema	cambagei
Amyema	Loranthaceae	Amyema	Loranthaceae
Amyema24	Loranthaceae	Amyema	spp
Anacardium49	Anacardiaceae	Anacardium	cashew
Anagallis151	Primulaceae	Anagallis	arvensis
Arachis12	Fabaceae	Arachis	hypogaea
Aristida123	Poaceae	Aristida	behriana
Arthropodium3	Asparagaceae	Arthropodium	milleflorum
Asparagaceae4	Asparagaceae	unknown Asparagaceae	spp
Asperula45	Rubiaceae	Asperula	spp
Asteraceae5	Asteraceae	unknown Asteraceae	spp
Asteraceae57	Asteraceae	unknown Asteraceae	spp
Austrodanthonia	Poaceae	Austrodanthonia	caespitosa
Austrodanthonia34	Poaceae	Austrodanthonia	spp
Austrostipa124	Poaceae	Austrostipa	Austrostipa
Avena35	Poaceae	Avena	barbata
Avena125	Poaceae	Avena	spp
Boraginaceae7	Boraginaceae	unknown Boraginaceae	spp
Boraginaceae61	Boraginaceae	unknown Boraginaceae	spp
Bossiaea85	Fabaceae	Bossiaea	buxifolia
Brachyloma84	Ericaceae	Brachyloma	daphnoides
Brassicaceae8	Brassicaceae	unknown Brassicaceae	spp
Brassicaceae64	Brassicaceae	unknown Brassicaceae	spp
Briza37	Poaceae	Briza	maxima
Briza36	Poaceae	Briza	minor
Bromus126	Poaceae	Bromus	Bromus
Bromus38	Poaceae	Bromus	catharticus
Callitris76	Cupressaceae	Callitris	spp
Campanulaceae9	Campanulaceae	unknown Campanulaceae	spp
Capsicum169	Solanaceae	Capsicum	spp
Carex78	Cyperaceae	Carex	appressa
Carex	Cyperaceae	Carex	breviculmis
Caryophyllaceae67	Caryophyllaceae	unknown Caryophyllaceae	spp

Casuarina69	Casuarinaceae	Casuarina	cunninghamiana
Casuarina70	Casuarinaceae	Casuarina	spp
Centaurium94	Gentianaceae	Centaurium	tenuiflorum
Cerastium	Caryophyllaceae	Cerastium	Cerastium
Chloris127	Poaceae	Chloris	truncata
Clematis154	Ranunculaceae	Clematis	spp
Correa163	Rutaceae	Correa	spp
Crassula75	Crassulaceae	Crassula	sieberiana
Crataegus158	Rosaceae	Crataegus	monogyna
Crepis55	Asteraceae	Crepis	spp
Crepis	Asteraceae	Crepis	tectorum
Cryptandra155	Rhamnaceae	Cryptandra	amara
Cynodon128	Poaceae	Cynodon	dactylon
Cyperaceae82	Cyperaceae	unknown Cyperaceae	spp
Dactylis139	Poaceae	Dactylis	spp
Daucus50	Apiaceae	Daucus	spp
Daviesia86	Fabaceae	Daviesia	genistifolia
Desmodium	Fabaceae	Desmodium	elegans
Desmodium13	Fabaceae	Desmodium	rhytidophyllum
Desmodium87	Fabaceae	Desmodium	spp
Dianella53	Asphodelaceae	Dianella	spp
Dichondra73	Convolvulaceae	Dichondra	spp
Dodonaea165	Sapindaceae	Dodonaea	viscosa
Dysphania	Amaranthaceae	Dysphania	pumilio
Echium59	Boraginaceae	Echium	spp
Echium6	Boraginaceae	Echium	vulgare
Einadia1	Amaranthaceae	Einadia	nutans
Eleocharis2	Cyperaceae	Eleocharis	acicularis
Eleocharis3	Cyperaceae	Eleocharis	mamillata
Eleocharis79	Cyperaceae	Eleocharis	spp
Eleocharis	Cyperaceae	Eleocharis	valleculosa
Eleusine140	Poaceae	Eleusine	spp
Enneapogon130	Poaceae	Enneapogon	spp
Epilobium116	Onagraceae	Epilobium	billardiereanum
Epilobium28	Onagraceae	Epilobium	spp
Eragrostis141	Poaceae	Eragrostis	curvula
Erodium95	Geraniaceae	Erodium	cicutarium
Eucalyptus112	Myrtaceae	Eucalyptus	rubida
Fabaceae17	Fabaceae	unknown Fabaceae	spp
Fabaceae93	Fabaceae	unknown Fabaceae	spp
Festuca142	Poaceae	Festuca	spp
Geranium96	Geraniaceae	Geranium	solanderi
Geranium19	Geraniaceae	Geranium	spp
Geranium20	Geraniaceae	Geranium	subulatostipulatum
Grevillea152	Proteaceae	Grevillea	robusta

Grevillea	Proteaceae	Grevillea	spp
Grimmia97	Grimmiaceae	Grimmia	laevigata
Grimmia98	Grimmiaceae	Grimmia	spp
Haloragaceae	Haloragaceae	unknown Haloragaceae	spp
Haloragis99	Haloragaceae	Haloragis	trigonocarpa
Hardenbergia88	Fabaceae	Hardenbergia	violacea
Hesperocyparis77	Cupressoideae	Hesperocyparis	spp
Hibbertia83	Dilleniaceae	Hibbertia	scandens
Hirschfeldia62	Brassicaceae	Hirschfeldia	incana
Holcus143	Poaceae	Holcus	spp
Hordeum131	Poaceae	Hordeum	vulgare
Hydrocotyle51	Araliaceae	Hydrocotyle	laxiflora
Hydrocotyle2	Araliaceae	Hydrocotyle	novae-zealandiae
Hypericum101	Hypericaceae	Hypericum	perforatum
Hypoxis102	Hypoxidaceae	Hypoxis	hygrometrica
Indigofera89	Fabaceae	Indigofera	australis
Ipomoea74	Convolvulaceae	Ipomoea	spp
Juncus22	Juncaceae	Juncus	articulatus
Juncus21	Juncaceae	Juncus	bufonius
Juncus	Juncaceae	Juncus	capitatus
Juncus105	Juncaceae	Juncus	spp
Kunzea113	Myrtaceae	Kunzea	ericoides
Lamiaceae23	Lamiaceae	unknown Lamiaceae	spp
Lamiaceae108	Lamiaceae	unknown Lamiaceae	spp
Lepidium63	Brassicaceae	Lepidium	africanum
Lepidosperma80	Cyperaceae	Lepidosperma	laterale
Leptospermum114	Myrtaceae	Leptospermum	spp
Linaria121	Plantaginaceae	Linaria	purpurea
Lolium132	Poaceae	Lolium	perenne
Lolium39	Poaceae	Lolium	spp
Lomandra52	Asparagaceae	Lomandra	multiflora
Luzula	Juncaceae	Luzula	campestris
Luzula106	Juncaceae	Luzula	spp
Lythrum109	Lythraceae	Lythrum	salicaria
Lythrum26	Lythraceae	Lythrum	spp
Malvaceae110	Malvaceae	unknown Malvaceae	spp
Medicago	Fabaceae	Medicago	polymorpha
Medicago14	Fabaceae	Medicago	sativa
Medicago90	Fabaceae	Medicago	spp
Microlaena133	Poaceae	Microlaena	avenacea
Microtis29	Orchidaceae	Microtis	spp
Moenchia10	Caryophyllaceae	Moenchia	spp
Musa111	Musaceae	Musa	banana
Myosotis60	Boraginaceae	Myosotis	spp
Myriophyllum100	Haloragaceae	Myriophyllum	verticillatum
Myrtaceae27	Myrtaceae	unknown Myrtaceae	spp

Myrtaceae115	Myrtaceae	unknown Myrtaceae	spp
Nassella134	Poaceae	Nassella	trichotoma
Orchidaceae117	Orchidaceae	unknown Orchidaceae	spp
Orobanche30	Orobanchaceae	Orobanche	minor
Oxalis118	Oxalidaceae	Oxalis	spp
Paronychia68	CaryophyllaceaeÂ	Paronychia	argyrocoma
Persicaria145	Polygonaceae	Persicaria	decipiens
Persoonia153	Proteaceae	Persoonia	asperula
Petrorhagia66	Caryophyllaceae	Petrorhagia	prolifera
Phalaris135	Poaceae	Phalaris	aquatica
Pinus119	Pinaceae	Pinus	spp
Pittosporaceae31	Pittosporaceae	unknown Pittosporaceae	spp
Pittosporaceae120	Pittosporaceae	unknown Pittosporaceae	spp
Plantago32	Plantaginaceae	Plantago	lanceolata
Plantago122	Plantaginaceae	Plantago	spp
Plantago33	Plantaginaceae	Plantago	varia
Poaceae40	Poaceae	unknown Poaceae	spp
Poaceae144	Poaceae	unknown Poaceae	spp
Polygonaceae41	Polygonaceae	unknown Polygonaceae	spp
Polygonaceae148	Polygonaceae	Polygonaceae	spp
Polygonum146	Polygonaceae	Polygonum	arenastrum
Pomaderris156	Rhamnaceae	Pomaderris	angustifolia
Portulaca150	Portulacaceae	Portulaca	oleracea
Proteaceae	Proteaceae	unknown Proteaceae	spp
Pultenaea91	Fabaceae	Pultenaea	spp
Romulea103	Iridaceae	Romulea	spp
Rosa159	Rosaceae	Rosa	rubiginosa
Rosaceae44	Rosaceae	unknown Rosaceae	spp
Rosaceae161	Rosaceae	unknown Rosaceae	spp
Rubiaceae46	Rubiaceae	unknown Rubiaceae	spp
Rubiaceae162	Rubiaceae	unknown Rubiaceae	spp
Rubus160	Rosaceae	Rubus	fruticosus
Rumex147	Polygonaceae	Rumex	spp
Salix164	Salicaceae	Salix	spp
Salvia107	Lamiaceae	Salvia	spp
Schoenus81	Cyperaceae	Schoenus	pennisetis
Scrophulariaceae47	Scrophulariaceae	unknown Scrophulariaceae	spp
Scrophulariaceae168	Scrophulariaceae	unknown Scrophulariaceae	spp
Senecio56	Asteraceae	Senecio	quadridentatus
Senecio	Asteraceae	Senecio	spp
Solanum104	Iridaceae	Solanum	nigrum
Sonchus58	Asteraceae	Sonchus	spp
Sorghum136	Poaceae	Sorghum	nitidum
Sporobolus	Poaceae	Sporobolus	africanus
Stackhousia71	Celastraceae	Stackhousia	monogyna

Stypandra54	Asphodelaceae	Stypandra	glauca
Themeda137	Poaceae	Themeda	triandra
Trifolium15	Fabaceae	Trifolium	angustifolium
Trifolium92	Fabaceae	Trifolium	spp
Trifolium18	Fabaceae	Trifolium	spp
Trifolium16	Fabaceae	Trifolium	subterraneum
Tripogonella138	Poaceae	Tripogonella	loliiformis
Typha170	Typhaceae	Typha	domingensis
Verbascum166	Scrophulariaceae	Verbascum	thapsus
Verbena171	Verbenaceae	Verbena	spp
Veronica167	Scrophulariaceae	Veronica	perfoliata
Wahlenbergia65	Campanulaceae	Wahlenbergia	spp
Wurmbea72	Colchicaceae	Wurmbea	dioica

Appendix C – Chapter Three

Appendix C Table 1. Complete list of plant species identified from germinated seeds grown in a greenhouse experiment. Samples collected across the Ginninderry Conservation Corridor, ACT, between April 2024 and March 2025. Nativeness pertains to the origin of the plant species and whether it is native or exotic and if it is found in the local classification as an invasive species.

Species	Common name	Nativeness	Functional group
Alternanthera denticulata	lesser joy weed	native	herb
Amaranthus retroflexus	redroot amaranth	exotic	herb
Anagallis arvensis	scarlet Pimpernel	exotic	herb
Argemone mexicana	Mexican prickly poppy	exotic	herb
Chenopodium album	fat hen	exotic	herb
Centaurium erythraea	Common centaury	exotic	herb
Cerastium tianschanicum	chickweed	exotic	forb
Conium maculatum	Poison hemlock	invasive	herb
Cynodon dactylon	couch grass	exotic	annual C4 grass
Cyperus eragrostis	Umbrella sedge	exotic	sedge
Digitaria ischaemum	smooth crabgrass	exotic	annual C4 grass
Digitaria sanguinalis	crabgrass	exotic	annual C4 grass
Dysphania pumilio	clammy goosefoot	native	herb
Eleusine tristachya	goose grass / sage	exotic	annual C4 grass
Eragrostis barrelieri	pitted love grass	exotic	annual C4 grass
Eragrostis cilianensis	stink grass	exotic	annual C4 grass
Eragrostis curvula	African lovegrass	invasive	perennial C4 grass
Eragrostis minor	little lovegrass	exotic	annual C4 grass
Festuca arundinacea	tall fescue	exotic	annual C3 grass
Festuca myuros	rat's-tail fescue	exotic	annual C3 grass
Holcus lanatus	velvet grass	exotic	perennial C3 grass
Hypericum perforatum	St John's Wort	invasive	herb
Hypochaeris radicata	flatweed	exotic	forb
Lepidium ferganense	peppercress	exotic	shrub
Lythrum hyssopifolia	lesser loosestrife	native	herb
Juncus bufonius	toad rush	native	herb
Malva neglecta	dwarf mallow	exotic	forb
Microleana stipoides	Weeping grass	native	perennial C3 grass
Modiola caroliniana	red-flowered mallow	exotic	forb
Nasturtium spp	Indian cress	exotic	herb
Paronychia brasiliana	Brazilian whitlow	exotic	herb
Panicum effusum	hairy panic grass	native	perennial C4 grass
Persicaria lapathifolia	pale smartweed	native	herb
Persicaria prostrata	creeping knotweed	native	herb
Persicaria. spp	Unknown species	native	herb
Plantago lancelota	ribwort	exotic	herb
Plantago gaudichaudii	bearded plantain	native	herb
Plantago major	common plantain	exotic	forb

Pleurosorus rutifolius	blanket fern	native	fern
Pleurosorus. spp	unknown fern	native	fern
Polypogon monspeliensis	annual beard grass	exotic	annual C3 grass
Portulaca oleracea	purslane	native	herb
Pyracantha angustifolia	firethorn	exotic	shrub
Rubus spp.	blackberry	invasive	shrub
Rumex acetosella	sheep sorrel	exotic	herb
Rytidosperma carphoides	short wallaby grass	native	perennial C3 grass
Setaria parviflora	slender pigeon grass	exotic	perennial C4 grass
Solanum nigrum	Blackberry nightshade	exotic	shrub
Solenogyne dominii	Smooth solenogyne	native	herb
Sonchus oleraceus	common sow thistle	exotic	herb
Sporobolus fertilis	Giant Parramatta Grass	exotic	perennial C4 grass
Sporobolus indicus	rat's-tail grass	exotic	perennial C4 grass
Stelaris media	Chickweed	exotic	forb
Trifolium angustifolium	narrow leaved clover	exotic	herb
Trifolium arvense	Hare's-foot clover	exotic	herb
Trifolium latinum	latine clover	exotic	herb
Trifolium glomeratum	Cluster clover	exotic	herb
Trifolium repens	White clover	exotic	herb
Trifolium spp.	clover	exotic	herb
Tropaeolum majus	Nasturtium	exotic	herb
Verbena bonariensis	purple top (tall verbena)	exotic	herb
Verbascum thapsus	Great mullein	exotic	herb
Verbena incompta	Purple top	exotic	herb
Verbena officinalis	Common Verbena	exotic	herb
Veronica anagallis-aquatica	Blue water speedwell	exotic	herb
Veronica. spp	unknown speedwell	native	herb

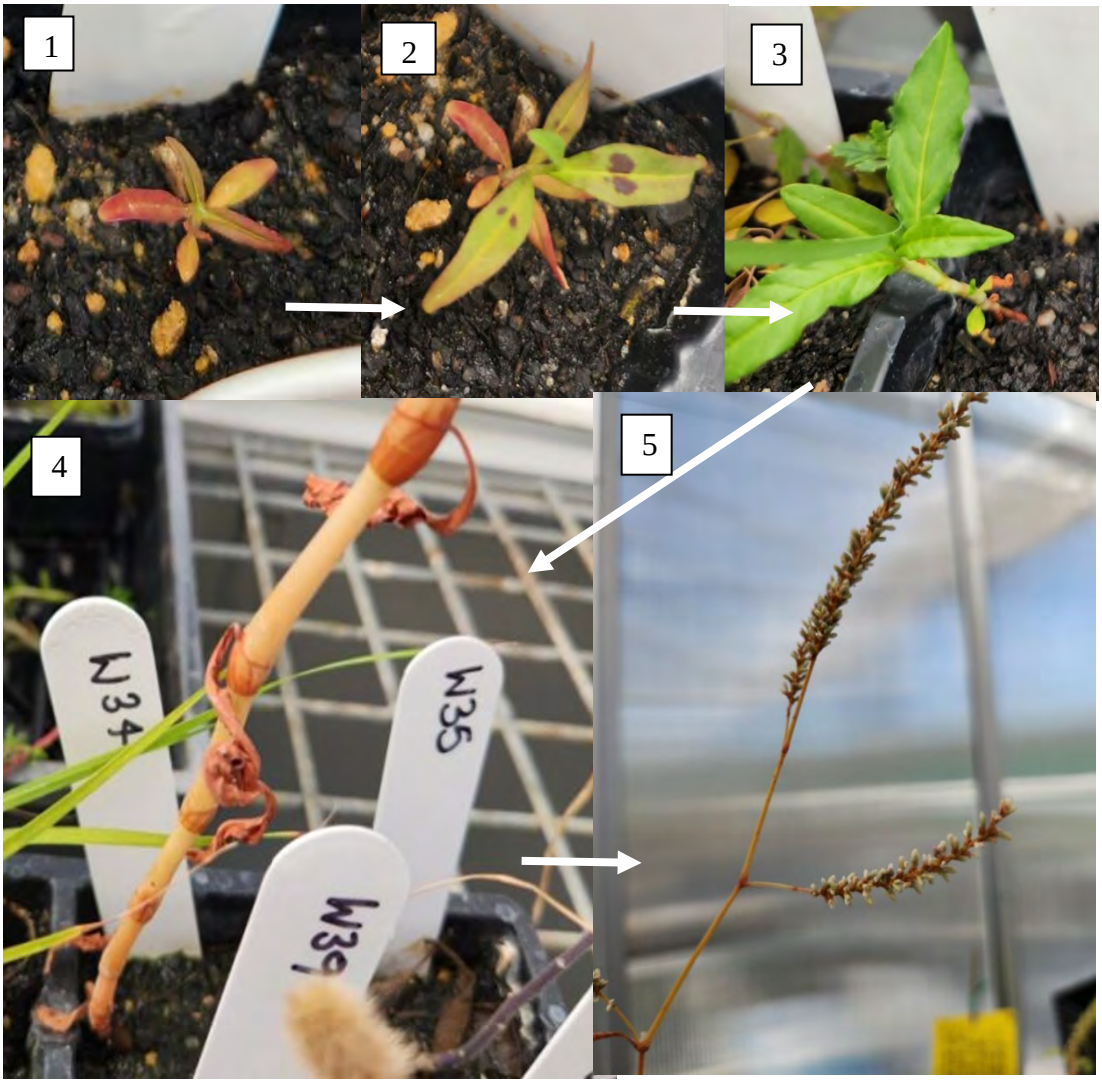
Appendix C. Table 2. List of primers used for the genetic identification of macropod faecal samples.

Primer	**Target Species**	**Sequence (5'-3')**	**Product size(bp)**	**Reference**
mrobF mrobR	Wallaroo	AGCACCCCACCACATATCAAA TGTGTGTAGGAGAGGAATAATAGG		This study
macf marR	Eastern grey kangaroo	GCATCCATCTTAATTCTCCTCA GGTTYTAGTATGTAGTTTTCAAA	250	Koehler et al. (2020a)
walF marR	Swamp wallaby	GCCCTACTTTCATTAGCAC GGTTYTAGTATGTAGTTTTCAAA	425	Koehler et al. (2020a)
Mrus_f Mruf_r	Red-necked wallaby	GCCCTTGGTTTCATACTCATACTTC TTAGTGGGTTGGCAGGAGAG	200	This study

Appendix C. Table 3. Sample size, weight (g), seedling count and species richness for each herbivore by season and total.

Herbivore	n	Season	weight (g)	# seedlings	species richness
EGK	6	Spring	29.71	8	1
Cow	6	Spring	74.05	44	22
Deer	36	Spring	175.33	1447	22
Macropod	39	Spring	116.43	18	3
Wallaroo	29	Spring	105.83	161	1
Wombat	19	Spring	111.87	50	10
EGK	8	Winter	42.73	5	3
Cow	11	Winter	191.73	272	6
Deer	36	Winter	132.09	581	24
Macropod	47	Winter	173.11	64	14
Wallaroo	62	winter	252.36	82	18
Wombat	41	Winter	494.68	78	9
EGK	18	Summer	57.16	8	5
Cow	16	Summer	1423.46	526	25
Deer	39	Summer	175.92	1059	19
Macropod	1	Summer	1.65	0	0
Wallaroo	36	Summer	130.62	120	8
Wombat	14	Summer	77.07	11	6
EGK	5	Autumn	10.11	7	3
Cow	12	Autumn	69.71	189	17
Deer	43	Autumn	105.51	125	30
Macropod	0	Autumn	0	0	0
Wallaroo	47	Autumn	149.55	66	11

Wombat	20	Autumn	114.82	23	11
EGK	37	Total	139.71	28	5
Cow	45	Total	1758.95	1031	25
Deer	154	Total	588.85	3212	30
Macropod	87	Total	291.19	82	14
Wallaroo	176	Total	638.36	429	18
Wombat	94	Total	798.44	162	11



Appendix C. Figure 1 Photo series of one germinated seedling as it grows over time to aid in identification.