Fighting fire with fauna: exploring connections between fire, fuel, and fauna

by

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Candidate's Declaration

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

MChard

Matthew Chard Date: 23/10/2023

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Acknowledgement of Country

I would like to pay my respects to the Traditional Custodians of the land that I live and work on. I acknowledge the continued connection to land, water and community of First Nations people and pay my respects to elder's past, present, and emerging. I acknowledge that sovereignty was never ceded and that this land was, and always will be, Aboriginal land.

My scientific research was conducted on the land of the Wreck Bay Community in Booderee National Park. I was so fortunate to be able to work in such a spectacular place and I dedicate this body of work to the land of Wreck Bay and Booderee. I would further like to acknowledge that this thesis was written on Ngunnawal/Ngunawal, Ngambri, Gadigal, Wodi Wodi, Dharug, Darkinjung and Awabakal lands.

As a non-indigenous person, I am aware this thesis was written under a westernised lens of science and does not incorporate indigenous knowledge or values.

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And finally, to my numerous siblings who mocked me for wanting to write about animals, I love you all and hope you Eat Apples and Dark Chocolate.

Preface

This thesis is being submitted as a compilation of published or submitted, peer-reviewed journal articles in accordance with the 'Thesis by Compilation' guidelines provided by the Fenner School of Environment and Society and the Australian National University. All papers are standalone pieces of scientific literature and, therefore, there is some unavoidable repetition within chapters. Due to editing from journals, there may be minor formatting differences between the papers in this thesis compared to the published counterparts.

In line with 'Thesis by Compilation' guidelines, an Extended Context Statement has been provided at the beginning of this thesis. The Extended Context Statement is not intended to be a complete literature review, but rather a framework for understanding the relationships between all aspects of the research. *Paper I*, *II*, *III* and *IV* each present a review of the literature relevant to the focus of that paper.

I was the major contributor to each of the papers presented in this thesis. This included developing research questions and experimental designs, experimental construction, data collection and analysis, and writing manuscripts. My supervisors (Claire Foster, David Lindenmayer, and Geoff Cary) and collaborators provided advice on conceptualisation, experimental design, experimental construction, data analysis, and manuscript revisions. The addition of different co-authors to each paper reflects contributions from collaborators, which are detailed below. The author contribution statements below have been agreed to in writing by all authors. Other assistance is acknowledged in the acknowledgments section at the end of each paper.

Paper I: Chard, M., Foster, C.N., Lindenmayer, D.B., Cary, G.J., MacGregor, C.I. and Blanchard, W. (2022) 'Time since fire influences macropod occurrence in a fire-prone coastal ecosystem' *Austral Ecology*, **47**(3), pp.507-518.

Word length: 7,673

Journal: Austral Ecology

Status: Published

Author contribution: conceptualisation & design - MC, CNF, DBL, GJC; data extraction and analysis - MC, WB; manuscript drafting - MC; manuscript revision - MC, CNF, DBL, GJC, CIM.

Paper II: Chard, M., Foster, C.N., Lindenmayer, D.B., Cary, G.J., MacGregor, C.I. and Blanchard, W. (2022) 'Post-fire pickings: Large herbivores alter understory vegetation communities in a coastal eucalypt forest' *Ecology and evolution*, **12**(4), p.e8828.

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Paper III: Chard, M., Foster, C.N., Lindenmayer, D.B., Cary, G.J., MacGregor, C.I. and Zylstra, P.J. (2023) ‘Fencing foragers fuels fires: Can large herbivores alter fire behaviour in coastal eucalypt forests?’

Word length: 9,802

Journal: Fire Ecology

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***Paper IV*:** Chard, M., Foster, C.N., Lindenmayer, D.B. and Cary, G.J. (2023) ‘Fighting fire with fauna: exploring the potential of using large herbivores to manage bushfire fuel in south-east Australia’

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Abstract

The role of animal-mediated influences on fire is poorly understood from an ecological and fire management perspective. As fire activity is predicted to worsen in fire-prone ecosystems, is it imperative to understand the connections between fire, fuel, and fauna. In this thesis, I examined the drivers of large native herbivore behaviour, and the subsequent impacts on fuel properties, to determine if herbivores can alter fire behaviour.

Large herbivores can alter vegetation structure, composition, and function, which are key drivers of fuel properties. However, it is currently unknown if fire management practices in eucalypt forests need to accommodate for large herbivore populations. Quantitative studies are required to measure large herbivore impacts on fuel properties. My study system was a fire-prone National Park in south-eastern Australia in which large herbivores were represented by three macropod species.

I first aimed to understand the drivers of macropod occurrence across my study system with respect to fire and vegetation. Analysis incorporated long-term spotlighting surveys; fire history data; and vegetation mapping. I found macropods preferentially selected for recently burnt patches likely due to the green pick available following a fire. Further, macropods were more likely to occur in forest vegetation.

Secondly, I constructed exclosure fences to manipulate macropod access to plots in forest vegetation that had been burnt during a wildfire in 2017. My study also incorporated a similar manipulative experiment, comprising smaller

exclosure fences, that had been constructed five years prior. Vegetation community metrics and fire behaviour projections were recorded in the experimental plots and compared between fencing treatments.

Browsing by macropods reduced measures of species richness, diversity, and evenness in understorey vegetation. This resulted in a depauperate vegetation community in plots exposed to post-fire herbivory compared to fenced plots. The palatability of plant species was the likely driver, as less palatable plants were dominant in browsed plots.

I found evidence for large herbivores to affect fire behaviour predictions, but the direction of these effects depended upon the model used and the elements of fuel each model considered. When one fire model that accounts mostly for dead fuel was used, herbivore browsing was predicted to create more moderate fire behaviour, potentially allowing more aggressive firefighting responses. Pronounced trends in other vegetation parameters considered by another fire model indicated that longer-term trends of herbivore browsing would see milder fire behaviour.

These findings highlighted the risk of drawing conclusions regarding large herbivore management if the fire model employed accounts for only some of the many vegetation characteristics affected by herbivory. This study demonstrated the capacity for large herbivores to alter fire behaviour with clearer trends likely to become apparent with more time.

The final chapter of my thesis aimed to synthesise current literature on large herbivore impacts on vegetation in forest ecosystems in south-eastern Australia. Viewing this research from a fire management perspective, I

assessed how large herbivores may be influencing aspects of fuel properties and the likely fire behaviour outcomes of such modifications. I explored this concept as a potential for a nature-based solution to manage fuel properties but urged caution to the long-term ramifications on vegetation communities and fire behaviour. I then provided a new framework for the future management of large herbivore populations to utilise large herbivores as a tool for managing bushfire fuel in forests.

My research identified some of the relationships between fire, fuel, and fauna within forests of south-eastern Australia. My research highlights the potential for herbivore-mediated changes to future fire regimes in forest ecosystems, an aspect that needs to be addressed in future fire management practices.

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Extended Context Statement

Introduction

Global trends show fire severity to be increasing as air temperatures rise and extreme weather events become more frequent (Kertész et al., 2017). Australian ecosystems, that have adapted to cope with fire, are being subject to more frequent catastrophic fires (Abram et al., 2021). These fire-adapted ecosystems are experiencing fires that are severe enough to cause adverse impacts on both wildlife (Dickman & McDonald, 2020) and their habitats (Ward et al., 2020). To reduce threats to Australian ecosystems due to the increased frequency of catastrophic fires, understanding the factors that drive changes in fire behaviour is vital to future fire management practices (Cruz et al., 2021). Further, greater protection needs to be placed on ecologically sensitive areas that are under threat of severe fire (Driscoll et al., 2010) and areas that threaten human life (Morgan et al., 2020).

The Australian landscape is synonymous with fire. For thousands of years, the indigenous custodians of the land used fire to manage, invigorate and nurture the land (Steffensen, 2020). Australian native flora and fauna have co-evolved with fire, often being able to persist and thrive following a fire event (Recher & Christensen, 1981; Trauernicht et al., 2015). However, areas, where burning practices were regularly conducted by First Nations peoples, were disrupted following the colonisation of Australia and the removal or restriction of indigenous land practices (Steffensen, 2020). Poor land management following this disruption to the fire cycle further exacerbated negative repercussions for

Australian ecosystems through land clearing, urbanisation, and the introduction of invasive plants and animals (Dickman & McDonald, 2020).

A major issue of contemporary Australian fire management is the proximity of human habitation to highly flammable forests (Lindenmayer et al., 2022). This is particularly pronounced in south-eastern Australia where the wildland-urban interface is most extensive, and continuing to expand (Morgan et al., 2020). Forests in these areas are dominated by *Eucalyptus* species that can support high-severity fires due to numerous factors including, but not limited to; the volatile oils contained in their leaves; the amount of dead fuel they produce; and stand structure (Gill & Zylstra, 2005). As human settlements continue to expand near, or within areas of high fire risk, fire management continues to focus on reducing the loss of human lives and reducing loss and damage to assets (AFAC, 2012). This needs to be balanced with healthy ecosystem functioning to ensure threats to biodiversity are similarly minimised (Driscoll et al., 2010).

Techniques employed in fire management in south-eastern Australian eucalypt forests range from preventative (Morgan et al., 2020) to responsive (Penney et al., 2019). While responsive measures occur during a fire event, preventative measures aim to reduce wildfire damage before a fire event (AFAC, 2012). Preventative measures can take the form of prescribed burning practices whereby a controlled fire is applied to a pre-determined area to attain desired management objectives (AFAC, 2012; Morgan et al., 2020). However, the efficacy of this technique has come into question, with evidence suggesting that prescribed burning may be driving increased fire risk (Zylstra et al., 2022). Another preventative measure involves the establishment and maintenance of asset protection zones whereby vegetation is cleared to form a physical buffer to reduce the likelihood of fires threatening human property (Driscoll et al., 2010). Methods of prescribed burning and clearing generally attempt to reduce the amount of fuel available to burn and reduce fuel connectivity (Gosper et al., 2013).

One aspect that is currently overlooked in preventative fire management is the impact of large herbivores on the landscape (Johnson et al., 2018). Large herbivores (> 2 kg as per Danell, 2006) can alter both fuel load and fuel structure through the removal and trampling of vegetation (Fuhlendorf et al., 2009). As large herbivores preferentially select more palatable plants within an ecosystem, this can alter the succession and persistence of plant species (Archibald et al., 2019). The response of plant species to herbivory is dependent on both foraging pressure and plant resilience (Strauss & Agrawal, 1999). Under some conditions, this can lead to the dominance of unpalatable, chemically-defended plant species as other palatable plants are removed, freeing up nutrients and space (Bakker et al., 2016; Leroux et al., 2020). Conversely, browsing may cause an increased abundance of highly palatable plants through positive nutrient cycling and facilitated seed dispersal (Augustine & McNaughton, 1998). The capacity for large herbivores to modify vegetation is then further compounded by other disturbances in the landscape such as fire (Archibald et al., 2019).

Following a fire in a eucalypt forest, vegetation communities undergo a process of recovery (Forsyth et al., 2012). This can be characterised by the germination of seeds and the regrowth of persisting plants (Bradstock et al., 2002). This provides an opportunity for herbivores to access highly nutritious and easily digestible plant matter often referred to as ‘green pick’ (Matthews et al., 2015). This phenomenon is coined ‘pyric herbivory’ whereby fire in the landscape drives herbivore foraging behaviour within an ecosystem (Fuhlendorf et al., 2009). Small mammals may prefer cover, but there is evidence that larger mammals prefer open habitat (anti-predator visibility) and can be attracted to burnt patches (Fuhlendorf et al., 2009). This increased foraging pressure in a post-fire environment can further shape plant communities (Archibald & Hempson, 2016). However, little is known about how eucalypt forest communities in south-eastern Australia respond to an increase in large herbivore browsing following a fire, although an effort is being made to document such changes (Foster et al., 2016). A logical progression for this research is to determine how vegetation communities subject to post-fire herbivory translate to altered fuel properties, consequently shaping future fire behaviour (Foster et al., 2020).

A drying climate is likely to further exacerbate large herbivore influences on vegetation in south-eastern Australia (Bradstock et al. 2014). Higher extreme temperatures may increase the curing of dead fuel material and reduce decomposition rates in eucalypt forest communities (Vandandorj et al. 2017). This may lead to an increased dead fuel load, potentially increasing future fire behaviour (Zylstra et al. 2022).

Large native herbivores in Australia are predominantly represented by macropods, marsupials within the family of *Macropodidae* such as kangaroos and wallabies (Menkhorst & Knight, 2004). These mammals can be grazers or browsers and are present in many Australian habitats (Coulson et al., 2010). Some macropod species, generally larger grazing species, have benefitted from post-colonial alterations to the landscape that were intended to aid agriculture such as tree removal, predator control, and the installation of permanent water sources (Read et al., 2021). The rise in macropod populations in some areas is a cause of concern for agricultural systems, animal welfare, and biodiversity (Pedler et al., 2021). Concerns are primarily derived from over-abundant macropod populations engaged in increased foraging that reduces the available feed for livestock or causes damage to farm crops (Morgan, 2021). The implications of overabundant macropods on vegetation communities in forest ecosystems are currently being explored (Dexter et al., 2013; Foster et al., 2015). Understanding the foraging behaviour of macropod species is critical to determining their influence on fuel properties and fire behaviour.

How macropods respond to fire is dependent on each species' response to the presence of green pick and the reduction of available cover (Meers & Adams, 2003). While evidence exists for both the attraction and avoidance of macropods, studies of eucalypt forest ecosystems often show that macropods are attracted to burnt patches likely due to the increased green pick following fire (Styger et al., 2010; Matthews et al., 2015; Bowman et al., 2021). Studies have found an increased presence of macropods following fire between 14 days (Meers & Adams, 2003) up to two years following a fire (Parkins et al., 2019).

Increased macropod presence following a fire in eucalypt forests has revealed significant modifications to understory vegetation communities (Foster et al., 2015). Post-fire herbivory from macropods resulted in a more depauperate understory community with manipulative field experiments revealing reduced measures of species richness, species diversity and evenness compared to areas where macropods are excluded (Dexter et al., 2013; Foster et al., 2015). Further, these studies found macropod foraging to increase measures of plant dominance, indicating that post-fire herbivory promoted the succession of the most dominant understory plants within a given plot. This was expected given dominant plants in forest understories are often less palatable for macropods (Archibald et al., 2019).

While this thesis is predominately concerned with the influence of macropods on forest vegetation communities, populations of other native and feral large herbivores are present within forests of south-eastern Australia. Feral herbivores, particularly feral ungulates, are a management concern in Australian forest communities due to their relative size (compared to native herbivores), diets, behaviour, morphology, and overabundance in some locations (Kieth & Pellow 2005; Davis et al. 2016; Atkinson et al. 2019). It is likely that feral herbivores may have a higher impact on vegetation communities in south-eastern Australia, compared to macropods, with evidence of altered vegetation biomass (Davis et al. 2016), modified plant structure (Coleman et al. 2014), and increasing the abundance of unpalatable plant species (Bell et al. 2022).

An understory dominated by unpalatable plants is a cause for concern as unpalatable plants, on average, have reduced moisture content and a higher concentration of volatile oils making them more flammable compared with palatable species (Archibald et al., 2019). Further, plant species such as bracken fern (*Pteridium esculentum*), a species of low palatability for macropods, are fast growing and senesce quickly (Dexter et al., 2013). The rapid life cycle of bracken, and its frond structure, produces large amounts of cured, well-aerated fuel in the understory (Mason et al. 2016). This may mean that post-fire herbivory from large herbivores in eucalypt forests is driving long-term increased fire potential as browsing transforms fuel properties (Foster et al., 2015). The influence of large herbivore browsing on fire behaviour needs to be quantified through fire modelling projections. It is imperative to determine how macropods, and large herbivores more generally, shape fuel properties and potentially alter fire behaviour.

Overview of Aims

This thesis explores the relationship between fire, fuel, and fauna, with the central aim of determining herbivore-mediated influences on fire behaviour (Table 1). This thesis is comprised of the following components: How do fire and vegetation affect large herbivore occurrence at a landscape scale? (*Paper I*); How does post-fire browsing from large herbivores alter understory plant communities? (*Paper II*); Can post-fire browsing from large herbivores alter fire behaviour? (*Paper III*); Can large herbivores be an effective tool to manage bushfire fuel in south-eastern Australia? (*Paper IV*).

I first needed to understand the influence of fire activity on large herbivore occurrence at a landscape scale (*Paper I*). This study confirmed that the large herbivores within the study area were attracted to burnt patches and that they were most likely to occur in forest vegetation. Using a manipulative field experiment, the next step was to determine how pyric herbivory responses influenced understory vegetation (*Paper II*). If large herbivores are altering the understory vegetation community, then that altered community should be characterised by modified fuel properties and fire behaviour. The logical progression was to model fire behaviour and compare areas that were browsed and unbrowsed by large herbivores (*Paper III*). Collectively, *Papers I*, *II*, and *III* aimed to understand the ecological processes surrounding fire behaviour in the study area and explore the connection of fire, fuel, and fauna.

While several studies have documented the capacity for large herbivores to modify understory vegetation assemblages in forest ecosystems in south-eastern Australia (e.g., Colman et al., 2014; Foster et al., 2015; Bennett et al., 2020), the effects of such changes on fire behaviour are rarely considered. I synthesised current literature on large herbivore interactions with vegetation and fire in forest ecosystems in south-eastern Australia (*Paper IV*). By comparing this body of literature with the findings from my empirical papers, I developed a management resource to determine if large herbivores may be utilised as a fire management tool. This last chapter provided valuable insights and practical land management advice for resource managers.

Table 1: Overview of research questions, aims and methods of the papers within this thesis.

Research Question	Aims	Method
Paper I: **How do fire and vegetation affect large herbivore occurrence at a landscape scale?**	• Investigate whether fire drives patterns of large herbivore occurrence • Quantify pyric herbivory responses of focal herbivores • Determine which vegetation community large herbivores prefer in the landscape	• Long-term ecological monitoring • Quantitative

***Paper II*:** **How does post-fire browsing from large herbivores alter understory plant communities?**	• Measure changes to understory plant community assemblages • Document morphological differences of the dominant plant species	• Manipulative field experiment • Quantitative
***Paper III*:** **Can post-fire browsing from large herbivores alter fire behaviour?**	• Quantify large herbivore influence on fire behaviour projections • Investigate multiple fire behaviour models and determine (if any) changes to firefighting responses	• Manipulative field experiment • Quantitative
***Paper IV*:** **Can large herbivores be an effective tool to manage bushfire fuel in south-eastern Australia?**	• Explore current literature for large herbivore responses to fire and large herbivore impacts on vegetation • Synthesise literature to explore how large herbivores may positively or negatively influence fuel properties • Construct a framework to assist resource managers in future fire management	• Literature synthesis • Qualitative

Study Area

The empirical papers in this thesis (*Papers I*, *II*, and *III*) are based on two field experiments conducted in Booderee National Park (BNP). *Paper I* incorporates monitoring data sourced from long-term ecological surveys that began in 2003 (Lindenmayer et al., 2008; 2016). *Papers II* and *III* incorporated a field experiment to manipulate large herbivore activity. Below, I provide a brief description of the study area and the species found across BNP relevant to this thesis. More detailed descriptions and a map of the study area are included in all empirical papers.

Booderee National Park is located on the south-eastern coast of Australia and is home to the Wreck Bay Aboriginal Community (35°08'13.3"S 150°41'37.4"E). The Park is ~ 6,500 ha and is jointly managed by the Wreck Bay Aboriginal Community and Parks Australia. BNP is dominated by Sydney Coastal dry sclerophyll vegetation with four dominant vegetation classes: forest; heathland; woodland; and shrubland (Taws, 1997). There is a well-documented fire history with records of fire type and extent dating back to 1957 (Westgate et al., 2012). BNP has experienced three bushfires that were high-severity crown fires in the past 20 years: 2003 (2,700 ha); 2007 (270 ha); and 2017 (1,600 ha). In addition, approximately 45 medium to low-intensity, controlled burns have occurred in Booderee National Park since 1957 ranging from 1.8 to 289 ha.

Three large macropod species are currently found in BNP: the eastern grey kangaroo (*Macropus giganteus*); swamp wallaby (*Wallabia bicolor*); and red-necked wallaby (*Notamacropus rufogriseus*). All three species have previously demonstrated pyric herbivory responses with most studies identifying a preference for recently burnt patches (Southwell & Jarman, 1987; Meers & Adams, 2003; Williamson et al., 2012; Foster et al., 2015; Parkins et al., 2019). A population of the long-nosed potoroo (*Potorous tridactylus*) also occurs in the park, but the species is extremely rare and under the weight threshold for ‘large herbivores’ (> 2 kg; Danell, 2006) which is the focus of this thesis.

As Booderee National Park lacks other large herbivore species that are not macropods, my conclusions and recommendations for *Papers I*, *II*, and *III* are primarily focused on the impacts of macropods in coastal eucalypt forests.

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Paper I: Time since fire influences macropod occurrence in a fire-prone coastal ecosystem

1.1 Foreword

Paper I explores the effect of fire and vegetation on macropod occurrence across Booderee National Park. Determining the drivers of macropod occurrence across the park may provide insights into fire-herbivore relationships. It was also imperative to determine if macropods in the park displayed evidence of pyric herbivory by preferentially selecting for burnt areas in the landscape as this underpins a key concept within my thesis. In this study, I examined the effect of fire history and vegetation type on macropod occurrence using a 16-year spotlighting dataset.

Chard, M., Foster, C.N., Lindenmayer, D.B., Cary, G.J., MacGregor, C.I. and Blanchard, W. (2022) 'Time since fire influences macropod occurrence in a fire-prone coastal ecosystem' Austral Ecology, 47(3), pp.507-518.

Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with https://policies.anu.edu.au/ppl/document/ANUP_003405

I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multi-author papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

Title: Time since fire influences macropod occurrence in a fire-prone coastal ecosystem

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Senior author or collaborating authors endorsement: I, Claire Foster endorse the above contribution statement

Matthew Chard	MChard	3/15/2023
Candidate	Signature	Date

Endorsed

Claire Foster	C.	15.03.2023
Primary Supervisor – Print Name	Signature	Date
Philip Gibbons	Philip Gibbons	17/3/2023
Delegated Authority – Print Name	Signature	Date

1.2 Abstract

Knowledge of animal responses to fire is fundamental to wildlife management in fire-prone ecosystems. Fire can influence the occurrence of large herbivores by altering the structure and composition of vegetation. However, how fire affects herbivore occurrence in many ecosystems is poorly understood. Large herbivores may be attracted to burnt areas due to higher foraging quality. Conversely, herbivores may avoid burnt areas due to heightened predation risk. We tested the influence of vegetation type and fire history variables on the occurrence of macropods at Booderee National Park in south-eastern Australia. We documented macropod occurrence at 107 long-term monitoring sites using spotlighting surveys conducted between 2003 and 2019. We modelled relationships between the occurrence of the eastern grey kangaroo (*Macropus giganteus*) and the swamp wallaby (*Wallabia bicolor*) with three fire history variables; time since fire, fire frequency, and burn context (the proportion of the area surrounding each site that was recently burnt), as well as their interaction with vegetation type. We found both macropod species selected recently burnt sites, likely due to a higher abundance of preferred plants at these sites. Increasing fire frequency was associated with a reduced occurrence of the eastern grey kangaroo. The occurrence of both macropod species was significantly higher in forest sites, possibly reflecting higher foraging quality of grass and shrub species compared to woodland, heathland and shrubland sites. We suggest that if fire is used as a management tool, it is important to recognise potential feedbacks from increased foraging pressure from large herbivores. Future fire management will need to avoid burning areas of sensitive vegetation if local herbivores display pyric herbivory responses, and/or avoid small scale burns which may concentrate foraging pressure.

Keywords: fire history, swamp wallaby, eastern grey kangaroo, time since fire, pyric herbivory

1.3 Introduction

Fire alters the structure and composition of vegetation and can influence the occurrence of herbivores within landscapes (Fuhlendorf et al., 2009; Rickbeil et al., 2017). As fire modifies resource availability and habitat suitability, herbivores can adapt to accommodate such disturbances (Bond & Keeley, 2005; Nimmo et al., 2018). The relationship between fire and herbivores in grass-dominated ecosystems has been well established under the banner of ‘pyric herbivory’ (herbivory shaped by fire) and researched globally (Fuhlendorf et al., 2009; Eby et al., 2014). Fire and herbivores act as competing consumers of vegetation which, through feedback mechanisms, alter the expression of both the fire regime (Krebs et al., 2010) and the habitat selection of herbivores (Nimmo et al., 2018). As global fire regimes are predicted to change as a result of human land use and climate change, it is imperative to evaluate how this will influence the future functioning of fire-prone ecosystems, including herbivore responses (Keeley, 2009; Earl & Simmonds, 2018; Johnson et al., 2018; Nimmo et al., 2018).

Fire-grazing interaction studies have revealed preferential foraging in recently burnt areas by large (> 2 kg) herbivores (Allred et al., 2011). In North America, barren-ground caribou (*Rangifer tarandus groenlandicus*), bison

(*Bison bison*) and cattle (*Bos taurus*) actively select recently burnt patches (Allred et al., 2011; Rickbeil et al., 2017). Similarly, many African ungulate species exhibit increased foraging pressure in areas following fire (Kimuyu et al., 2014; Archibald & Hempson, 2016; Donaldson et al., 2018). The underlying mechanism for this phenomenon is predominantly post-fire vegetation succession. New growth of vegetation is stimulated by fire through the removal of competition and increases of both available nutrients and space (Bond & Van Wilgen, 1996). Fire also can stimulate seed release and germination of certain plant species (Ooi, 2012). Relative to older vegetation, new growth (post-fire) is more nutritious, more readily digestible, and more easily accessible for herbivores (Eby et al., 2014). Conversely, some (often smaller) herbivore species have been found to avoid burnt areas, likely due to heightened predation risk as fire removes available cover (Banks et al., 2011; Hale et al., 2016; Puig-Gironès et al., 2018). If recently burnt patches in landscapes influence the occurrence of herbivores (positively or negatively), future fire management practices should ideally account for these behavioural changes.

While fire-herbivory interactions have been identified in many environments, the focus of these studies has typically been on ungulate species in grass-dominated systems (Danell, 2006; Fuhlendorf et al., 2009). Fire-herbivory studies of non-ungulate herbivores are uncommon, particularly in open forest environments. Australia contains many fire-prone environments, but the continent lacks native ungulate species. Instead, macropods occupy the role of the dominant large native herbivore in many Australian ecosystems (Southwell et al., 1973, 1999; Southwell, 1987). Macropod species are classified as either grazers and/or generalist browsers that forage on a range of plant foods (Coulson et al., 2010). Fire has been identified as a driver which alters macropod responses in several ecosystems (Ritchie et al., 2008; Styger et al., 2010; Williamson, Doherty and Di Stefano, 2012; Foster et al., 2015). Macropod focused fire-herbivory research has revealed occurrence responses to aspects of fire that are: positive (Meers & Adams, 2003; Styger et al., 2010); negative (Caughley et al., 1985; Styger et al., 2010); both positive and negative (Ritchie et al., 2008); or absent (Geary et al., 2020). The directionality of these responses is dependent on both the foraging preferences of the macropod species as well as the type of ecosystem in which the fire occurred.

There is a need to quantify how fire influences habitat use by macropods as this may affect regenerating vegetation communities. Further, research on macropod responses to fire has typically been short-term (Hale et al., 2016; Nimmo et al., 2018). Within open eucalypt forests, macropods have displayed positive associations with fire frequency (Dexter et al., 2013; Lindenmayer et al., 2016) and utilised the edges of burnt patches (Parkins et al., 2019). Increased browsing pressure from macropods within burnt patches of south-eastern Australian coastal eucalypt forest has resulted in an altered understory vegetation community (Foster et al., 2015). It is critical to incorporate long-term monitoring into animal movement studies to increase the reliability of measured change (Nimmo et al., 2018).

In this study, we used a 16-year dataset to quantify temporal relationships between the occurrence of two macropod species, vegetation type and three fire history variables including: time since fire, fire frequency and burn context (defined as the proportion burnt of the area surrounding a site). Our objective was to identify which vegetation and fire history variables had the greatest influence on the occurrence of macropods within a coastal environment in south-eastern Australia. The two macropod species we investigated were the eastern grey kangaroo (*Macropus giganteus*) and the swamp wallaby (*Wallabia bicolor*).

We predicted that vegetation type would significantly influence the occurrence of both macropod species in Booderee National Park. We postulated that the probability of occurrence of both the eastern grey kangaroo and the swamp wallaby would be greater in open forest (hereafter referred to as 'forest') than woodland, heathland and shrubland due to (comparatively) higher forage quality (nitrogen content, water content and dry matter digestibility; Moser et al., 2006). Food quality has previously been identified as influencing habitat selection for both species (Moore et al., 2002; Swan et al., 2008; Di Stefano et al., 2009).

We also expected that both macropod species would preferentially select for recently burnt patches as fire stimulates the sprouting and germination of many grasses, forbs and shrubs which both species preferentially select for (Jaremovic & Croft, 1987; Moore et al., 2002; Swan et al., 2008; Leonard et al., 2010; Foster et al., 2016).

Repeated fires will promote the dominance of fire-resistant or early successional species, such as grasses and ferns, altering the composition of a vegetation community (Foster et al., 2018; Archibald et al., 2019). Further, successive fires decrease structural complexity which results in increased visibility for both herbivores and their predators (Bond et al., 2004; Bond &

Keeley, 2005). We predicted a higher occurrence of the grazing eastern grey kangaroo with increased fire frequency as grasses become more abundant and dominant (Moore et al., 2002). Conversely, we expected a lower occurrence of the browsing swamp wallaby with increased fire frequency due to changes in the quality, abundance and distribution of their preferred food as well as increased predator risk (Swan et al., 2008; Foster et al., 2018).

The landscape context of fire may also influence macropod occurrence. Larger swathes of burnt patches should benefit the eastern grey kangaroo which prefers open habitats for foraging (Moore et al., 2002). The constraints on the optimal foraging behaviour of the swamp wallaby relate to forage quality and lateral cover (Di Stefano et al., 2009). Therefore, increased fire size should reduce swamp wallaby occurrence but areas that are patchily burnt may promote swamp wallaby foraging where they have sufficient access to both food and protection from predation.

We considered other hypothesis involving interactions between the fire history variables and vegetation type (Table S1). For example, dense understory vegetation should return more quickly following fire in heathland compared to the other vegetation types (Gill, 1975). This faster recovery may reduce the optimal foraging window (in terms of accessibility and grass abundance) for the eastern grey kangaroo but may quickly reestablish the dense cover favoured by the swamp wallaby. As each vegetation type will respond differently to each fire variable due to differences in structure and plant species composition (Foster et al., 2017), we predicted the addition and/or interaction of these fire and vegetation variables will also result in varied responses from both the eastern grey kangaroo and swamp wallaby.

The large temporal and spatial scale of our study enabled insights into macropod occurrence in response to both vegetation and fire. We expected the change in occurrence of both macropod species across the landscape to reflect the optimal foraging behaviour. By investigating the role fire plays in the occurrence of macropods, we aimed to elucidate the mechanisms that drive habitat and foraging preferences of macropods.

1.4 Methods

Study area

We conducted this study at Booderee National Park (BNP; 35.1489415° S, 150.6454625° E) on the south-east coast of Australia, approximately 200 km south of Sydney (Fig 1). The park is ~6500 ha in area and co-managed by the Wreck Bay Aboriginal Community and Parks Australia. The dominant vegetation classes are forest (45.1%), heathland (15.3%), woodland (12.9%) and shrubland (9.5%; Fig 1b; Taws, 1997). These vegetation types are distinguished by the height, cover and identity of the canopy layers: forest (trees have touching crowns, usually > 20 m tall), woodland (trees have separated crowns, usually < 20 m tall), heathland (treeless, shrubs usually < 2 m tall) and shrubland (treeless, shrubs usually > 2 m tall).

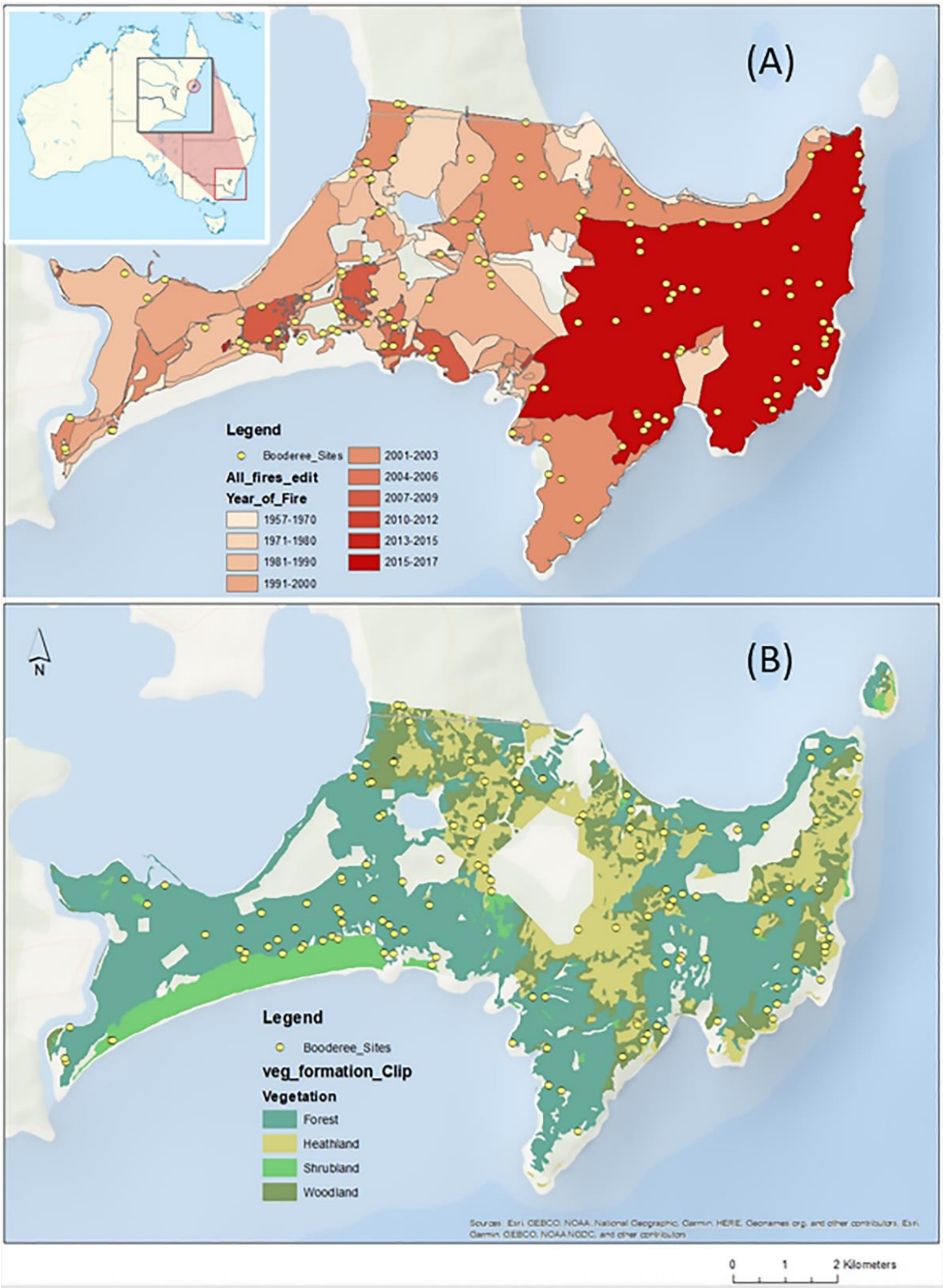

Figure 1: Map of Booderee National Park (35.1489415° S, 150.6454625° E) and the location of the reserve in Australia. Map (A) shows the fire history of the park since 1957. Yellow dots are the location of the long-term monitoring sites used for collecting spotlighting data. Fire history extents were combined by decade up until 2000 after which fires were combined every two years (for display purposes only). Mapped fires include any instance of fire within the park (bushfire, hazard reduction burn, back burn, etc.). Map (B) shows the distribution of the four dominant vegetation types within the park: forest (45.1%), heathland (15.3%), woodland (12.9%) and shrubland (9.5%).

Each vegetation type is dominated by an understory (< 2 m) of: *Pteridium esculentum* and *Lomandra longifolia* in forest; *P. esculentum*, *Banksia serrata*, *Lambertia formosa*, *Acacia longifolia*, *A. suavolens*, and *L. longifolia* in woodlands; *B. ericifolia*, *Allocasuarina distyla*, *Isopogon anemonifolius*, *Hakea teretifolia* and other *Leptospermum* or *Melaleuca* species in heathland; and in shrubland communities the understorey is often sparse owing to the dense growth of the midstory but is comprised of *P. esculentum*, *L. longifolia* and *Hibbertia scandens* (Lindenmayer et al., 2008). Further, many of the species within each of the vegetation types, including the canopy trees (*Eucalyptus* and *Corymbia*) are not killed by fire and can resprout from aboveground epicormic buds following fire (Gill, 1975; Ingwersen, 1977). Fires in the forest and woodland vegetation types in Booderee National Park are therefore not stand-replacing.

BNP has a well-documented fire history with records of fire type and extent dating back to 1957 (Fig 1a). Since our long-term monitoring sites were first established in 2003, BNP has experienced three bushfires that were high intensity, crown fires: 2003 (2,700 ha), 2007 (270 ha) and 2017 (1,600 ha). Further, approximately 45 medium to low intensity, controlled burns have occurred in BNP since 1957. These have ranged from 1.8 to 289 ha in size.

Study species

There has been an active program of intensive feral predator control in BNP for two decades, resulting in an increase in populations of macropods (Dexter et al., 2012; Lindenmayer et al., 2016). Three large macropod species are currently found within BNP, being the eastern grey kangaroo, swamp wallaby, and red-necked wallaby (*M. rufogriseus*). All three species have previously demonstrated pyric herbivory responses with most studies identifying a preference for recently burnt patches (Southwell and Jarman, 1987; Meers and Adams, 2003; Williamson, Doherty and Di Stefano, 2012; Foster et al., 2015; Parkins et al., 2019). A population of the long-nosed potoroo (*Potorous tridactylus*) also occurs in the park but the species is extremely rare and under the weight threshold for "large herbivore" (> 2 kg; Danell, 2006).

As a grazing species, the eastern grey kangaroo actively selects forage patches in lawns and open forests due to abundant grass species (Brunton et al., 2018). The eastern grey kangaroo will congregate in mobs and use vigilance strategies to reduce predation risk (Banks et al., 2000). The swamp wallaby is solitary and selects areas in which to forage based on both food quality and predator avoidance, with locations of increased horizontal cover being 'safer' environments (Di Stefano et al., 2009; Hradsky et al., 2017). Biomass data, corresponding to potential food availability within each vegetation type, indicates higher availability of preferred plants may be present in forest and woodland sites for the eastern grey kangaroo and forest sites for the swamp wallaby (Table S3).

In BNP, the main predator for macropod species is the introduced red fox (*Vulpes vulpes*). Predation by foxes was previously found to be significantly higher for the swamp wallaby compared to the eastern grey kangaroo within our study area (9.1% and 0.9% of fox diet respectively; Roberts et al., 2006). Furthermore, studies in similar ecosystems (eucalypt forest on the south-east coast of Australia) have shown that the presence of meso-predators, such as foxes, significantly increased following fire potentially elevating predation risk for macropods (Hradsky et al., 2017).

Spotlight surveys

In 2003, we established 109 monitoring sites with another 20 sites added in 2007 (Fig 1). Each site is 100 m in length and was confined to one vegetation class. We used nocturnal line-transect sampling with spotlights to count fauna along each transect within a 20-minute timeframe. Counts were not conducted when weather was poor (rain, high wind, fog or heavy cloud cover). Surveys were conducted annually from 2003-2007 with each site being surveyed once. From 2007 onwards, surveys have been conducted biennially with the most recent occurring in 2019. For further description of the spotlighting methodology see Lindenmayer et al. (2008).

Of the 129 sites surveyed by spotlighting, we focused on 107 sites located in the four major vegetation types (Veg): forest (42% of total surveys), woodland (23%), heathland (25%) and shrubland (10%). The eastern grey kangaroo and swamp wallaby were analysed separately with counts being converted to presence/absence data as recounting individuals was a possibility. There were insufficient records of the red-necked wallaby from the spotlighting data to include in our analysis.

Data analysis

We used data on macropod presence/absence to quantify relationships with vegetation type and fire history variables. Site-level data allowed for factors such as time since fire, fire frequency and burn context to be calculated for each site in each survey year. We completed analyses using statistical packages in R (Core, R Team, 2016).

The field protocol for this study entailed a single spotlighting transect survey in any given year and this precluded employing statistical assessments of detection/occupancy. It is therefore possible that some of the effects we identified may be due to changes in sampling efficacy as vegetation matured, rather than changes in occurrence. However, this effect is expected to be small as, within our 16-year dataset, there have only been 63 cases of unidentified macropods (presence indicated by footfalls) which is markedly lower than confirmed sightings for the eastern grey kangaroo (149) and the swamp wallaby (196).

Time since fire (TSF) was calculated at every survey date as the time (in years) since a fire last occurred at a site. Fire frequency (FF) was the number of fires that have occurred at a site between 1957 and the survey date. Both TSF and FF were standardised to Z-scores, that is, having zero mean and standard deviation = 1.

Burn context (BC) was calculated as the proportion of a defined area surrounding each site that had recently burnt. Using the core home range (50% isopleth) of both the eastern grey kangaroo (11.45 ha; Viggers and Hearn 2005) and the swamp wallaby (2.7 ha; Troy & Coulson, 1993), we calculated the proportion of the area surrounding each site which had been burnt in the year before each survey was conducted. A one-year period was selected as our temporal scale, as previous research (in the same ecosystem) found foraging effort from macropods to peak within 9 months post-fire (Foster et al., 2015). To calculate a percentage of the surrounding area that was burnt, we used a combination of ‘intersect’, ‘buffer’ (‘raster’ package; Hijmans et al. 2013), ‘gSimplify’ (‘rgeos’ package; Bivand et al. 2017), and ‘unionSpatialPolygons’ (‘maptools’ package; Bivand et al. 2020).

Year was fitted using a cubic polynomial (‘poly’ function from the ‘stats’ package; Core, R Team, 2016) to allow for the natural variation in macropod sightings through time. Year was included in all models as well as a random site variable.

Before progressing to model construction, collinearity of the variables was calculated using ‘check_collinearity’ in the ‘performance’ package and found to be low (VIF < 5; Lüdecke, 2018). We also assessed spatial correlation between sites for each year using ‘testSpatialAutoCorrelation’ in the ‘DHARMa’ package, with the smallest Moran’s I probability for the eastern grey kangaroo ($p = 0.2244$) and the swamp wallaby ($p = 0.0749$) indicating that the occurrence of both species was not spatially correlated (Hartig, 2017).

We then constructed generalised linear mixed models with a binomial distribution using the ‘glmmTMB’ package (Magnusson et al., 2017). We ran 15 models using each individual fire history variable and the addition/interaction of vegetation type for both macropod species (Table S1). We identified the top performing models using delta AICc (ΔAICc < 2), for the occurrence of the eastern grey kangaroo and the swamp wallaby (Murray et al., 2019).

Using the top performing model, we used the ‘predict’ function in the ‘stats’ package in conjunction with the ‘glmmTMB’ package to produce model predictions (Core, R Team, 2016; Magnusson et al., 2017). For predictions, all variables other than the variable of interest were held at their median value, or at the ‘forest’ value for vegetation type. To determine significant differences between vegetation types we utilised the ‘emmeans’ package (Lenth et al., 2018).

1.5 Results

Over 16 years, 1,079 spotlight surveys were conducted. Surveys in which a macropod was detected yielded 149 instances of the eastern grey kangaroo and 196 instances of the swamp wallaby. The results from the top performing models are reported below (Tables 1 and 2).

Model Selection

Of the 15 models constructed, two models were found to best explain the occurrence of the eastern grey kangaroo and three models for the swamp wallaby (ΔAICc < 2; Table S2). The two top performing models for the eastern grey kangaroo were Veg + TSF + FF (ΔAICc = 0.00) and Veg + TSF + FF + BC (ΔAICc = 1.99; Table 1). The top performing models for the swamp wallaby were: Veg + TSF (ΔAICc = 0.00) and Veg + TSF + BC (ΔAICc = 1.15; Table 2). A third model, Veg x TSF, was also found to perform well (ΔAICc = 1.37) for swamp wallaby occurrence (Table S2). Unless stated otherwise, reported results refer to the top performing model for both macropod species.

Responses

Vegetation was found to significantly influence the occurrence of both macropod species (Fig. 2a, b). The probability of occurrence of the eastern grey kangaroo was significantly higher in forest (0.17, 95% confidence interval 0.07

to 0.37) compared to woodland (0.08, 0.03 to 0.22), heathland (0.07, 0.02 to 0.19) and shrubland (0.03, 0.01 to 0.13). The occurrence of the eastern grey kangaroo was lowest in shrubland. Swamp wallaby occurrence was significantly higher in forest sites (0.34, 0.27 to 0.42) compared with the other three vegetation types. Swamp wallaby occurrence was similar in woodland (0.21, 0.15 to 0.29), heathland (0.18, 0.13 to 0.25) and shrubland (0.18, 0.11 to 0.29).

As time since fire increased, the probability of occurrence of the eastern grey kangaroo and the swamp wallaby decreased (Fig 2c, d). The interaction of vegetation type and time since fire was included only in the third-ranked model for the swamp wallaby (Table S2). While the interaction was included within the model, there was no significant influence on occurrence.

Fire frequency was found to negatively influence the occurrence of the eastern grey kangaroo (Fig 2e). The effect of the number of fires was not included in any of the top performing models for the swamp wallaby. Burn context was included in the second-ranked models for both macropod species but, in both cases, was not statistically detectable (Table 2).

Variation in occurrence increased with year for both species but was significant only for the swamp wallaby (Fig 2f). The occurrence of the swamp wallaby significantly changed with year, peaking in 2008, then declining.

Table 1: Results of the top-ranked GLMMs on the occurrence of the eastern grey kangaroo and the effects of vegetation type and fire history variables: time since fire (TSF), fire frequency (FF) and burn context (BC). Reference states for comparison was 'Forest' vegetation type. Year was included as a cubic polynomial. Site was included as a random term for each model.

	Top ranked model				**Second ranked model**			
Predictors	Est.	SE	Z	P	Est.	SE	Z	P
Intercept	-1.795	0.181	-9.925	**<0.001**	-1.787	0.184	-9.728	**<0.001**
Year – linear	6.8	3.791	1.794	0.073	6.505	3.978	1.635	0.102
Year – quadratic	-4.601	3.488	-1.319	0.187	-4.371	3.611	-1.211	0.226
Year – cubic	4.167	3.556	1.172	0.241	4.019	3.601	1.116	0.264
Heathland	-0.888	0.301	-2.95	**0.003**	-0.889	0.301	-2.954	**0.003**
Shrubland	-1.674	0.513	-3.265	**0.001**	-1.676	0.513	-3.269	**0.001**
Woodland	-0.713	0.305	-2.338	**0.019**	-0.713	0.305	-2.341	**0.019**
TSF	-0.733	0.183	-4.011	**<0.001**	-0.739	0.185	-3.996	**<0.001**
FF	-0.363	0.148	-2.452	**0.014**	-0.362	0.148	-2.449	**0.014**
BC					-0.136	0.579	-0.235	0.814
Observations	1079				1079			
Marginal R^2 / Conditional R^2	0.185 / 0.244				0.185 / 0.244			

Table 2: Results of the top-ranked GLMMs on the occurrence of the swamp wallaby and the effects of vegetation type and fire history variables: time since fire (TSF), fire frequency (FF) and burn context (BC). Reference states for comparison was 'Forest' vegetation type. Year was included as a cubic polynomial. Site was included as a random term for each model.

	Top ranked model				**Second ranked model**			
Predictors	Est.	SE	Z	P	Est.	SE	Z	P
Intercept	-1.454	0.134	-10.826	**<0.001**	-1.489	0.141	-10.577	**<0.001**
Year – linear	0.806	3.438	0.234	0.815	2.018	3.725	0.542	0.588
Year – quadratic	-11.715	3.239	-3.617	**<0.001**	-12.737	3.459	-3.683	**<0.001**
Year – cubic	13.785	3.345	4.121	**<0.001**	14.573	3.493	4.172	**<0.001**
Heathland	-0.851	0.234	-3.634	**<0.001**	-0.845	0.234	-3.606	**<0.001**
Shrubland	-0.86	0.314	-2.736	**0.006**	-0.85	0.314	-2.703	**0.007**
Woodland	-0.667	0.236	-2.821	**0.005**	-0.661	0.236	-2.797	**0.005**
TSF	-0.28	0.108	-2.582	**0.01**	-0.263	0.109	-2.408	**0.016**
BC					0.467	0.485	0.961	0.336
Observations	1079				1079			
Marginal R^2 / Conditional R^2	0.15 / 0.15				0.20 / 0.20			

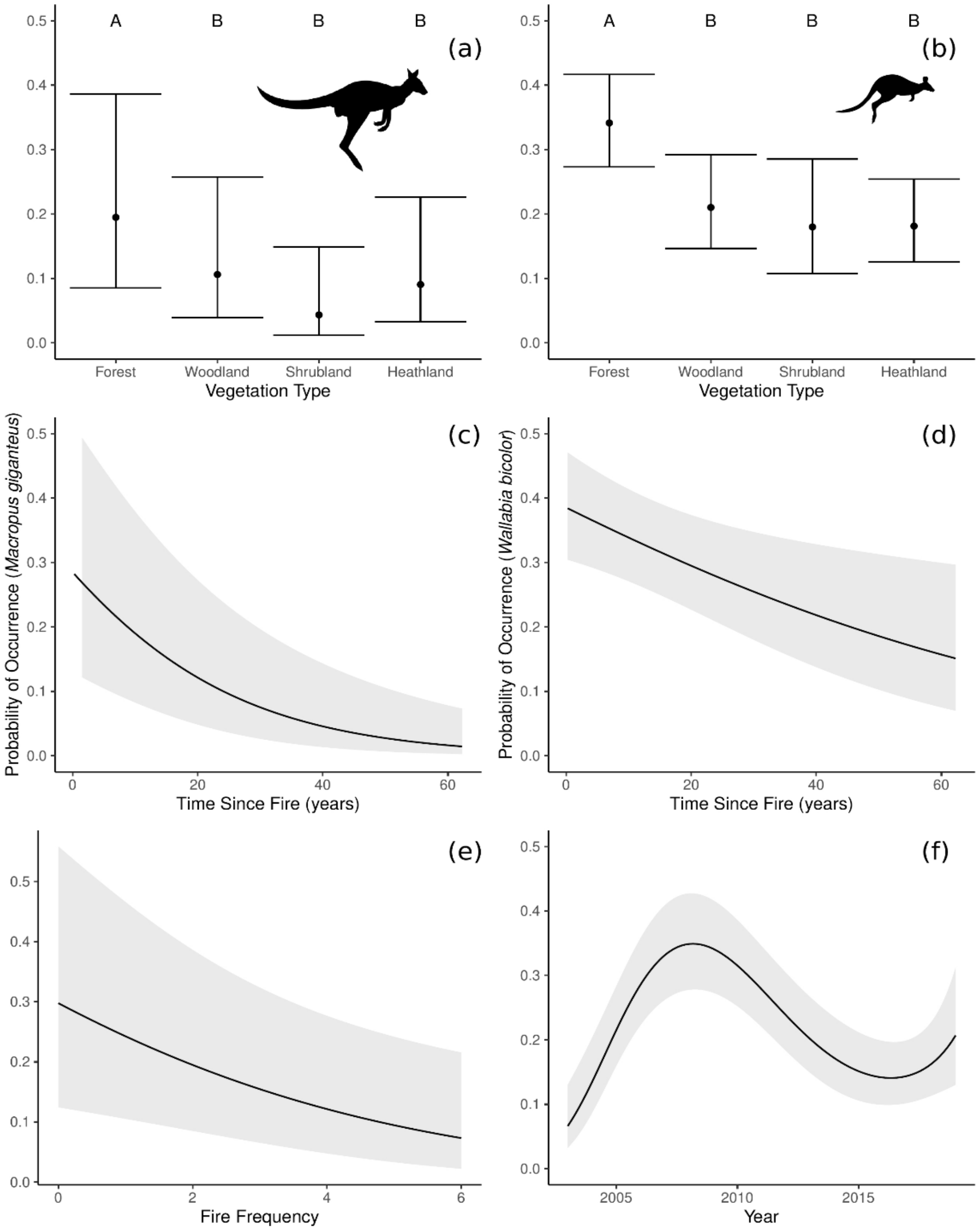

Figure 2: Probability of occurrence of two macropod species (±95% Confidence Interval) from 16 years of spotlighting data in Booderee National Park. Occurrence of eastern grey kangaroo in the left column and the swamp wallaby on the right. Figures (a) & (b) compare vegetation types with letters above indicating significant differences within individual figures only. Figures (c) & (d) model macropod occurrence with time since last fire at a site. Figure (e) shows the occurrence of the eastern grey kangaroo with fire frequency. Figure (f) shows occurrence of the swamp wallaby through time using an orthogonal polynomial. Graphs were constructed from predictions calculated from the top performing model (see text) with other covariates being held at their median value to predict probability.

1.6 Discussion

Quantifying inter-relationships between herbivores and fire is critical to predicting key aspects of ecosystem dynamics in fire-prone environments (Danell, 2006). We quantified long-term relationships between vegetation, fire history, and macropod occurrence to address the question: Which fire history variables influence the presence and absence of macropods? We found evidence that vegetation type and two of three fire history variables influenced the occurrence of macropod species. Our key findings were: (1) macropod occurrence declined strongly with time since fire; (2) fire frequency negatively influenced the occurrence of the eastern grey kangaroo, and (3) both macropod species were more likely to occur in forest communities compared to the other vegetation types.

Fire response

The occurrence of the eastern grey kangaroo and the swamp wallaby was strongly influenced by time since fire; both species selected sites that had recently burned. Fire can reduce canopy cover and re-invigorate understory vegetation allowing grasses and forbs to sprout (Whelan, 1995). These plants are preferred by both grazing and browsing macropods and this may explain higher levels of occurrence in the recently burnt sites (Di Stefano & Newell, 2008; Swan et al., 2008; Leonard et al., 2010). The increased occurrence of the swamp wallaby in recently burnt sites may also indicate that swamp wallabies were favouring forage quality over predator avoidance or that, despite fire, there was enough in-situ lateral vegetation cover to satisfy nocturnal safety requirements (Swan et al., 2008). The swamp wallaby has been shown to select for nocturnal sites of higher foraging quality (Di Stefano et al., 2009). As such, the spotlighting surveys in this study may only be reflecting nocturnal occurrence patterns which may not be congruent with daylight habitat selection.

The observed response to time since fire within the landscape suggests that macropods are engaging in pyric herbivory (Fuhlendorf et al., 2009). This supports findings from Foster et al. (2015) who demonstrated that foraging pressure by macropods increased in recently burnt patches and decreased over time. Our study confirmed a similar response of macropods occurrence in post-fire environments using a longer timeframe (16 years dataset compared to 2 years). Results for both species highlights a sharp and a steady decline in occurrence with increasing time since fire for the eastern grey kangaroo and the swamp wallaby, respectively. The stronger response from the eastern grey kangaroo may be indicative of the increased germination of grass species following shortly after fire (Gosper et al., 2013). This would also explain the steadier decline for the swamp wallaby as their preferred food sources of shrubs and herbs are slower growing, so post-fire increases in food would be observed over a longer timeframe (Mason et al., 2016). Further, this relationship may not exclusively be a response to fire, but perhaps a response to early successional environments, as the swamp wallaby has been found previously to select for disturbed habitats such as forests following timber harvesting (Di Stefano et al., 2007; Di Stefano & Newell, 2008). Regardless, if both macropod species are preferentially selecting burnt/disturbed patches, more research is required to assess the potential feedbacks that increased foraging pressure may have on the regenerating vegetation.

Fire frequency was found to influence only the eastern grey kangaroo. This negative relationship was unexpected as repeated fires should promote fire-tolerant species, such as grasses which are preferred by kangaroos (Archibald & Hempson, 2016). Our finding also contrasts with previous research within the same ecosystem which found a weak positive relationship with increased fire frequency for the eastern grey kangaroo (Lindenmayer et al., 2016). The number of fires in our study was calculated over 62 years (1957-2019), compared with the 35 years used by Lindenmayer et al. (2016), which may contribute to the differing results. Our findings indicate repeated fires may reduce habitat quality for the eastern grey kangaroo. While fire-tolerant grasses are prevalent within our study area have been found to respond positively to repeated fires (Foster et al., 2017), long-term exposure to high fire frequencies may reduce the nutritional quality of available forage through volatilisation or leaching of nutrients (Pellegrini et al., 2018; Bowd et al., 2019). The lack of response of fire frequency for the swamp wallaby was consistent with results from Lindenmayer et al. (2016).

Burnt context was included only within the second-ranked models and was not significantly associated with the occurrence of either macropod species. The lack of response to burn context, and a strong response to time since fire, implies that both macropod species preferentially select for burnt sites regardless of the extent of the surrounding burnt area in our study system. This may be due, in part, to low predator densities during the study period (Dexter et al., 2013) as well as the high degree of vegetation heterogeneity within Booderee National Park (Taws, 1997), which may fill the place of fire heterogeneity in providing a diversity of habitats within a macropod home range.

The effects of fire variables were not found to differ between vegetation types for either macropod species. This may be because such effects were weak in comparison with individual fire effects, with the fresh pick available following a fire event driving the occurrence patterns across all vegetation types. Alternatively, it might be the case that fire effects differed between vegetation types in a way that was not reflected in the models tested. A more intensive survey effort would be needed to enable testing of such nonlinear interactions between vegetation type and fire variables.

Vegetation preference

We found that the eastern grey kangaroo was more likely to occur in forest communities. This was expected as this species has been shown to select for relatively open patches with grasses (Moore et al., 2002). We also expected heathland and shrubland communities to support fewer eastern grey kangaroos due to the dense vegetation and low grass abundance (Taws, 1997; Moore et al., 2002). The response within the woodland habitat may reflect either lower quality or lower abundance of grass species, compared to forest sites (Taws, 1997; Moser et al., 2006).

Swamp wallaby occurrence was significantly higher in forest habitats than in woodland, heathland and shrubland communities. This may be due to the non-forest communities having relatively poorer foraging quality for browsing herbivores (Taws, 1997; Moser et al., 2006). As forest communities in BNP are more open than other vegetation communities, it is possible that food quality is a more important driver of swamp wallaby occurrence than predator avoidance. Our findings are consistent with other studies where swamp wallabies selected nocturnal habitats with high forage quality (Swan et al., 2008; Di Stefano et al., 2009). Future radio tracking of swamp wallabies in BNP would be required to determine whether habitat selection differed throughout a 24-hour period and allow for comparison of foraging quality with the overall amount of cover (a possible proxy for predator avoidance).

1.7 Conclusion

Our study has demonstrated how the eastern grey kangaroo and swamp wallaby occurrence is influenced by both fire history and vegetation type. Management of ecological drivers of herbivore occurrence will have direct and indirect impacts on ecosystem structure and function. As feedbacks from increased foraging of large herbivores can have positive or negative influences on vegetation succession (Persson et al., 2000; Forbes et al., 2019), identifying burning practices that deter or encourage macropod occurrence can be vital. Our study has shown that this preference for recently burnt habitats takes place at the landscape scale. Given the high numbers of macropods present in the park, integrating herbivores into fire management considerations may be necessary to ensure post-fire recovery of vegetation communities.

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1.10 Supplementary Material

Table S1: Candidate hypotheses, predictions, and models associated with patterns of occurrence of macropods in Booderee National Park. Sightings of macropod species were recorded on transects, occurrence converted to binary (present[1] – absent[0]), and presence related to preferred vegetation type (broad vegetation classification: F - forest; W - woodland; H - heathland; S - shrubland) and aspects of fire history: time since fire (TSF; time from last instance of fire), fire frequency (FF; total number of fires since 1957) and burnt context (BC; proportion of area surrounding a site that has been burnt). Hypotheses 1–4 were developed through review of the literature and 5–14 reflect potential multivariate processes governing macropod spatial dynamics. Predictions were developed a priori, assuming standardized variables (see text). The constant (C) variable within each the candidate set included year as a cubic polynomial and site as a random variable. [a, e, g] (Moore, Coulson and Way, 2002); [b, h] (Di Stefano et al., 2009); [c] (Leonard, Kirkpatrick and Marsden-Smedley, 2010); [d] (Swan et al., 2008); [f] (Foster et al., 2018)

Model	*Hypothesis*	*Predicted Association (direction)*											
		Vegetation Type				TSF	FF	BC	Interaction				C
		F	W	H	S				F:	W:	H:	S:	
						Eastern Grey Kangaroo							
1	Vegetation type[a]	+	+	-	-								0
2	Time since fire[c]					-							0
3	Fire frequency[e]						+						0
4	Burnt context[g]							+					0
5	Veg type + TSF	+	+	-	-	-							0
6	Veg type + FF	+	+	-	-		+						0
7	Veg type + BC	+	+	-	-			+					0
8	Veg type x TSF	+	+	-	-	-			-	-	-	-	0
9	Veg type x FF	+	+	-	-		+		+	+	+	+	0
10	Veg type x BC	+	+	-	-			+	+	+	+	+	0
11	Veg type + TSF + FF	+	+	-	-	-	+						0
12	Veg type + TSF + BC	+	+	-	-	-		+					0
13	Veg type + FF + BC	+	+	-	-		+	+					0
14	Veg type + TSF + FF + BC	+	+	-	-	-	+	+					0
15	Constant only												0
						Swamp Wallaby							
1	Vegetation type[b]	+	+	-	-								0
2	Time since fire[d]					-							0
3	Fire frequency[f]						-						0
4	Burnt context[h]							+/-					0
5	Veg type + TSF	+	+	-	-	-							0
6	Veg type + FF	+	+	-	-		-						0
7	Veg type + BC	+	+	-	-			+/-					0
8	Veg type x TSF	+	+	-	-	-			-	-	-	-	0
9	Veg type x FF	+	+	-	-		-		-	-	-	-	0
10	Veg type x BC	+	+	-	-			+/-	+	+	-	-	0
11	Veg type + TSF + FF	+	+	-	-	-	-						0
12	Veg type + TSF + BC	+	+	-	-	-		+/-					0
13	Veg type + FF + BC	+	+	-	-		-	+/-					0
14	Veg type + TSF + FF + BC	+	+	-	-	-	-	+/-					0
15	Constant only												0

Table S2: Model selection ranked results from a GLMM analysis of vegetation type (V), time since fire (TSF), fire frequency (FF) and burnt context (BC) influences on macropod occurrence. The constant (C) variable within each candidate set included year as a cubic polynomial and site as a random variable. Dashed line indicates threshold for best performing model selection (ΔAICc < 2).

Eastern Grey Kangaroo

Number	*Covariates*	*DF*	*Log-likelihood*	*AICc*	*ΔAICc*	w_i	*Conditional R²*
11	V + TSF + FF	10	-346.32	712.85	**0.00**	0.60	0.24
14	V + TSF + FF + BC	11	-346.29	714.83	**1.99**	0.22	0.24
5	V + TSF	9	-349.26	716.69	3.84	0.09	0.25
8	V * TSF	12	-346.55	717.40	4.55	0.06	0.28
12	V + TSF + BC	10	-349.23	718.66	5.81	0.03	0.25
1	V	8	-355.54	727.21	14.36	0.00	0.22
7	V + BC	9	-355.47	729.11	16.26	0.00	0.22
6	V + FF	9	-355.53	729.22	16.37	0.00	0.22
13	V + FF + BC	10	-355.47	731.14	18.29	0.00	0.22
2	TSF	6	-359.63	731.34	18.50	0.00	0.25
10	V * BC	12	-353.97	732.23	19.38	0.00	0.99
9	V * FF	12	-354.24	732.78	19.93	0.00	0.26
15	*C*	5	-366.18	742.41	29.56	0.00	0.21
4	BC	6	-366.05	744.18	31.33	0.00	0.21
3	FF	6	-366.15	744.37	31.52	0.00	0.20

Swamp Wallaby

Number	*Covariates*	*DF*	*Log-likelihood*	*AICc*	*ΔAICc*	w_i	*Conditional R²*
5	V + TSF	9	-417.79	853.75	**0.00**	0.33	0.15
12	V + TSF + BC	10	-417.35	854.90	**1.15**	0.19	0.16
8	V * TSF	12	-415.42	855.12	**1.37**	0.17	0.20
11	V + TSF + FF	10	-417.77	855.75	2.00	0.12	0.15
14	V + TSF + FF + BC	11	-417.33	856.90	3.15	0.07	0.16
10	V * BC	12	-417.38	859.06	5.31	0.02	0.92
6	V + FF	9	-420.51	859.19	5.44	0.02	0.13
1	V	8	-421.61	859.36	5.61	0.02	0.13
7	V + BC	9	-420.64	859.44	5.69	0.02	0.14
13	V + FF + BC	10	-419.74	859.69	5.94	0.02	0.14
9	V * FF	12	-418.03	860.35	6.59	0.01	0.15
2	TSF	6	-427.47	867.02	13.27	0.00	0.13
4	BC	6	-429.77	871.63	17.87	0.00	0.13
15	C	5	-430.97	872.01	18.25	0.00	0.12
3	FF	6	-430.68	873.44	19.69	0.00	0.12

Table S3: Average cover of plants within the four major vegetation classes found in Booderee National Park and the palatability and total cover of potential food for two macropod species. Table was adapted from data recorded by Taws (1998). Vegetation surveys were conducted four years post fire (for full methodology see Taws 1998). Palatability data was sourced from diet studies of the eastern grey kangaroo (Taylor 1984; Davis et al. 2008) and the swamp wallaby (Hollis et al. 1986; Di Stefano et al. 2008) with "H" and "L" indicating high or low palatability for each species respectively. Note: tree species listed are mostly edible only in their seedling/sapling life stage for the swamp wallaby.

Veg Class	*Species*	*Cover (%)*	*Life Form*	*Palatability*	
				Eastern Grey Kangaroo	**Swamp Wallaby**
Forest	*Pteridium esculentum*	3.38	Fern		L
	Lomandra longifolia	0.275	Sedges/Rhizomatous Perennials	L	H
	Acacia longifolia	2.01	Tree/Tree Seedlings		H
	Hibbertia scandens	0.93	Shrub		H
	Imperata cylindrica	0.45	Grass	H	L
	Stephania japonica	0.18	Vine		H
		Total cover of potential food (%)		**0.725**	**7.225**
Woodland	*Lepidosperma concavum*	0.46	Sedges/Rhizomatous Perennials	L	L
	Lomandra glauca	0.106	Sedges/Rhizomatous Perennials	L	L
	Pteridium esculentum	0.28	Fern		L
	Anisopogon avenaceus	0.026	Grass	H	L
	Lambertia formosa	0.36	Shrub		H
	Ceratopetalum gummiferum	0.36	Tree/Tree Seedlings		H
	Xanthosia pilosa	0.016	Shrub		
	Gonocarpus teucrioides	0.026	Sub-shrubs		H
	Platysace lanceolata	1.26	Shrub		H
		Total cover of potential food (%)		**0.592**	**2.878**
Heathland	*Allocasuarina distyla*	2.025	Tree/Tree Seedlings		H
	Cyathochaete diandra	0.344	Sedges/Rhizomatous Perennials		L
	Xanthorrhoea australis	1.44	Sedges/Rhizomatous Perennials		
	Lambertia formosa	1.08	Shrub		H
	Isopogon anemonifolius	1.35	Shrub		
	Entolasia stricta	0.007	Grass	H	L
	Phyllota phyllicoides	0.788	Shrub		H
	Pimelea linifolia	0.344	Shrub		H
		Total cover of potential food (%)		**0.007**	**4.588**
Shrubland	*Leptospermum laevigatum*	3.12	Shrub		
	Lepidosperma concavum	0.722	Sedges/Rhizomatous Perennials	L	L
	Banksia integrifolia	0.86	Tree/Tree Seedlings		L
	Dichondra repens	0.005	Herb/Forb		H
	Gonocarpus teucrioides	0.188	Sub-shrubs		H
	Kennedia rubicunda	0.045	Vine		H
	Acacia suaveolens	0.003	Shrub		H
	Hardenbergia violacea	0.006	Sub-shrubs		H
		Total cover of potential food (%)		**0.722**	**1.829**

Paper II: Post-fire pickings: Large herbivores alter understory vegetation communities in a coastal eucalypt forest

2.1 Foreword

Paper I identified that the large herbivores in my study area displayed a preference for burnt patches and forest communities. A wildfire in 2017, that burnt a large area of forest, presented an opportunity to measure the impact of large herbivore browsing in a post-fire environment. Alongside a previous experiment developed five years prior, I constructed a larger-scale experiment to manipulate large herbivore presence via fencing. In this study, vegetation community measures were recorded and compared between fencing treatments.

Chard, M., Foster, C.N., Lindenmayer, D.B., Cary, G.J., MacGregor, C.I. and Blanchard, W. (2022) 'Post-fire pickings: Large herbivores alter understory vegetation communities in a coastal eucalypt forest' *Ecology and evolution*, 12(4), p.e8828.

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Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with https://policies.anu.edu.au/ppl/document/ANUP_003405

I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multi-author papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

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Senior author or collaborating authors endorsement: I, Claire Foster endorse the above contribution statement

Matthew Chard	MChard	3/15/2023
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Delegated Authority – Print Name	Signature	Date

2.2 Abstract

1. Fire and herbivores alter vegetation structure and function. Future fire activity is predicted to increase, and quantifying changes in vegetation communities arising from post-fire herbivory is needed to better manage natural environments.

2. We investigated the effects of post-fire herbivory on understory plant communities in a coastal eucalypt forest in south-eastern Australia. We quantified herbivore activity, understory plant diversity, and dominant plant morphology following a wildfire in 2017 using two sizes of exclosures. Statistical analysis incorporated the effect of exclusion treatments, time since fire, and the effect of a previous prescribed burn.

3. Exclusion treatments altered herbivore activity, but time since fire did not. Herbivory reduced plant species richness, diversity and evenness and promoted the dominance of the most abundant plants within the understory. Increasing time since fire reduced community diversity and evenness and influenced morphological changes to the dominant understory plant species, increasing size and dead material while decreasing abundance. We found the legacy effects of a previous prescribed burn had no effect on herbivores or vegetation within our study.

4. Foraging by large herbivores resulted in a depauperate vegetation community. As post-fire herbivory can alter vegetation communities, we postulate that management burning practices may exacerbate herbivore impacts.

5. Future fire management strategies to minimise herbivore-mediated alterations to understory vegetation could include aggregating management burns into larger fire sizes or linking fire management with herbivore management. Restricting herbivore access following fire (planned or otherwise) can encourage a more diverse and species-rich understory plant community. Future research should aim to determine how vegetation change from post-fire herbivory contributes to future fire risk.

Keywords: macropod – large herbivore – post-fire – herbivory – vegetation community

2.3 Introduction

Fire and herbivores are consumers of vegetation, modifying the structure and function of plant communities (Bond & Keeley, 2005). Interactions between these disturbances can occur in ecosystems where both fire and herbivores are prevalent. However, few studies have implemented manipulative field studies to measure the long-term responses of forest vegetation to both fire and herbivory (Royo & Carson, 2006; Nuttle et al., 2013; Foster et al., 2016). As forest ecosystems are likely to face increased fire activity in the future (Bowman et al., 2009), more research that quantifies interactions between fire and herbivory on plant communities is required.

Fire can encourage or deter herbivore foraging (Fuhlendorf et al., 2010; Allred et al., 2011). Research into fire-herbivore relationships, under the banner of ‘pyric herbivory’, has emphasised the capacity for fire to influence foraging selection by herbivores (Allred et al., 2011). Large herbivores (> 2 kg) can be attracted to burnt patches due to increased abundance of new growth and more favourable physical or chemical accessibility to food (Danell et al., 2006; Allred et al., 2011; Foster et al., 2016). However, limited research has been conducted on the next logical question within fire-prone ecosystems, which is: How does the vegetation community respond when it is burnt, and then foraged? Manipulative experiments are required to answer this question.

Information on changes in vegetation communities arising from post-fire herbivory may guide future fire management practices. Large herbivores can alter plant succession following a fire through foraging, trampling, and alterations in nutrients (by defecation, urination, decomposition of carcasses, etc.; Persson et al., 2000; Forbes et al., 2019). Herbivores actively select for more palatable species which either leads to the dominance of unpalatable, chemically-defended plant species or an increased abundance of highly palatable plants through nutrient cycling and seed dispersal (Augustine & McNaughton, 1998; Bakker et al., 2016; Leroux et al., 2020). Changes to above-ground plant biomass is a direct modification of in situ fuel load (Archibald & Hempson, 2016). Fire also can promote the abundance of more-flammable plants (through positive feedback loops) that are often less palatable for herbivores (due to lower moisture content, increased tannins/oils, higher carbon-nitrogen ratios, etc.; Archibald & Hempson, 2016). As dominant plant species can influence fire risk (Cheney et al., 2012; Zylstra et al., 2016), quantifying the changes to plant communities from post-fire herbivory will be paramount to future wildfire management and predictions (Figure 2).

Figure 1: Large herbivores present in our study, the (A) swamp wallaby (*Wallabia bicolor*) and the (B) eastern grey kangaroo (*Macropus giganteus*). Photo credit: C. N. Foster & J. Clarke

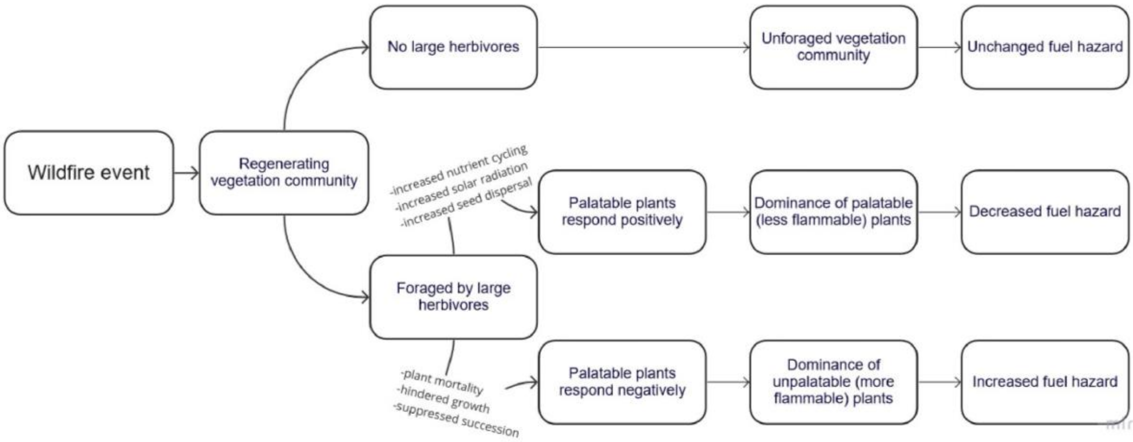

Figure 2: Hypothesised outcomes of foraging from large herbivores following a fire event in a eucalypt forest environment.

We aimed to answer the question: How does post-fire herbivory alter understory plant communities and physical attributes of the dominant plants in a eucalypt forest? We used a manipulative field study at Booderee National Park that modified large herbivore activity through different levels of fencing. At all plots, we tested the effects of fencing treatments and time since fire on herbivore activity, vegetation community measures, and morphological responses of the dominant understory plant. Where applicable, we also investigated the effect of the previous prescribed burn (5 years prior) applied to selected plots. We expected large herbivores to be attracted to recently burnt areas due to the availability of fresh growth and herbivore occurrence would decline over time as the vegetation regenerates (Allred et al., 2011). This response has been observed following prescribed burns in eucalypt forest (Foster et al., 2015; Parkins et al., 2019). However, it is possible this effect will be less evident following a larger wildfire where herbivores have a larger area of burnt space to select from.

While fire can reduce habitat complexity (Parkins et al., 2019), the interaction of fire and (increased) herbivory may result in an altered vegetation community with reduced species diversity (Foster et al., 2015). Fire will promote germination and growth of understory plants, resulting in a short-term increase in species richness (Ross et al., 2002). Species richness within the understory plant community typically decreases with time since fire due to increased competition and reduced space (Foster et al., 2018). Large herbivores can dramatically alter the recovering understory vegetative community by preferentially selecting the more palatable species (Persson et al., 2000). We expect that this should result in a decrease in community measures such as richness, diversity, and evenness and promote the dominance of less palatable plants within burnt patches (Foster et al., 2016). In addition, we expect the influence of the prior prescribed burn to exacerbate herbivore impacts following a wildfire as the vegetation has been subject to a short (5 year) fire interval and may be more sensitive to further disturbance compared to areas that were not subject to the prescribed burn (Furlaud et al., 2018).

A particular concern for managers of our study area has been the increase in dominance of the fern *Pteridium esculentum* (bracken) in the understory vegetation (Dexter et al., 2013). Current management of Booderee National Park is based on the understanding that abundant large herbivore populations, coupled with recurrent fires (prescribed burns and wildfires), is promoting bracken dominance (Dexter et al., 2013). Bracken has reduced palatability for larger herbivores (Di Stefano & Newell, 2008) and is an early-successional and fire-resistant plant (Tolhurst & Turvey, 1992). The ramifications for both biodiversity and future fire risk resulting from a bracken-dominated understory are currently unknown. We aimed to provide quantitative evidence on the effect that post-fire herbivory has on the morphology and abundance of bracken.

By focusing our study in a post-wildfire eucalypt forest, we predicted that: (1) exclosure treatments would reduce herbivore activity and herbivore activity would decline with increasing time since fire; (2) increased herbivore activity and increasing time since fire would reduce the species richness, diversity and evenness of the plant community and increase understory dominance of unpalatable understory species; and (3) increased herbivore activity and increasing time since fire would alter morphological measures of the dominant understory plant, promoting larger plants and higher abundance within plots. Further, we predicted the influence of the previous prescribed burn would exacerbate herbivore impacts. Plots subject to the prescribed burn followed by large herbivore browsing were expected to have lower initial plant diversity prior to the 2017 fire (Foster et al., 2015). Therefore, the 2017 wildfire and subsequent foraging by large herbivores was expected to further decrease plant diversity and increase dominant plant abundance at sites burnt in 2012.

2.4 Methods

Study area

We conducted this study at Booderee National Park (35.1489415° S, 150.6454625° E; Figure 3) on the southeast coast of Australia, approximately 200 km south of Sydney. The Park is ~6,500 ha in area and co-managed by the Wreck Bay Aboriginal Community and Parks Australia. The dominant vegetation class in the park is Sydney Coastal Dry Sclerophyll Forest (45% of the park area) which is characterised by canopy species of *Eucalyptus pilularis*, *Corymbia gummifera*, and *E. botryoides*, midstory species of *Banksia serrata* and *Monotoca eliptica*, and an understory dominated by *P. esculentum*, *Lomandra longifolia* and *Lepidosperma concavum* (Taws, 1997).

Study species

Three species of macropod in Booderee National Park meet the “large herbivore” classification (> 2 kg; *sensu* Danell et al., 2006). They are the eastern grey kangaroo (*Macropus giganteus*); swamp wallaby (*Wallabia bicolor*); and red-necked wallaby (*M. rufogriseus*). No other large terrestrial herbivore species are currently found in Booderee National Park. All three macropods have previously demonstrated pyric herbivory responses with most studies identifying a preference for recently burnt patches due to a higher quality of foraging resources (Southwell & Jarman, 1987; Meers & Adams, 2003; Foster et al., 2015; Parkins et al., 2019).

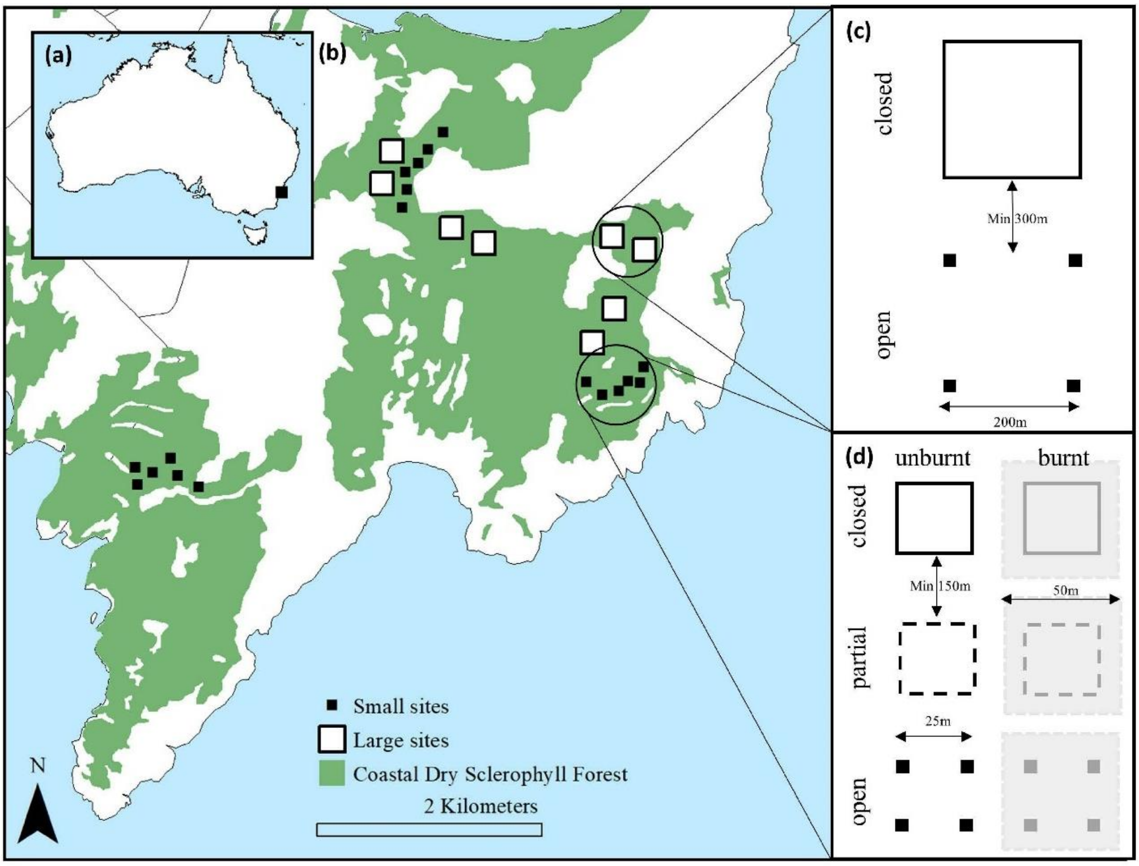

Figure 3: Study location and experimental design showing: (a) Location of Booderee National Park, Australia; and (b) The distribution of the small and large plots across the park. All plots were located within coastal dry sclerophyll forest (in green) and had been burnt in the 2017 wildfire. Eight large plots were paired into four blocks and 18 small plots were grouped into 3 blocks; (c) and (d) highlight the design within each block for both large and small plots respectively. Note half of the small plots were subject to a prescribed burn conducted in 2012.

Of the three macropod species, the eastern grey kangaroo and the swamp wallaby are the most common in Booderee National Park (Chard et al., 2022). While density measures have not been conducted for any macropod species, previous research analysing conditional abundance of the swamp wallaby peaked between 2007 – 2013 compared to when surveys began in 2003 (Lindenmayer et al., 2016). Further, managers have been concerned with the growing population of macropods in Booderee National Park (Dexter et al., 2013). Previous research in the study area found both species preferentially selected forest vegetation communities (Chard et al., 2022). The eastern grey kangaroo is a grazing species, targeting grass species such as Imperata cylindrica and Themeda triandra (Brunton et al., 2018). The swamp wallaby is a browsing species that will forage on most understory plants in a forest community with a preference for forb species (Di Stefano & Newell, 2008). For more detailed descriptions on each species preferred plant foods see Chard et al. (2022).

Study design

We quantified the interacting effects of post-fire herbivory on vegetation communities using two randomised, blocked experiments. In June 2012, we established three blocks of six 25 x 25 m plots (0.0625 ha, hereafter referred to as ‘small’ plots) within Sydney Coastal Dry Sclerophyll Forest, with plots spaced 150 m apart and blocks 2 km apart. We manipulated grazing pressure by macropods using three methods of fencing: (1) open (i.e no fencing), (2) partial fencing - intermediate access with gates at two corners of the plot which were opened or closed at two-month intervals and (3) closed (completely fenced). We constructed 1.1 m tall fences which prevented access by macropods (Foster et al., 2015). We conducted low-intensity, prescribed burns in August 2012 within half of the plots in each block so that each fencing treatment had one burnt and one unburnt pair. Controlled fires were extinguished after burning a 50 x 50 m area and removing approximately 95% of the understory vegetation. This facilitated examination of two burning treatments across three herbivory measures within all three blocks. Although a wildfire in 2017 burnt all plots, we describe our small plots as ‘burnt’ or ‘unburnt’ as per the initial prescribed burn conducted in 2012.

In September 2017, a wildfire burned 1,600 ha of Booderee National Park, including each small experimental block, again removing approximately 95% of the understory vegetation. In our study, we recorded time since fire as time since the 2017 wildfire. In July 2018, we established an additional four blocks of two 200 x 200 m plots (4 ha, hereafter referred to as ‘large’ plots) in forest vegetation. Large plots were spaced 300 m apart and blocks at least 2 km apart. Again, we manipulated herbivore grazing pressure using two randomly allocated fencing treatments: (1) open (no fencing); and (2) closed (completely fenced).

Data collection

We conducted scat surveys every two months from October 2018 to February 2020 in all plots, within two 25 m x 2 m transects (small plots), and four 50 m x 2 m transects (large plots), in which macropod scats were counted and removed from the transect. We used macropod scat counts as an index of herbivore activity, as macropods defecate primarily while feeding (Johnson et al., 1987; Murphy & Bowman, 2007). Note, it was assumed in this study that macropods will digest and deposit all vegetation at a similar rate. We conducted vegetation surveys annually in spring, in all plots. We used five point-intercept transects of 20 m (small plots) and four 50 m transects (large plots) within each plot to record understory plant species (< 3 m in height) at 1 m intervals. We used site-level data to calculate four vegetation community measures: species richness, diversity (Simpson’s reciprocal index – 1/D), evenness (Shannon evenness index), and dominance (Berger-Parker index; Magurran, 2013). Using the same point-intercept transects, when a bracken plant was present, we recorded its physical attributes including width (measured parallel with the transect), height to bottom-most frond, top height, and percentage of dead vegetation. We also recorded the number of bracken plants intercepted at the 20 or 50 points along each transect. Both scat and vegetation surveys encompassed the post-wildfire period from September 2018 to February 2020.

Data analysis

We analysed the influence of exclosure fences, time since fire, and the 2012 prescribed burn on: (1) scat counts, (2) plant community measures and (3) bracken attributes in R (Core, R Team, 2016). We fit models from a candidate set of nine models (small plots) and two models (large plots) for each response in a Bayesian framework using the 'brms' package (Bürkner, 2017). The models we constructed used all possible combinations of exclusion treatment (open/partial/closed), time since fire, and prescribed burn (burnt/unburnt) for each response variable (Table S1; S2; S3). We selected appropriate regression distributions for each variable after testing for assumptions of normality and homogeneity of variance (see Tables S1; 2; 3; Hanea et al., 2015).

Our response variables were: (1) number of macropod scats, with scat counts being summed at two-month intervals for small plots to allow for effective analysis of the partial treatments (as every second count was effectively zero); (2) understory plant richness, diversity, evenness, and dominance, with vegetation measures calculated using the 'diversityresult' function from the 'BiodiversityR' package (Kindt & Kindt, 2019); and (3) bracken width, height to bottom frond, top height, count of individuals, and percentage of dead material. We treated time since fire as a continuous variable for scat surveys, standardised using the ‘scale’ function so that the mean was zero with a standard deviation of one. We included season (for scat surveys) and block as a fixed effect in each model as well as the random effect of plot. We expected a seasonal effect resulting in reduced herbivore activity in the summer months as macropod defecation rates decrease and scat decay increases (Perry & Braysher, 1986). We selected appropriate priors for each model and the Rhat values were deemed acceptable (all values = 1; Gelman & Rubin, 1992).

The models were fit using Markov chain Monte-Carlo methods. We ran four chains, each with with 3,000 iterations with the first 1,000 iterations discarded as burn-in for the sampler. We based our inference on the importance of the hypothesised interactions by selecting the most parsimonious model using lowest weighted Akaike Information Criterion (WAIC; ≤ 2) and simplest model using the ‘loo’ package (Burnham & Anderson, 2002; Vehtari et al., 2017). We selected AIC over the Bayesian Information Criterion (BIC) to allow the inclusion of more potential predictors in the model (Aho et al., 2014). We present results for most parsimonious models for macropod scats, vegetation community measures and bracken morphology from small and large plots.

Table 1: Results from Bayesian generalized linear model analysing whether macropod scats in small (25 m x 25 m) and large (200 m x 200 m) plots are influenced by fire (burnt/unburnt), herbivore access (open/partial/closed) and time since fire.

	Small Plots		**Large Plots**	
Coefficient	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*
Intercept	**2.40**	**0.99, 3.98**	**4.33**	**2.61, 5.60**
Herbivory (Partial)	**-1.45**	**-2.38, -0.51**		
Herbivory (Closed)	**-7.76**	**-12.91, -5.31**	**-1.55**	**-2.72, -0.13**
Fire (Burnt)	-0.48	-1.42, 0.43		
Time Since Fire	0.48	-0.09, 1.07	-0.17	-0.46, 0.11
Summer	0.20	-1.11, 1.47	**-1.20**	**-1.98, -0.44**
Autumn	-0.01	-1.61, 1.58	-0.75	-1.61, 0.18
Winter	0.50	-0.98, 2.01	0.32	-0.49, 1.11
Block B	0.16	-0.93, 1.24	-0.07	-1.50, 1.60
Block C	0.45	-0.63, 1.51	-1.22	-2.75, 0.47
Block D			-0.13	-1.63, 1.55
N	18 $_{\text{plot}}$		8 $_{\text{plot}}$	
Obvs.	126		67	
Marginal R^2/ Conditional R^2	0.474/ 0.492		0.589/ 0.629	

Estimates (log-scale) and 95% credible intervals are shown for the most parsimonious models (by WAIC and model simplicity; see Appendix S1 for model selection table). Rows that are in bold indicate that credible intervals do not overlap zero. Reference states for comparisons in small plots were open, unburnt plots sampled in 2018. Reference states for comparisons in large plots were open plots sampled in 2018.

2.5 Results

Herbivore activity

Our exclosure treatments altered herbivore activity (Table 1). The best performing model for both small and large plots did not include any interaction terms (Table S1). In both small and large plots, scat counts were highest in the open treatment and lowest in the closed treatments (Figure 4). We found in the small plots that partial treatments had scat counts at intermediate levels between open and closed treatments. Time since fire did not influence herbivore activity in either large or small plots. Further, we detected no effect of the previous prescribed burns in the small plots. Season only affected scat counts in the large plots, with counts being lower in summer months. Notably, scat counts in the large, closed plots were not zero (11.9 ± 6.5 SE), indicating some level of macropod intrusion within the exclosure fences (Figure 4).

Vegetation community

Three years of vegetation surveys yielded 74 plant species in the understory community. We found herbivore activity and time since fire altered understory community measures in both small and large plots (Figures 5; 6).

In small plots, the interaction of herbivory and time since fire was included in the selected models for diversity and dominance (Table S1). However, the confidence intervals for both interaction effects overlapped with zero indicating a weak effect (Table 2). Richness, diversity and evenness measures in small, open plots was lower compared to partially-closed and closed plots (Figure 5a; b; c). As time since fire increased, community measures in small, open plots revealed a decreasing trend for richness, diversity, and evenness. This trend was similar in partially-closed plots with 2018 richness, diversity and evenness measures higher compared to 2019 and 2020 surveys. However, in small, closed plots where macropods were fully excluded, diversity and evenness measures were higher in 2020 compared to 2019. In small plots, there was a greater proportion of dominant species present in open plots compared to partially-closed and closed plots (Figure 5d). As time since fire increased, dominance measures in small plots that were open and partially-closed steadily increased, with 2018 measures being lower compared to 2019 and 2020. Again, small plots that were macropod-free were characterized by an initial increase in dominance measures from 2018 to 2019, but then a decrease in 2020.

In large plots, the interaction of herbivory and time since fire was included in richness, diversity, and evenness models (Table S2). The confidence intervals for the interaction effect for species richness overlapped with zero (Table 3). We observed comparable trends to small plots within large plots, with richness, diversity and evenness measures being lower in open plots compared to closed (Figure 6a; b; c). For large, open plots, increasing time since fire negatively affected richness, diversity, and evenness, with the highest measures observed in 2018 which subsequently decreased in 2019 and 2020. A different trend for time since fire was apparent for large, closed plots whereby measures of richness, diversity and evenness initially decreased from 2018 to 2019, but then increased in 2020. Dominance measures within large plots were higher in open plots, although confidence intervals overlapped with zero. We found time since fire to influence community dominance with measures being higher in 2019 compared to both 2018 and 2020 (Figure 6d). Large, open plots revealed an increasing trend for dominance as time since fire increased, while dominance in closed plots peaked in 2019 before decreasing the following year.

Comparison of experimental blocks for small plots revealed Block C to have significantly higher measures of species diversity and evenness and lower measures of dominance compared to Blocks A and B (Table 2). Similarly, in the large plots, Block A supported significantly higher species richness, diversity and evenness compared to the other three blocks (Table 3). However, Block C had the highest values for plant dominance.

Dominant plant morphology

During the three years of vegetation surveys, we measured 3,468 individual P. esculentum plants. The interaction effect of herbivore activity and time since fire was included only in models for bottom height and for the count of individuals for small plots (Table S3). In small plots, the bottom heights of bracken plants were higher within partial and closed plots in 2019 compared to both 2018 and 2020 (Figure 7b). The number of bracken plants within small plots decreased with time since fire and they were more abundant within closed plots in 2019 (Figure 7e; Table 4). Within large plots, we found bracken width to be altered by herbivore activity, with plants in open plots being wider (Figure 8a).

As time since fire increased, bracken plants were wider and taller within both small and large plots in 2019 and 2020 compared to 2018 (Table 4; 5). In small plots, the amount of dead material on bracken plants was greater in 2019 and 2020 compared to 2018 (Figure 7d). The number of bracken plants in both small and large plots declined with time since fire (Figure 7e; 8e).

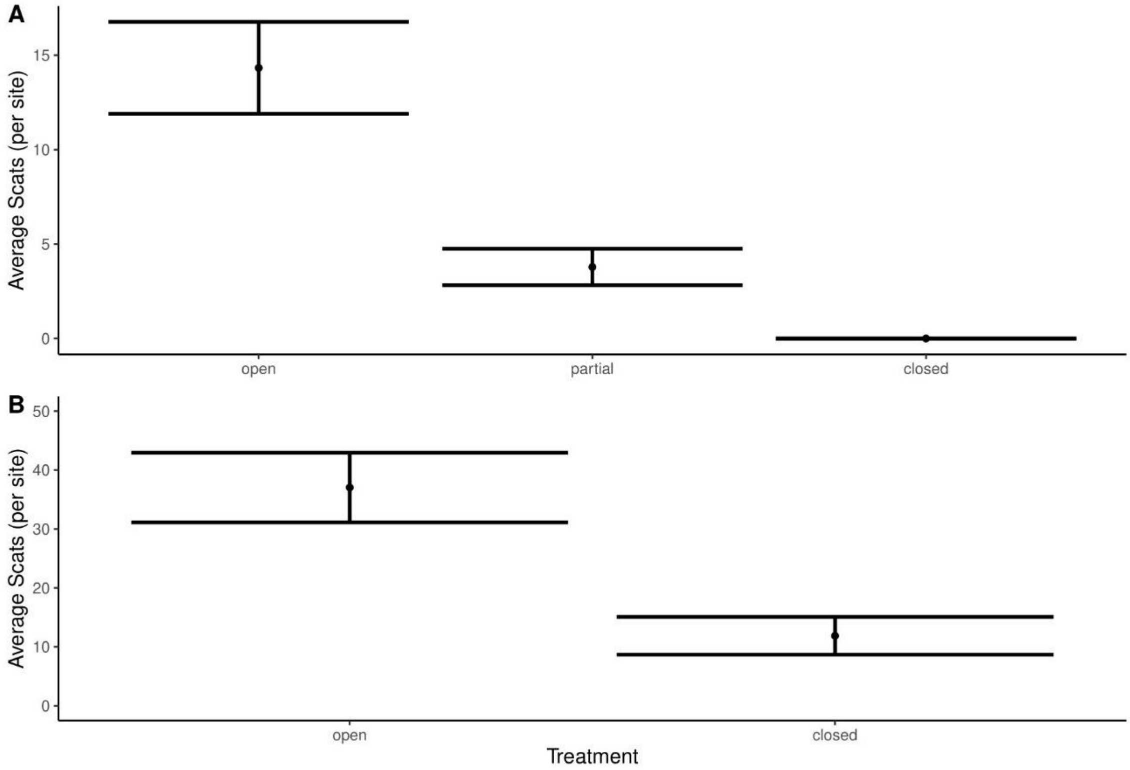

Figure 4: The average abundance of macropod scats found in (A) small plots and (B) large plots. Small plots were 25 m x 25 m and had three levels of fencing (open/closed/partial) to alter macropod access. Large plots were 200 m x 200 m and had two level of fencing (open/closed) to alter macropod access. Values are means and 95% credible intervals from plots located in forest vegetation.

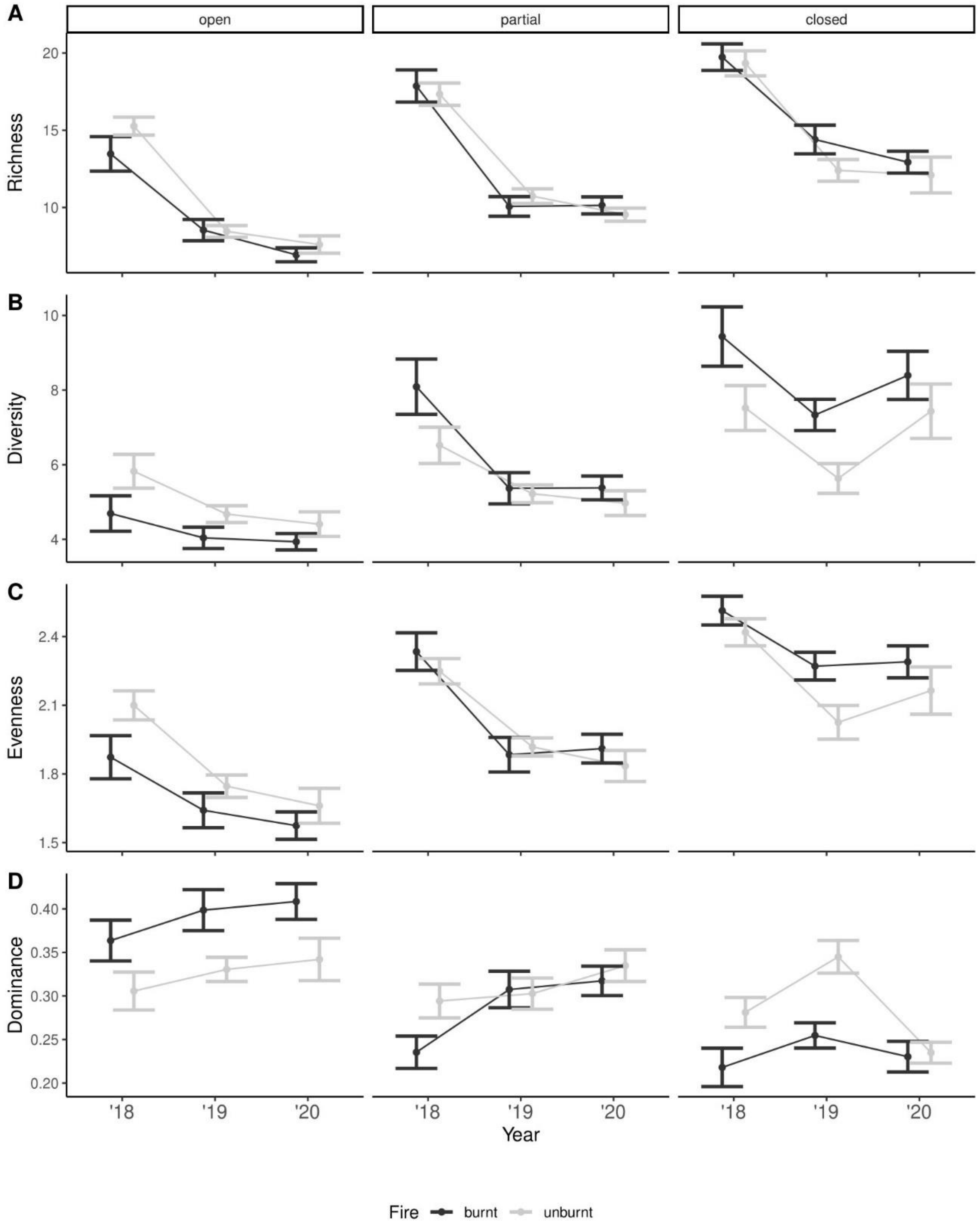

Figure 5: Response of plant community measures of (A) species richness, (B) diversity (Simpson's reciprocal index, 1/D), (C) evenness (Simpson's evenness, $E_{1/D}$) and (D) dominance (Berger-Parker, d) to fire (unburnt/burnt) and herbivory (open/partial/closed) through time. Values are means and 95% credible intervals from small plots (25 m x 25 m) in forest vegetation.

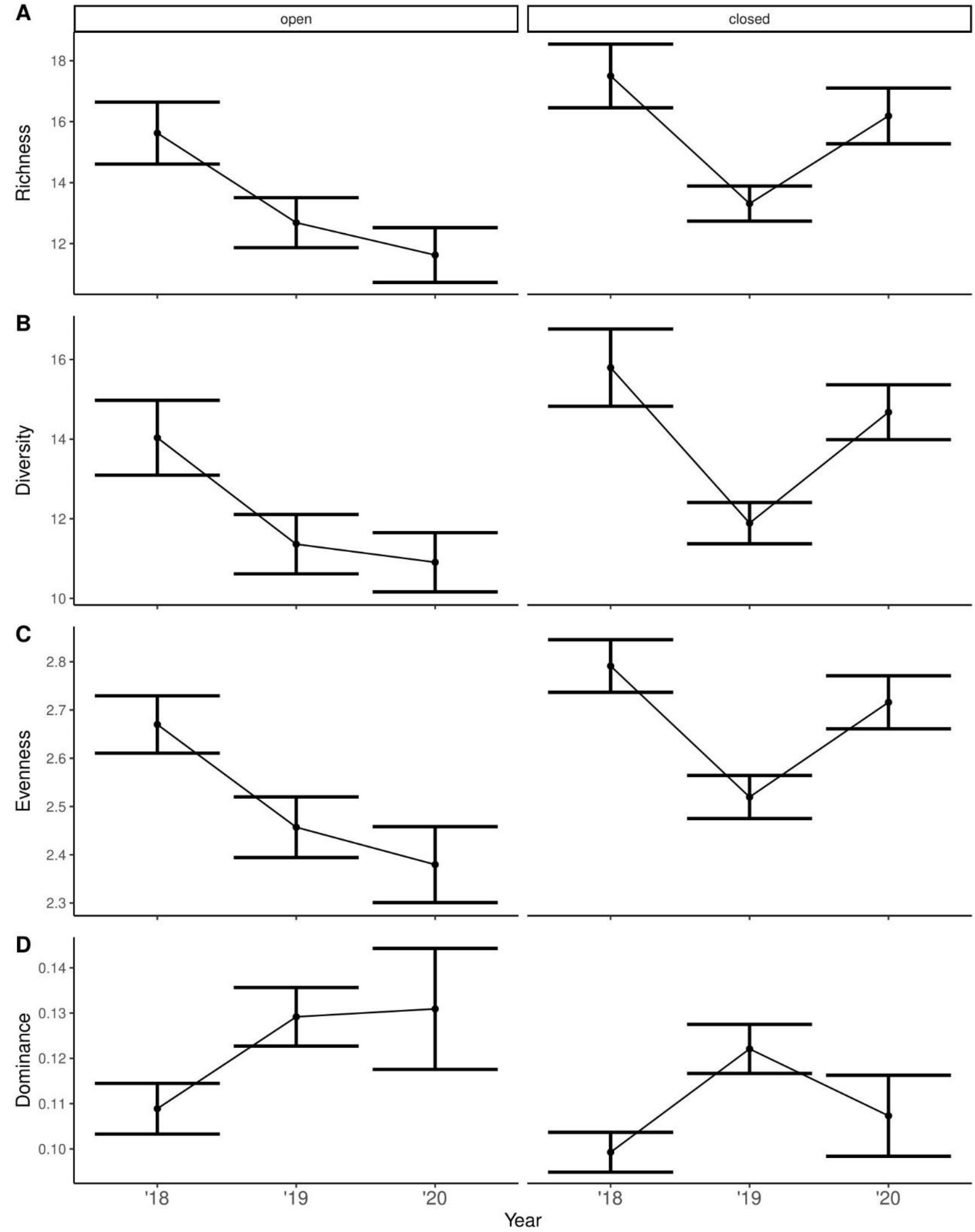

Figure 6: Response of plant community measures of (A) species richness, (B) diversity (Simpson's reciprocal index, 1/D), (C) evenness (Simpson's evenness, E1/D) and (D) dominance (Berger- Parker, d) herbivory (open/closed) through time. Values are means and 95% credible intervals from large plots (200 m x 200 m) located in forest vegetation.

Table 2: Results from Bayesian generalized linear model analysing whether plant species richness, diversity (Simpson's reciprocal index, 1/D), evenness (Simpson's evenness, $E_{1/D}$) and dominance (Berger-Parker, d) in 25 m x 25 m plots are influenced by fire (burnt/unburnt), herbivore access (open/partial/closed) and year (2018/19/20).

	Species Richness		**Simpson's Diversity (1/D)**		**Shannon's Evenness ($E_{1/D}$)**		**Berger-Parker Dominance (d)**	
Coefficient	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*
Intercept	**2.57**	**2.39, 2.75**	**1.5**	**1.28, 1.71**	**1.93**	**1.75, 2.11**	**0.36**	**0.30, 0.42**
Herbivory (Partial)	**0.23**	**0.05, 0.39**	**0.33**	**0.11, 0.56**	**0.25**	**0.08, 0.43**	**-0.07**	**-0.13, -0.01**
Herbivory (Closed)	**0.41**	**0.24, 0.57**	**0.49**	**0.26, 0.71**	**0.5**	**0.32, 0.67**	**-0.08**	**-0.15, -0.02**
Fire (Burnt)	0	-0.14, 0.14	0.04	-0.12, 0.21	0.02	-0.12, 0.17	-0.01	-0.05, 0.04
Year (2019)	**-0.47**	**-0.55, -0.40**	**-0.19**	**-0.31, -0.06**	**-0.35**	**-0.41, -0.28**	**0.04**	**0.01, 0.07**
Year (2020)	**-0.55**	**-0.63, -0.46**	**-0.16**	**-0.28, -0.02**	**-0.33**	**-0.39, -0.27**	0.03	-0.00, 0.07
Block B	-0.05	-0.22, 0.12	-0.04	-0.23, 0.17	-0.06	-0.24, 0.13	0	-0.06, 0.05
Block C	0.15	-0.02, 0.31	**0.28**	**0.09, 0.48**	**0.24**	**0.07, 0.42**	**-0.07**	**-0.13, -0.01**
Partial:2019			-0.11	-0.28, 0.06			0	-0.04, 0.05
Closed:2019			-0.08	-0.25, 0.08			0.02	-0.03, 0.06
Partial:2020			-0.17	-0.34, 0.01			0.03	-0.02, 0.08
Closed:2020			0.09	-0.08, 0.26			-0.04	-0.09, 0.01
N	18 $_{plot}$		18 $_{plot}$		18 $_{plot}$		18 $_{plot}$	
Observations	270		270		270		270	
Marginal R^2/ Conditional R^2	0.683 / 0.745		0.527 / 0.623		0.597 / 0.675		0.402 / 0.525	

Estimates and 95% credible intervals are shown for the most parsimonious models (by WAIC and model simplicity; see Appendix S2 for model selection table). Rows that are in bold indicate that credible intervals do not overlap zero. Reference states for comparisons were open, unburnt plots sampled in 2018.

Table 3: Results from Bayesian generalized linear model analysing whether plant species richness, diversity (Simpson's reciprocal index, 1/D), evenness (Simpson's evenness, $E_{1/D}$) and dominance (Berger-Parker, d) in 200 m x 200 m plots are influenced by herbivore access (open/partial/closed) and year (2018/19/20).

	Species richness		**Simpson's Diversity (1/D)**		**Shannon's Evenness ($E_{1/D}$)**		**Berger-Parker Dominance (d)**	
Coefficient	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*
Intercept	**3.01**	**2.81, 3.20**	**2.87**	**2.70, 3.02**	**2.94**	**2.76, 3.10**	**0.09**	**0.06, 0.11**
Herbivory (Closed)	0.11	-0.10, 0.32	0.13	-0.03, 0.29	0.12	-0.04, 0.29	-0.01	-0.03, 0.01
Year (2019)	**-0.21**	**-0.40, -0.03**	**-0.21**	**-0.33, -0.10**	**-0.21**	**-0.33, -0.10**	**0.02**	**0.01, 0.04**
Year (2020)	**-0.3**	**-0.49, -0.11**	**-0.26**	**-0.37, -0.15**	**-0.29**	**-0.40, -0.18**	0.01	0.00, 0.03
Block B	**-0.31**	**-0.55, -0.09**	**-0.28**	**-0.48, -0.10**	**-0.30**	**-0.48, -0.09**	0.02	-0.01, 0.05
Block C	**-0.49**	**-0.73, -0.25**	**-0.47**	**-0.66, -0.28**	**-0.49**	**-0.69, -0.28**	**0.05**	**0.02, 0.07**
Block D	**-0.31**	**-0.54, -0.07**	**-0.28**	**-0.45, -0.10**	**-0.29**	**-0.50, -0.09**	0.02	-0.00, 0.05
Closed:2019	-0.06	-0.32, 0.19	-0.06	-0.23, 0.10	-0.06	-0.22, 0.10		
Closed:2020	0.22	-0.03, 0.47	**0.19**	**0.03, 0.35**	**0.22**	**0.05, 0.38**		
N	8_{plot}		8_{plot}		8_{plot}		8_{plot}	
Observations	96		96		96		96	
Marginal R^2/ Conditional R^2	0.689 / 0.690		0.655 / 0.662		0.669 / 0.677		0.371 / 0.370	

Estimates and 95% credible intervals are shown for the most parsimonious models (by WAIC and model simplicity; see Appendix S2 for model selection table). Rows that are in bold indicate that credible intervals do not overlap zero. Reference states for comparisons were open plots sampled in 2018.

Table 4: Results from Bayesian generalized linear model analysing whether *Pteridium esculentum* (bracken) morphology including: plant width, height to bottom frond, height to top, percentage of dead material on each plant and number of plants in 25 m x 25 m plots are influenced by fire (burnt/unburnt), herbivore access (open/partial/closed) and year (2018/19/20).

	Width (cm)		**Bottom Height (cm)**		**Top Height (cm)**		**Dead (%)**		**Count**	
Coefficient	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*
Intercept	**60.23**	**55.30, 65.30**	**28.01**	**23.60, 33.11**	**58.96**	**52.33, 65.21**	**0.45**	**0.07, 0.86**	**4.12**	**3.65, 4.59**
Herbivory (Partial)	0.55	-3.80, 4.80	1.02	-3.00, 5.28	0.24	-4.75, 4.80	-0.27	-0.57, 0.01	-0.12	-0.61, 0.37
Herbivory (Closed)	2.03	-2.11, 6.81	2.87	-1.62, 7.70	2.06	-2.73, 8.20	-0.07	-0.40, 0.27	-0.42	-0.91, 0.10
Fire (Burnt)	-0.23	-4.20, 3.74	0.77	-3.07, 4.55	0.40	-4.18, 5.24	0.16	-0.09, 0.41	0.11	-0.28, 0.49
Year (2019)	**5.74**	**3.32, 8.28**	**3.35**	**0.80, 5.75**	**10.42**	**8.17, 12.68**	**-0.43**	**-0.76, -0.11**	**-0.31**	**-0.47, -0.16**
Year (2020)	1.17	-1.23, 3.61	**5.68**	**3.25, 8.28**	**10.29**	**7.91, 12.68**	**-0.59**	**-0.93, -0.24**	**-0.47**	**-0.63, -0.30**
Block B	0.68	-3.38, 4.92	0.75	-3.48, 4.86	0.15	-4.59, 5.25	-0.13	-0.42, 0.18	0.04	-0.43, 0.51
Block C	1.58	-2.41, 6.09	3.17	-1.19, 8.36	1.11	-3.53, 6.34	-0.29	-0.65, 0.05	-0.42	-0.88, 0.04
Partial:2019			**3.54**	**0.26, 7.27**					-0.11	-0.35, 0.12
Closed:2019			**4.26**	**0.93, 8.16**					**0.27**	**0.04, 0.50**
Partial:2020			0.09	-3.09, 3.31					0.15	-0.09, 0.38
Closed:2020			1.28	-2.24, 5.19					0.04	-0.23, 0.32
N	18 $_{\text{plot}}$		18 $_{\text{plot}}$		18 $_{\text{plot}}$		18 $_{\text{plot}}$		18 $_{\text{plot}}$	
Observations	2210		2210		2210		2210		53	
Marginal R^2/ Conditional R^2	0.018 / 0.061		0.046 / 0.112		0.053 / 0.189		0.001 / 0.001		0.084 / 0.733	

Estimates and 95% credible intervals are shown for the most parsimonious models (by WAIC and model simplicity; see Appendix S2 for model selection table). Rows that are in bold indicate that credible intervals do not overlap zero. Reference states for comparisons were open, unburnt plots sampled in 2018.

Table 5: Results from Bayesian generalized linear model analysing whether *Pteridium esculentum* (bracken) morphology including: plant width, height to bottom frond, height to top, percentage of dead material on each plant and number of plants in 200 m x 200 m plots are influenced by herbivore access (open/partial/closed) and year (2018/19/20).

	Width (cm)		Bottom Height (cm)		Top Height (cm)		Dead (%)		Count	
Coefficient	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*	*Est.*	*CI (95%)*
Intercept	**51.33**	**45.37, 56.53**	**25.73**	**20.58, 30.33**	**50.00**	**42.32, 57.03**	-0.22	-0.85, 0.43	**3.68**	**2.95, 4.41**
Herbivory (Closed)	**-5.67**	**-9.85, -0.48**	0.22	-3.45, 4.58	-5.22	-11.41, 1.36	-0.03	-0.44, 0.37	0.17	-0.47, 0.85
Year (2019)	**9.62**	**6.22, 13.19**	**2.66**	**0.08, 5.23**	**11.66**	**8.42, 15.04**	0.19	-0.27, 0.64	**-0.2**	**-0.33, -0.07**
Year (2020)	**8.65**	**4.86, 12.43**	**7.33**	**4.77, 10.07**	**18.15**	**14.60, 21.79**	0.39	-0.07, 0.88	**-0.44**	**-0.59, -0.31**
Block B	**14.41**	**9.00, 20.84**	**8.18**	**3.09, 13.40**	**17.07**	**8.65, 26.01**	-0.17	-0.74, 0.39	0.76	-0.14, 1.66
Block C	2.27	-4.65, 8.94	2.05	-3.74, 7.86	-0.68	-9.68, 8.56	0.05	-0.58, 0.65	-0.26	-1.17, 0.72
Block D	4.48	-1.30, 10.75	-0.45	-5.87, 4.86	2.31	-6.48, 10.98	-0.06	-0.64, 0.50	0.64	-0.23, 1.52
N	8_{plot}		8_{plot}		8_{plot}		8_{plot}		8_{plot}	
Observations	1257		1257		1257		1257		24	
Marginal R^2/ Conditional R^2	0.087 / 0.090		0.064 / 0.065		0.162 / 0.175		0.001 / 0.001		0.765 / 0.767	

Estimates and 95% credible intervals are shown for the most parsimonious models (by WAIC and model simplicity; see Appendix S2 for model selection table). Rows that are in bold indicate that credible intervals do not overlap zero. Reference states for comparisons were open plots sampled in 2018.

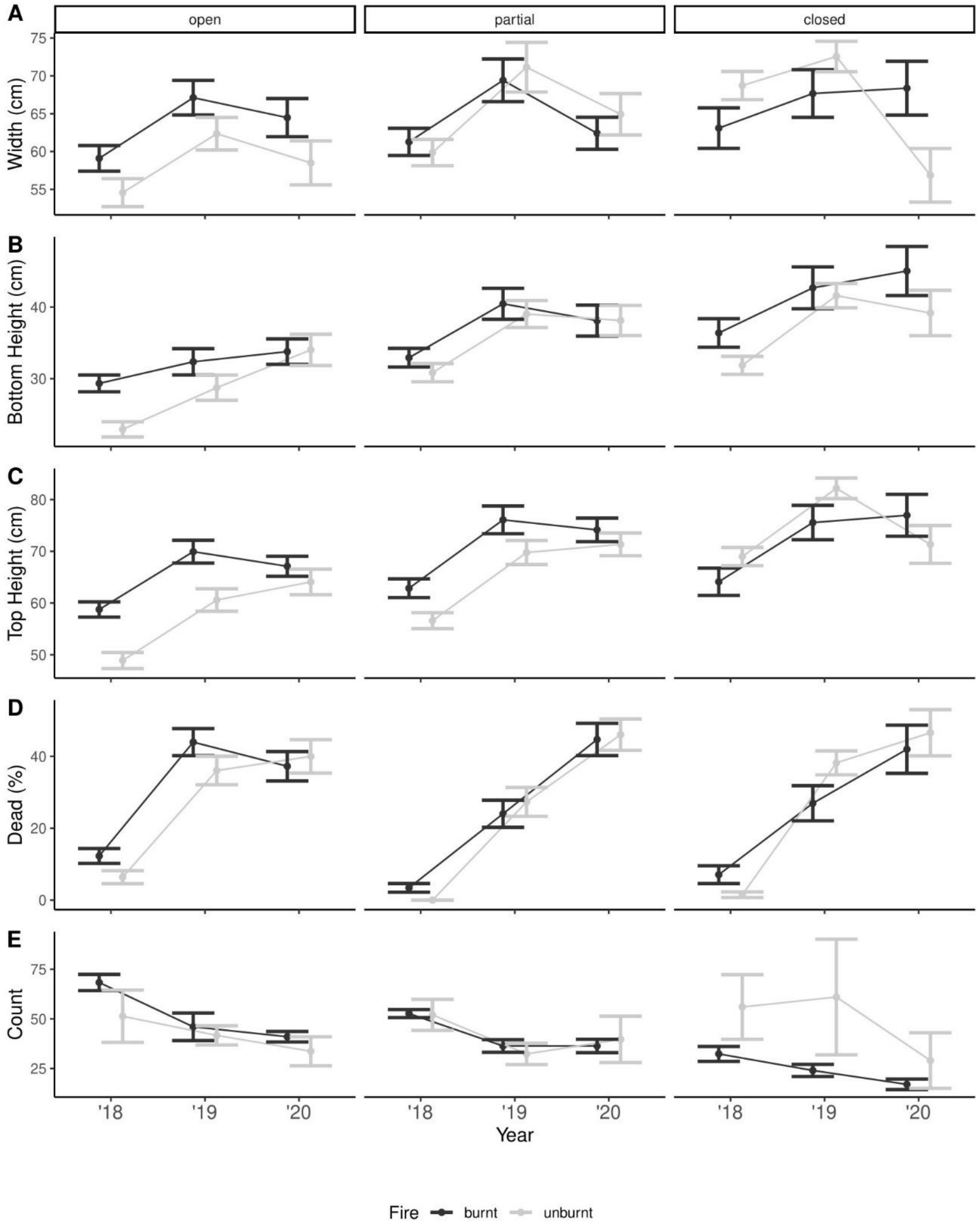

Figure 7: Morphological responses of the dominant understory bracken (Pteridium esculentum) of (A) width, (B) height to bottom frond, (C) top height, (D) percent of dead material and (E) number of plants to fire (unburnt/burnt) and herbivory (open/partial/closed) through time. Values are means and 95% credible intervals from small plots (25 m x 25 m) located in forest vegetation.

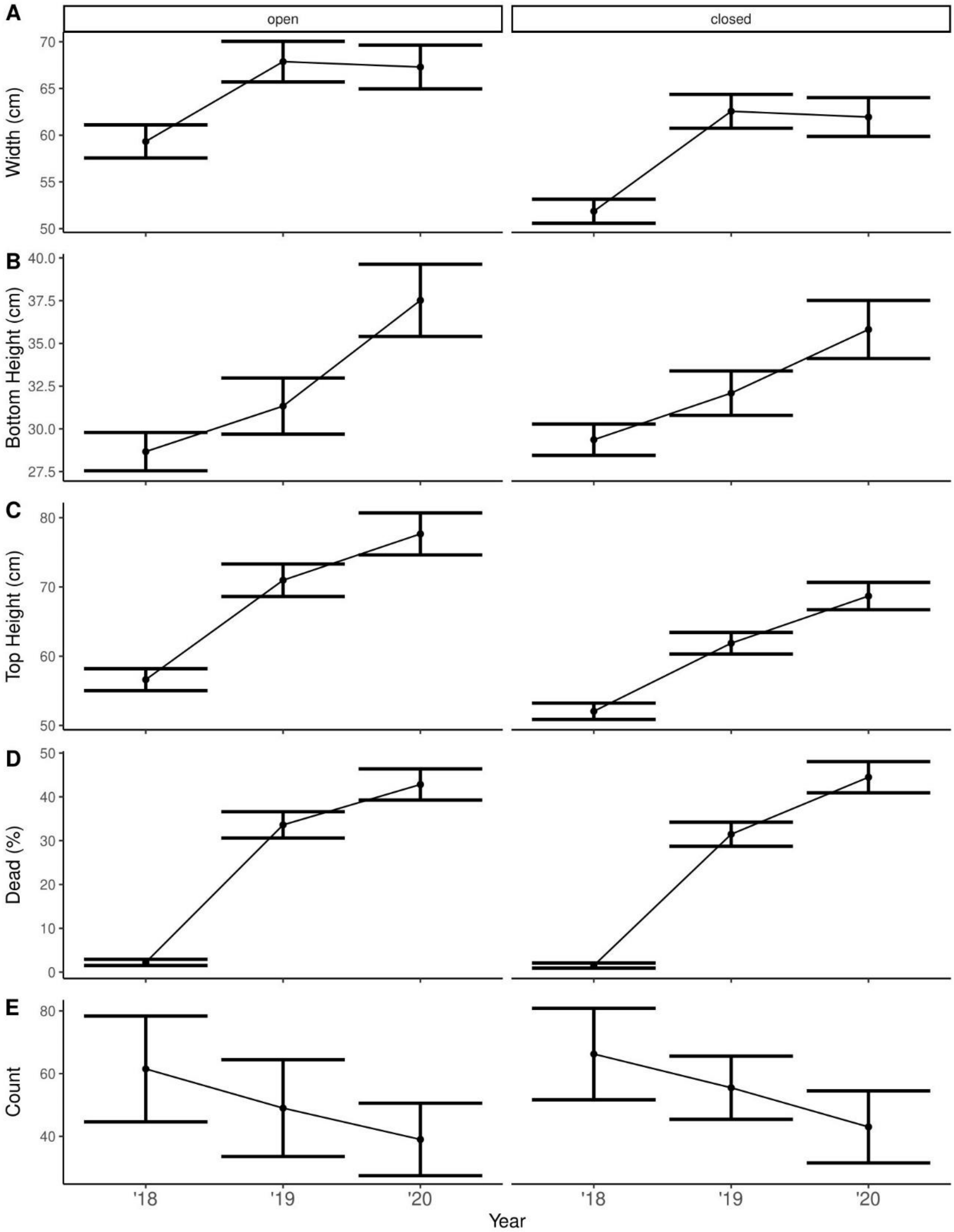

Figure 8: Morphological responses of the dominant understory bracken (Pteridium esculentum) of (A) width, (B) height to bottom frond, (C) top height, (D) percent of dead material and (E) number of plants to herbivory (open/closed) through time. Values are means and 95% credible intervals from large plots (200 m x 200 m) located in forest vegetation.

2.6 Discussion

The interactive effect of herbivory and fire on vegetation structure, composition and dynamics is important but often overlooked (Foster et al., 2020). We used a manipulative exclosure experiment to address the question: How does post-fire herbivory alter understory plant diversity and dominant plant attributes in a coastal eucalypt forest? We found evidence that herbivore exclusion and time since fire, and their interaction altered the understory plant community. Our key findings were that: (1) herbivore activity was reduced by the exclusion fences, but there was no evidence of a time since fire effect; (2) the exclusion of herbivores generally resulted in a richer, more diverse, and more even vegetation community; (3) time since fire was the strongest driver of morphological changes in bracken, which dominated the understory; and, (4) the influence of the previous prescribed burns had no apparent legacy effects on vegetation measures.

Post-fire herbivore activity

Fencing treatments reduced herbivore activity in partially-closed and closed plots, but there was no time since fire effect. A lack of a time since fire effect was surprising as the macropod species present within our study have previously shown a selective preference for recently burnt patches (Southwell & Jarman, 1987; Meers & Adams, 2003; Foster et al., 2015; Hradsky et al., 2017; Parkins et al., 2019). This result might be explained by the large size of the 2017 wildfire (1,600 ha) compared with other studies that focused on smaller burns (31 ha, Southwell and Jarman, 1987; 1 ha, Meers and Adams, 2003; 226 ha, Dexter et al., 2013; 0.25 ha, Foster et al., 2015; 714 ha, Hradsky et al., 2017). Macropods may be selecting for burnt patches within our study area but, due to the large size of the 2017 wildfire, increased occurrence may have been distributed over a large area, resulting in only a nuanced effect at our study plots. If fire size is impacting herbivore response, future prescribed burning practices may need to accommodate local herbivore density. To confirm this, more investigations would be required to determine the relationship between fire size and herbivore density.

Shifting vegetation communities

Knowledge of modifications to vegetation communities by large herbivores within fire-prone ecosystems is increasing (Tuft et al., 2012; Crowther et al., 2016). We found that post-fire herbivory reduced plant species richness, diversity and evenness and increased plant dominance measures. This was expected as foraging pressure by large herbivores has been shown to decrease diversity and increase species dominance in other ecosystems (Bakker et al., 2006; Tuft et al., 2012; Connor et al., 2021). This finding confirms that increased foraging pressure from large herbivores following a wildfire also results in a more depauperate vegetation community, consistent with previous studies of smaller prescribed/experimental burns (Foster et al., 2015; Parkins et al., 2019).

Our study revealed that the richest and most diverse plant communities occurred directly after fire. These findings are consistent with earlier studies indicating richness decreases with increasing time since fire (Ross et al., 2002; Foster et al., 2018). Higher species richness immediately after fire was expected in eucalypt forest understory as fire typically stimulates new growth and the germination of seedlings, and many species can re-sprout after fire

(Dixon et al., 2018). Further, within large plots, we observed that with increasing time since fire, herbivore exclusion promoted a more diverse and more even community. Preventing large herbivores from accessing burnt patches may therefore promote a richer and more diverse understory.

Morphology of bracken

The increase in *P. esculentum* dominance within Booderee National Park has been an ongoing concern for resource managers (Dexter et al., 2013). However, this study did not uncover evidence of differences in bracken morphology with altered herbivore activity. This was surprising as we expected this unpalatable plant species to thrive in plots accessible to macropods where increased foraging of palatable plants would reduce interspecies competition with bracken (Archibald & Hempson, 2016). Previous research indicated high plant diversity in understory forest communities can positively affect the biomass and survivability of all plants (Cook-Patton et al., 2014). It is possible that bracken is experiencing a win-win scenario in post-fire landscapes, whether browsed or unbrowsed. Increased herbivory may be reducing interspecies competition by decreasing species diversity, promoting the dominance of bracken. Conversely, reduced herbivory may be accommodating positive interspecific interactions from increased species diversity, resulting in healthier bracken plants.

Our findings indicate that increasing time since fire led to the reduced abundance and altered physical attributes of bracken plants. The amount of dead material on bracken increased with increasing time since fire in small plots. This dead material may contribute directly to fire risk by increasing potential fire behaviour (Cheney et al., 2012). However, no changes were observed within the large plots. Potential differences in our results may be due to the difference between time since exclosure (nine years vs three years) or the time to establishing the larger manipulative experiment following the wildfire in 2017 (10 months). The latter effect may have allowed macropods to modify the understory before the fences affected herbivore activity, reducing the contrast between plots. Extending the survey to future years may reveal important findings as dead biomass of bracken usually peaks at four to seven years following disturbance (Bray, 1991; Parkins et al., 2019). Longer-term datasets (> 3 years) may be required to document post-fire bracken growth within forested communities.

Fire history

We found no evidence that previous prescribed burns in 2012 influenced herbivore activity, vegetation community measures, or bracken morphology following the 2017 wildfire. This was surprising as repeated fires at short intervals (five years in our study) have been observed to drive large herbivores to suppress palatable plants, locally decreasing plant diversity, while promoting the dominance of unpalatable, fire-resistant plants like bracken (Pietrzykowski et al., 2003; Archibald & Hempson, 2016; Wyse et al., 2016). This may be because of strong effects of the 2017 fire and herbivory masked any remaining effects on vegetation of the 2012 fires. It is possible that effects of the short fire interval may become apparent with increasing time since fire (i.e. reduced effect of 2017 fire), where impacts on slower growing species, and in particular obligate seeding shrub species, become easier to detect.

2.7 Conclusion

Our study highlights the impacts of post-fire herbivory on vegetation communities. Post-fire herbivory decreases richness, diversity, and evenness measures and increases the dominance of few species leading to a more depauperate vegetation community. Future management of forest ecosystems should account for local populations of large herbivores. Increased understory plant diversity may be achieved by reducing herbivore numbers or preventing access to burnt patches following fire. Conversely, where herbivore impacts align with management goals (e.g. control of palatable weeds, or reducing fuel biomass for fire hazard reduction) small prescribed burns may be effective in concentrating foraging pressure by herbivores in target areas.

2.8 Acknowledgements

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2.10 Supplementary Material

Table S1: Model selection results from an analysis of herbivory (open/partial/closed), fire (unburnt/burnt), and time since fire (TSF, continuous) influences on macropod scats. Bayesian generalized linear models were constructed with negative binomial distribution. Within all models, season and block were included as fixed effects and plot was included as a random effect. Results are ranked based of WAIC for small (25 m x 25 m) and large (200 m x 200 m) plots. The most parsimonious model, indicated in bold, was selected from the simplest (ie. least variables) model under the WAIC threshold of 2 (indicated by dashed line).

SMALL PLOTS			
Model	**Model Description**	**WAIC**	**SE**
4	Herbivory+Fire+TSF + Herbivory:TSF	0.00	0.00
1	**Herbivory+Fire+TSF**	**0.30**	**3.34**
6	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF	0.35	2.20
2	Herbivory+Fire+TSF + Herbivory:Fire	1.34	3.94
3	Herbivory+Fire+TSF + Fire:TSF	1.44	3.54
7	Herbivory+Fire+TSF + Fire:TSF + Herbivory:TSF	1.69	1.26
8	Herbivory+Fire+TSF + Herbivory:Fire+ Herbivory:TSF + Fire:TSF	1.74	2.64
5	Herbivory+Fire+TSF + Herbivory:Fire+ Fire:TSF	1.90	3.98
9	Herbivory+Fire+TSF + Herbivory:Fire+ Herbivory:TSF + Fire:TSF + Herbivory:Fire:TSF	1.98	4.33
LARGE PLOTS			
Model	**Model Description**	**WAIC**	**SE**
1	**Herbivory+TSF**	**0.00**	**0.00**
2	Herbivory+TSF + Herbivory:TSF	0.77	2.40

Table S2: Model selection results from an analysis of herbivory (open/partial/closed), fire (unburnt/burnt), and time since fire (TSF, continuous) influences on vegetation community measures. Plant community measures were species richness, diversity (Simpson's reciprocal index, 1/D), evenness (Simpson's evenness, $E_{1/D}$) and dominance (Berger-Parker, d). Bayesian generalized linear models were constructed with Poisson, for species richness, or Gaussian distribution. Within all models, block was included as a fixed effect and plot was included as a random effect. Results are ranked based of WAIC for small (25 m x 25 m) and large (200 m x 200 m) plots. The most parsimonious model, indicated in bold, was selected from the simplest (ie. least variables) model under the WAIC threshold of 2 (indicated by dashed line).

	SMALL PLOTS		
Model	**Model Description**	**WAIC**	**SE**
	Species Richness		
4	Herbivory+Fire+TSF + Herbivory:TSF	0.00	0.00
6	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF	0.16	0.91
1	**Herbivory+Fire+TSF**	**0.73**	**3.40**
2	Herbivory+Fire+TSF + Herbivory:Fire	0.79	3.50
7	Herbivory+Fire+TSF + Fire:TSF + Herbivory:TSF	2.06	1.21
8	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF	2.70	1.63
3	Herbivory+Fire+TSF + Fire:TSF	2.75	3.72
5	Herbivory+Fire+TSF + Herbivory:Fire+ Fire:TSF	3.32	3.85
9	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF + Herbivory:Fire:TSF	5.86	2.62
	Simpson's Diversity		
6	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF	0.00	0.00
4	**Herbivory+Fire+TSF + Herbivory:TSF**	**0.28**	**2.04**
7	Herbivory+Fire+TSF + Fire:TSF + Herbivory:TSF	2.65	2.93
8	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF	3.41	2.01
1	Herbivory+Fire+TSF	4.14	7.67
2	Herbivory+Fire+TSF + Herbivory:Fire	4.59	6.90
9	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF + Herbivory:Fire:TSF	5.78	4.97
3	Herbivory+Fire+TSF + Fire:TSF	7.76	7.36
5	Herbivory+Fire+TSF + Herbivory:Fire+ Fire:TSF	7.82	7.99
	Shannon's Evenness		
1	**Herbivory+Fire+TSF**	**0.00**	**0.00**
2	Herbivory+Fire+TSF + Herbivory:Fire	0.26	1.86
4	Herbivory+Fire+TSF + Herbivory:TSF	0.77	5.16
6	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF	1.13	5.60
3	Herbivory+Fire+TSF + Fire:TSF	2.41	2.54
5	Herbivory+Fire+TSF + Herbivory:Fire+ Fire:TSF	2.52	3.08

7	Herbivory+Fire+TSF + Fire:TSF + Herbivory:TSF	3.89	5.48
8	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF	4.30	5.90
9	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF + Herbivory:Fire:TSF	6.88	7.74
	Berger-Parker Dominance		
8	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF	0.00	0.00
7	Herbivory+Fire+TSF + Fire:TSF + Herbivory:TSF	0.28	2.08
4	**Herbivory+Fire+TSF + Herbivory:TSF**	**1.12**	**4.87**
6	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF	1.16	4.22
9	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF + Herbivory:Fire:TSF	2.04	4.79
1	Herbivory+Fire+TSF	6.64	7.09
2	Herbivory+Fire+TSF + Herbivory:Fire	6.69	8.48
3	Herbivory+Fire+TSF + Fire:TSF	6.70	7.91
5	Herbivory+Fire+TSF + Herbivory:Fire+ Fire:TSF	8.10	7.67
	LARGE PLOTS		
Model	**Model Description**	**WAIC**	**SE**
	Species Richness		
2	**Herbivory+TSF + Herbivory:TSF**	**0.00**	**0.00**
1	Herbivory+TSF	2.21	2.78
	Simpson's Diversity		
2	**Herbivory+TSF + Herbivory:TSF**	**0.00**	**0.00**
1	Herbivory+TSF	3.08	7.14
	Shannon's Evenness		
2	**Herbivory+TSF + Herbivory:TSF**	**0.00**	**0.00**
1	Herbivory+TSF	8.98	7.06
	Berger-Parker Dominance		
1	**Herbivory+TSF**	**0.00**	**0.00**
2	Herbivory+TSF + Herbivory:TSF	1.89	3.54

Table S3: Model selection results from an analysis of herbivory (open/partial/closed), fire (unburnt/burnt), and time since fire (TSF, continuous) influences on morphological measurements of the dominant understory bracken (*Pteridium esculentum*). Morphological responses include width, height to bottom frond, top height, percent of dead material and number of plants. Bayesian generalized linear models were constructed with Poisson (for count data), zero-one-inflated (for percent data) or Gaussian distribution. Within all models, block was included as a fixed effect and plot was included as a random effect. Results are ranked based of WAIC for small (25 m x 25 m) and large (200 m x 200 m) plots. The most parsimonious model, indicated in bold, was selected from the simplest (ie. least variables) model under the WAIC threshold of 2 (indicated by dashed line).

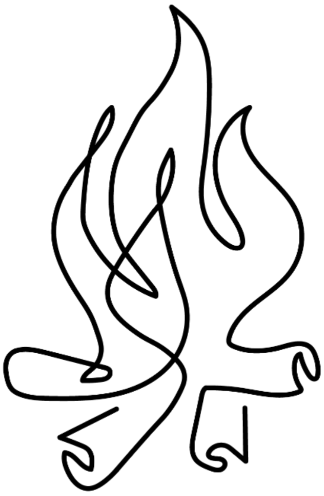
	SMALL PLOTS		
Model	**Model Description**	**WAIC**	**SE**
	Width (cm)		
1	**Herbivory+Fire+TSF**	**0.00**	**0.00**
4	Herbivory+Fire+TSF + Herbivory:TSF	0.26	2.31
6	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF	0.31	2.36
3	Herbivory+Fire+TSF + Fire:TSF	0.40	1.36
2	Herbivory+Fire+TSF + Herbivory:Fire	0.59	2.88
9	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF + Herbivory:Fire:TSF	0.64	0.12
7	Herbivory+Fire+TSF + Fire:TSF + Herbivory:TSF	1.05	2.74
8	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF	1.18	2.75
5	Herbivory+Fire+TSF + Herbivory:Fire+ Fire:TSF	1.39	1.42
	Bottom Height (cm)		
4	**Herbivory+Fire+TSF + Herbivory:TSF**	**0.00**	**0.00**
6	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF	0.34	0.26
7	Herbivory+Fire+TSF + Fire:TSF + Herbivory:TSF	1.50	0.66
8	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF	1.67	0.66
1	Herbivory+Fire+TSF	3.01	4.34
2	Herbivory+Fire+TSF + Herbivory:Fire	3.46	1.54
9	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF + Herbivory:Fire:TSF	3.51	4.31
3	Herbivory+Fire+TSF + Fire:TSF	4.46	4.34
5	Herbivory+Fire+TSF + Herbivory:Fire+ Fire:TSF	4.90	4.31
	Top Height (cm)		
1	**Herbivory+Fire+TSF**	**0.00**	**0.00**
2	Herbivory+Fire+TSF + Herbivory:Fire	0.58	0.15
3	Herbivory+Fire+TSF + Fire:TSF	2.15	1.60
5	Herbivory+Fire+TSF + Herbivory:Fire+ Fire:TSF	2.75	1.57
4	Herbivory+Fire+TSF + Herbivory:TSF	3.30	1.93
6	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF	3.74	1.94
7	Herbivory+Fire+TSF + Fire:TSF + Herbivory:TSF	5.42	2.56

8	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF	5.66	2.54
9	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF + Herbivory:Fire:TSF	6.91	2.82
	Dead (%)		
1	**Herbivory+Fire+TSF**	**0.00**	**0.00**
3	Herbivory+Fire+TSF + Fire:TSF	2.69	2.31
2	Herbivory+Fire+TSF + Herbivory:Fire	3.92	0.66
4	Herbivory+Fire+TSF + Herbivory:TSF	5.47	2.45
5	Herbivory+Fire+TSF + Herbivory:Fire+ Fire:TSF	6.62	2.39
6	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF	7.58	3.64
7	Herbivory+Fire+TSF + Fire:TSF + Herbivory:TSF	8.94	2.67
8	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF	10.38	6.02
9	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF + Herbivory:Fire:TSF	10.85	3.89
	Count		
7	Herbivory+Fire+TSF + Fire:TSF + Herbivory:TSF	0.00	0.00
6	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF	1.31	5.80
8	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF	1.56	1.90
4	**Herbivory+Fire+TSF + Herbivory:TSF**	**1.73**	**5.20**
9	Herbivory+Fire+TSF + Herbivory:Fire + Herbivory:TSF + Fire:TSF + Herbivory:Fire:TSF	2.72	5.39
3	Herbivory+Fire+TSF + Fire:TSF	11.46	11.97
5	Herbivory+Fire+TSF + Herbivory:Fire+ Fire:TSF	12.80	11.99
1	Herbivory+Fire+TSF	14.52	16.59
2	Herbivory+Fire+TSF + Herbivory:Fire	15.70	16.67
	LARGE PLOTS		
Model	**Model Description**	**WAIC**	**SE**
	Width (cm)		
1	**Herbivory+TSF**	**0.00**	**0.00**
2	Herbivory+TSF + Herbivory:TSF	3.79	1.96
	Bottom Height (cm)		
1	**Herbivory+TSF**	**0.00**	**0.00**
2	Herbivory+TSF + Herbivory:TSF	3.53	2.49
	Top Height (cm)		
1	**Herbivory+TSF**	**0.00**	**0.00**
2	Herbivory+TSF + Herbivory:TSF	3.22	2.53
	Dead (%)		
1	**Herbivory+TSF**	**0.00**	**0.00**
2	Herbivory+TSF + Herbivory:TSF	3.41	2.10
	Count		
1	**Herbivory+TSF**	**0.00**	**0.00**
2	Herbivory+TSF + Herbivory:TSF	3.90	0.76

Paper III: Fencing foragers fuels fires: Can large herbivores alter fire behaviour in coastal eucalypt forests?

3.1 Foreword

Following my findings that large herbivores impact post-fire vegetation communities (*Paper II*), this study aimed to quantify whether the modifications to vegetation produced altered fire behaviour projections. Modelling of fire behaviour has never been applied to vegetation that has been altered by large herbivores in a forest ecosystem. By quantifying changes to projected fire behaviour, I wanted to determine if large herbivores were reducing or increasing projected fire behaviour.



Chard, M., Foster, C.N., Lindenmayer, D.B., Cary, G.J., MacGregor, C.I. and Zylstra, P.J. (2023) 'Fencing foragers fuels fires: Can large herbivores alter fire behaviour in coastal eucalypt forests?'

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Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with https://policies.anu.edu.au/ppl/document/ANUP_003405

I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multi-author papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

Title: Fencing foragers fuels fires: Can large herbivores alter fire behaviour in coastal eucalypt forests?

Authors: Chard, M., Foster, C.N., Lindenmayer, D.B., Cary, G.J., MacGregor, C.I. and Zylstra, P.J.

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Contribution to paper: Author contribution: conceptualisation & design - MC, CNF, DBL, CIM, GJC; data collection - MC, CNF, CIM; data analysis - MC with additional input from CNF, PJZ, GJC; manuscript first draft - MC; discussion extensive revision - MC, PJZ; manuscript revision - MC, CNF, DBL, GJC, CIM, PJZ.

Senior author or collaborating authors endorsement: I, Claire Foster endorse the above contribution statement

Matthew Chard Candidate	MChard Signature	3/15/2023 Date

Endorsed

Claire Foster Primary Supervisor – Print Name	Signature	15.03.2023 Date
Philip Gibbons Delegated Authority – Print Name	Philip Gibbons Signature	17/3/2023 Date

3.2 Abstract

Background: Large herbivores may alter forest fire behaviour by modifying fuel properties, although this has rarely been quantified. If large herbivores can modify fuel to a degree that changes fire behaviour, we need to know if this is beneficial or detrimental to wildfire management aims. We investigated herbivore impacts on simulated fire behaviour using a large-scale field experiment in an Australian eucalypt forest, where herbivore activity was manipulated by fencing. Our study incorporated four large (4 ha) exclosure plots with paired unfenced controls, and six small (0.0625 ha) exclosures, each matched with an unfenced control and a partially-closed treatment. We quantified effects of exclosure fencing on fuel properties including surface litter depth, plant height, and plant cover, and used these measurements to project flame height and rate of fire spread using three fire behaviour models (FFDM, Vesta Mk 2 and FRaME), under four weather scenarios.

Results: We found evidence for large herbivores to affect fire behaviour predictions, but the direction of these effects depended upon the model used. When some herbivore-affected parameters were considered, the Vesta Mk 2 model predicted that under some conditions, herbivores would reduce fire behaviour allowing for direct attack, rather than indirect firefighting approaches.. Conversely, pronounced trends in other vegetation parameters considered only by the FRaME model indicated that longer-term trends would see milder fire behaviour where herbivory had a weaker effect.

Conclusions: Our study highlights the risk of drawing misleading conclusions on large herbivore management if modelling and field data collection do not account for all trends in vegetation affected by herbivory. Considering the changes occurring in both fire regimes and herbivore populations globally, it is critical to further investigate and quantify the effects of herbivores on fuel properties in fire-prone forests and we implore the use of appropriate fire models and long-term data.

Keywords: flame height - Forest Fire Danger Meter - FRaME - herbivory - macropod - post-fire - rate of fire spread - Vesta Mk 2

3.3 Introduction

Predicted increases in future fire activity globally (Andela et al. 2019), mean that variation in fuel properties within forest vegetation need to be monitored (Gale et al. 2021). Large herbivores have the capacity to alter fuel properties in forests, via post-fire browsing, which may translate to modified fire behaviour (Kerns et al. 2011, Raffaele et al. 2011, Johnson et al. 2018, Rouet-Leduc et al. 2021). Manipulative experiments are required to quantify such changes to determine if large herbivores are significantly influencing fire behaviour in forests (Foster et al. 2020).

Large herbivores modify forest community composition via browsing, trampling, and alterations in nutrients (by defecation, urination, and decomposition of carcasses, Persson et al. 2000, Forbes et al. 2019). The degree of modification to vegetation, and subsequently fuel properties, depends on the intensity of browsing pressure and how plant species respond to browsing (Danell 2006). Palatable plants may respond positively to low-moderate levels of herbivory through increased nutrient cycling, increased solar radiation, and greater seed dispersal (Archibald et al. 2019). However, intense browsing pressure may reduce palatable plant abundance by stunting growth or by complete removal (Kerns et al. 2011).

Following fire, palatable plants can experience increased browsing pressure as the regenerating vegetation presents a readily accessible food source for herbivore populations in forest ecosystems (Eby et al. 2014, Read et al. 2021a). This is evident in pyric herbivory relationships, whereby post-fire browsing by large herbivores is focused within burnt areas (Allred et al. 2011, Foster et al. 2015, Bielski et al. 2018). Increased browsing in post-fire forest ecosystems may promote the development of an altered vegetation community in which less palatable species (e.g., low moisture, high carbon to phosphorus ratio, more tannins) persist in the understory due to reduced competition (Blackhall et al. 2015). Less palatable plants generally contain more volatile oils and senesce or cure at a faster rate, potentially increasing available fuel in the understory (Archibald et al. 2019). Comparisons between post-fire forest ecosystems that are browsed versus unbrowsed are required to monitor changes in vegetation, and consequently, fuel properties (Haslem et al. 2011, Chard et al. 2022a).

Altered fire behaviour driven by large herbivore browsing has rarely been quantified in the context of forest ecosystems (Foster et al. 2020). As such, we know relatively little about the likely magnitude or direction of impact. Previous research in forest ecosystems has found that browsing from large herbivores promoted the dominance of flammable plant species, potentially increasing fire severity (Foster et al. 2016, Archibald et al. 2019, Chard et al. 2022a). However, where large herbivores consume or trample large amounts of biomass, they may modify the understory vegetation to a degree whereby the resulting amount and structure of live and dead fuel results in reduced fire severity (McCaw et al. 2012, Zylstra et al. 2022). Large herbivores can also affect the accumulation of leaf litter in forests, either positively or negatively, via direct (e.g., trampling) or indirect (e.g., altered nutrient cycling) pathways (Wardle and Bardgett 2004). Finally, it is likely that the effects of herbivores on fire behaviour will vary with time since fire as the various fuel strata re-accumulate and plant succession is altered (Taylor et al. 2014, Dixon et al. 2019).

In this study, we used a large-scale manipulative field experiment, and three fire behaviour models, to answer two interrelated questions. (1) Does post-fire browsing from large herbivores alter measured fuel properties in a coastal eucalypt forest? And (2) to what extent do resultant changes in fuel properties influence projected fire behaviour? To test these questions, we compared fuel properties including: (i) surface litter depth; (ii) height of near-surface and elevated plants; (iii) number of plants in near-surface and elevated strata; and the projected fire behaviour measures of flame height; and rate of fire spread with respect to herbivore exclosure treatments. We predicted large herbivore browsing to promote the persistence of more flammable plants in the understory (Foster et al. 2016, Chard et al. 2022a) and expected this to increase projected flame height and rate of fire spread. Inference was then made as to how changes to fire behaviour predictions may alter firefighting responses. Such insights into post-fire herbivory effects on fire behaviour may inform future fire management.

3.4 Methods

Study area

Our study was conducted at Booderee National Park, Jervis Bay (-35.1338°, 150.6860°), which is a ~6500 ha area on the south-east coast of Australia, approximately 200 km south of Sydney (Fig. 1a). Booderee National Park is owned by the Wreck Bay Aboriginal Community and is jointly managed by Traditional Owners and Parks Australia.

Sydney Coastal Dry Sclerophyll Forest (hereafter referred to as forest) is the dominant vegetation type in the park (45% of area, Fig. 1b, Taws 1997). This vegetation community is characterized by canopy species of *Eucalyptus pilularis*, *Corymbia gummifera*, and *Eucalyptus botryoides*, with mature trees exceeding 20 m in height and the crowns touching. The midstory is comprised of *Banksia serrata*, *Monotoca eliptica* and several *Acacia* species. It has an understory dominated by *Pteridium esculentum*, *Lomandra longifolia* and *Lepidosperma concavum*.

Three macropod species exist in Booderee National Park that are categorized as “large” herbivores (> 2 kg, as per Danell 2006). The swamp or black wallaby (*Wallabia bicolor*) is a specialist browser that forages on a range of plants in the understory (Di Stefano and Newell, 2008, Dexter et al. 2013). The eastern grey kangaroo (*Macropus giganteus*) and the red-necked wallaby (*Notamacropus rufogriseus*) are grazing species. In Booderee National Park, swamp wallaby and eastern grey kangaroo occurrence is higher in forest than other vegetation types (Chard et al. 2022b) and their abundance has steadily increased over the past 15 years (Lindenmayer et al. 2018). This rise in macropod populations has been accompanied by an alteration in the composition of the understory vegetation toward less palatable but more flammable species and is causing concern to park managers (Dexter et al. 2013, Foster et al. 2016, Chard et al. 2022a).

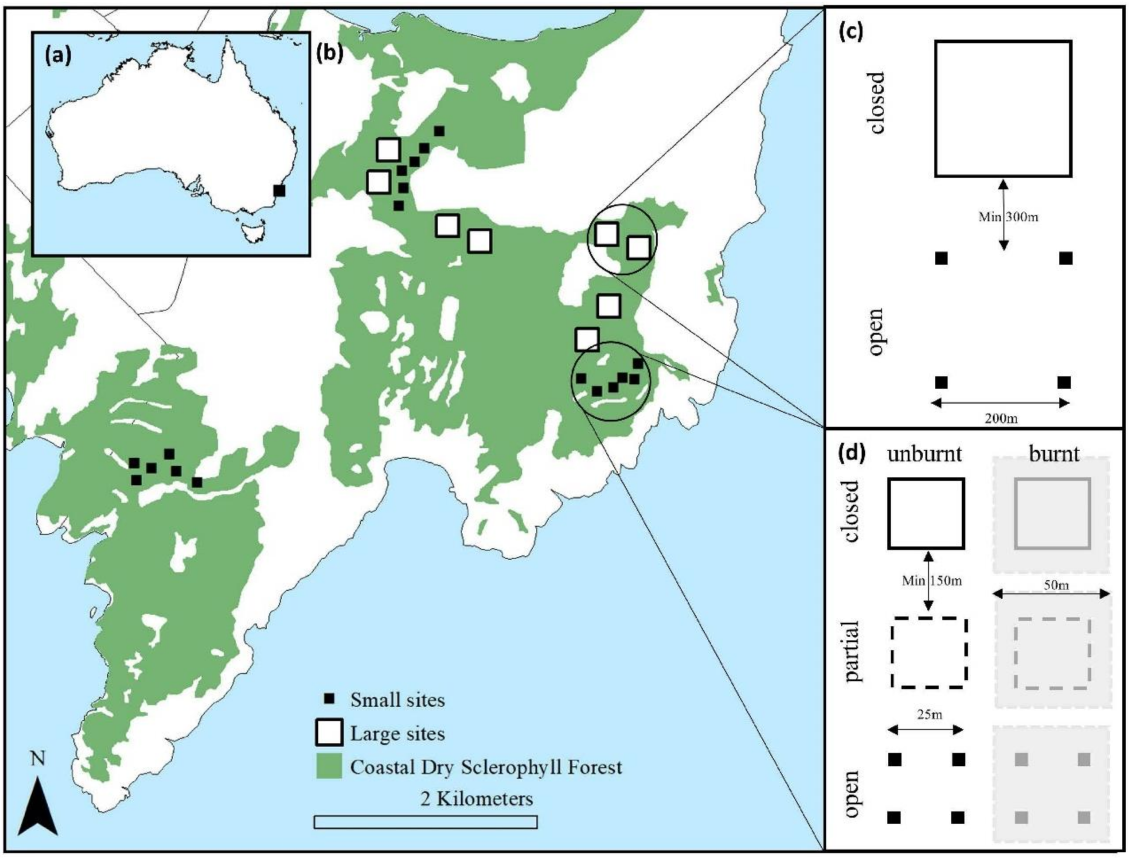

Figure 1: Study location and experimental design showing: (a) Location of Booderee National Park, NSW, Australia (-35.1338°, 150.6860°); (b) The distribution of the large (4 ha) and small (0.0625 ha) plots across the park. All plots were in coastal dry sclerophyll forest (in green) and had been burnt in the 2017 wildfire. Eight large plots were paired into four blocks and 18 small plots were grouped into 3 blocks; (c) and (d) outline the design in each block for both large and small plots respectively. Note half of the small plots were subject to an experimental burn conducted in 2012.

Study design

We quantified the impact of herbivory on fuel properties and fire behaviour predictions using a manipulative field experiment in which we altered herbivore activity. In June 2012, four experimental blocks, each comprised of six 25 m x 25 m (0.0625 ha) plots were established in forest communities. Plots were spaced 150 m apart and experimental blocks were at least 2 km apart. Herbivore activity was manipulated by altering accessibility using three fencing methods: no fencing (open); partially fenced, with gates in the fence being open or closed at two-month intervals (partial or partially-closed); and fenced (closed). Fences were constructed using a 1.1 m tall stock fence and topped with black plastic to increase visibility. Fences are checked and maintained every two months. In August 2012, low severity experimental burns were conducted in half of the plots in each block, to remove 95% of the understory vegetation as part of related research (Foster et al. 2015, 2016). Each block of six plots consisted of a pair of each herbivore exclusion treatment with one being burnt or unburnt by low severity fire in 2012 (Fig. 1d). This facilitated the analysis of two burning treatments across three levels of herbivory manipulation.

In September 2017, a wildfire burnt ~1,600 ha of Booderee National Park. This included three of the four experimental blocks, and an estimated 95% of the understory vegetation was burnt at these plots. The unburnt block was excluded from this study, so all plots had consistent time since fire. To understand whether the effects observed in small exclosure sites could be replicated at larger scales, four additional experimental blocks were established in burnt forest communities in July 2018. The four blocks of two 200 m x 200 m (4 ha) plots were established with plots spaced 300 m apart and blocks situated at least 2 km apart (Fig. 1c). These larger plots were of a similar design to the smaller plots and included a white sighting top-wire to increase visibility. Herbivore activity was manipulated in the larger plots using two fencing treatments: no fencing (open); and fenced (closed). Macropod scat monitoring over the period 2018 to 2020 indicated that while some incursions into large exclosures did occur, herbivore activity was four to five times higher in open than closed plots (Chard et al 2022b). Throughout the rest of the study, we refer to the 0.0625 ha and 4 ha plots as ‘small’ and ‘large’ plots, respectively. For both small and large plots, scat surveys have shown the fencing technique effectively excludes all macropod species in our study area with only minor incursions due to tree falls or other fence damage (Foster et al. 2015, Chard et al. 2022a).

Fire models

We employed three fire modelling approaches to test the effects of large herbivore exclusion on projected fire behaviour. Each of the three fire models we employed incorporated at least one fuel property that large herbivores could potentially influence in a coastal eucalypt forest. The models vary in complexity and use for fire management practices in Australian eucalypt forests (Cruz et al. 2015, Zylstra 2021).

The first, and least complex, model was the McArthur Mk 5 Forest Fire Danger Meter (FFDM, McArthur 1973). The FFDM incorporates data on fuel load, slope, and weather variables (Table S1) to project flame height and rate of fire spread in eucalypt forests (Noble et al. 1980, Cruz et al. 2015). While the FFDM does not account for fuel structure, and hence may not be ideal for investigation of herbivore effects on forest fire, this model has been employed by other studies of animal effects on fire (Nugent et al. 2014, Hayward et al. 2016), and its inclusion therefore allowed for direct comparison with these earlier studies.

The second model, Vesta Mk 2 (Cruz et al. 2021) was selected as it is employed by fire management agencies in Australia, and incorporates some elements of fuel structure, including height and estimated fuel load at several strata in a forest stand. The model also incorporates weather and topographic data, and analyses fire spread in three distinct phases of fire propagation as fire intensity increases (Cruz 2021).

The third, and most complex model, was the Fire Research and Modelling Environment (FRaME, Zylstra et al. 2016, Zylstra 2021). This model was selected as it is able to account for many of the potential effects of herbivores on forest fuel properties, including effects on plant species composition, architecture and spacing in all forest strata (Zylstra et al. 2016). Alongside spatial dimensions, species-specific flammability traits of the dominant plants in the community are incorporated to produce fire behaviour predictions (Zylstra 2021).

Measured fuel properties

We monitored vegetation metrics annually in 2018, 2019, and 2020, one-, two- and three-years post-wildfire (Chard et al. 2022a). To test large herbivore effects on projected fire behaviour, we analysed fuel property measures from data collected in the spring of 2020, three years post-wildfire, being the longest time since fire of our experiment. Further, we included only 2020 data in our modelling and analysis for this paper because, in the vegetation types in our study site, vegetation one- and two-years post-fire does not usually contain sufficient fuel to carry a wildfire (Dixon et al. 2018).

All fuel property surveys were conducted by the same individual (MC) to reduce the potential for observer-induced heterogeneity in the data. In each plot, we conducted surface litter measurements at five survey points in the small plots and nine survey points in large plots, distributed evenly across each plot. At every survey point, we took three measurements of surface litter depth using a ruler and drop circle and recorded the mean of these (Hines et al. 2010). For each plot we calculated the average depth of the surface litter and converted measurements to fuel loads (t ha^{-1}) using a conversion table (Hines et al. 2010).

We measured near-surface and elevated vegetation structure and composition in each plot using five 20 m transects (small plots), and four 50 m transects (large plots) that were evenly distributed throughout each plot. Using the point intercept technique, plant species were recorded at 1 m intervals along each transect. In addition to recording the number and identity of each understory plant species intercepted at each point, we recorded the physical dimensions of dominant plant species by measuring all individuals of species that occurred in at least 10% of points on a single transect (two points for small plots, five points for large plots). The physical traits measured for each individual plant were crown width (parallel with the transect line), height to the base of the crown and height to the top of the crown. Further, the proportion of dead foliage on each plant was visually estimated. We categorised near-surface plants as having contact with the surface fuel from the base of the foliage (i.e., a crown base height of zero). Elevated plants had clear separation between the surface fuel and the first leaf such that a low intensity fire (flame height of less than 0.5 m) may pass beneath elevated plants without consuming much, if any, of it (Hines et al. 2010). These data allowed us to compile for each plot the comprehensive suite of vegetation structure and composition metrics required to implement the FRaME model (Table S1). The mean height of plants in the elevated fuel stratum was also calculated for each plot and used as the measure of elevated fuel height in Vesta Mk2 calculations (Table S2).

In addition to understory vegetation, the FRaME model required measures of midstory and canopy vegetation structure. We measured midstory and canopy vegetation metrics at each plot using a wandering quarter survey (Catana 1963). Surveys began at the north-eastern corner of small plots and the center of large plots. For small plots, one wandering quarter was conducted at a south-west bearing. In large plots, four wandering quarters were conducted, one for each compass bearing (N, E, S and W). From the starting point, for both midstory and canopy strata, the nearest plant was identified within 45° either side of the bearing. After noting the plant species, we then measured the distance to the trunk and crown width with a tape measure. We measured tree crown (top and bottom height) metrics using a clinometer. The proportion of dead material was then visually estimated. From that plant, the next closest plant in the same stratum was identified based on the same bearing, 45° either side, and measurements were repeated. We continued measuring plants until we recorded ten individual plants for each bearing, or the boundary of the plot was reached. As macropods were unlikely to directly modify aspects of the midstory and canopy strata in the timeframe of our study, measures were averaged across each experimental block, so that differences in fuel properties between plots included in fire models were in surface, near-surface, and elevated fuel strata only. Further data required for the FRaME model, such as plant traits, were sourced from existing datasets (Table S1).

Estimated fuel properties

In addition to measured fuel properties, the FFDM and Vesta MK2 models required estimates of dead fuel in the near-surface and elevated strata which we collected at each plot following survey methods developed by Gould et al. (2008). Estimates were made at the same five (small plots) or nine (large plots) survey points at which litter depth measurements were taken. We visually estimated near-surface and elevated fuel hazard scores of dead fuels in a 5 m radius circle of the survey point. Fuel hazard scores ranged from 0 - 4, whereby 0 represented no, or little, dead material present in that stratum and a 4 represented an extreme fuel hazard with high fuel cover and relatively high proportions of dead material (Gould et al. 2008). Fuel hazard scores were averaged for both near-surface and elevated fuels in each plot and converted measurements to fuel loads (t ha^{-1}) using a conversion table (Hines et al. 2010).

Fire behaviour predictions

We modelled flame height and rate of fire spread projected by the three fire behaviour models, using their relevant inputs, under four weather scenarios (Table 1). Three of the weather scenarios were selected to reflect possible wildfire conditions for the study area and were based on the conditions recorded on the day of the three most recent medium to large wildfires that have occurred in Booderee National Park (December 2003, October 2007, and September 2017, Bureau of Meteorology 2021). The fourth weather scenario was the average summer weather for Booderee National Park collated from nearby weather stations (Point Perpendicular Lighthouse and the Jervis Bay Airfield, Bureau of Meteorology 2021). We defined summer as the period between December and January (average conditions derived from 2001 – 2021), due to these months having elevated fire danger rating at the study area. While a summer month, we excluded February as the study area typically experiences high rainfall and relatively high humidity during this month, resulting in reduced fire danger overall (Bureau of Meteorology, 2021).

To further provide fire management context to measured predictions of fire behaviour, we overlayed threshold values of flame height and rate of fire spread to our results which indicate appropriate firefighting responses to wildfires (Table 2). Responses to wildfires include direct, parallel, and indirect methods of fire suppression or mitigation as described by the Department of Fire and Emergency Services (DFES 2014). Direct measures refer to offensive attacks on head fires or fire flanks and require firefighters to be close (< 10 m) to the flame zone. Parallel attacks are conducted at a safe distance from the fire zone whereby containment lines are constructed and backburning is performed to restrict the advancement of a wildfire. Indirect methods are utilised when a wildfire is too intense or dangerous and involves back burning, defending properties, and evacuating people from at-risk areas. All thresholds were adapted from Penney et al. (2019) and include a maximum failure threshold where, facing extreme wildfires, any action is likely to fail.

Table 1: Weather scenario variables used to project fire behaviour measures including temperature (T), humidity (H), wind speed (U10), drought factor (DF) and dead fuel moisture content (MC). Three weather scenarios were selected using weather conditions recorded on the day of the three most recent medium to large wildfires that occurred in Booderee National Park (Bureau of Meteorology, 2021). The fourth weather scenario was the average summer weather for Booderee National Park.

Set	Description	Code	Date	T (C°)	H (%)	U_{10} (km hr^{-1})	DF	MC (%)
1	Wildfire	WF03	22/12/2003	24.3	43.5	22.0	7.5	7.7
2	Wildfire	WF07	29/10/2007	27.1	20.0	32.0	9.3	4.7
3	Wildfire	WF17	14/09/2017	15.6	64.0	20.0	5.5	10.4
4	Summer average	SuAv	Dec-Jan (2001-21)	24.4	21.1	17.0	4.9	4.9

Table 2: Description of threshold ranges and limits indicating the appropriate firefighting course of action to a fire event. Thresholds were adapted from Penney et al. (2019).

Threshold	Method	Techniques employed
Flame height (m)		
0 – 2	Direct	Apply suppressants from handheld attack lines or machines
2 – 3	Parallel	Construct containment lines parallel to the fire line then burn out the intervening fuel
3 – 10	Indirect	Building containment lines, backburning, defending properties and focusing on evacuation of people and livestock.
10+	Fail	Indirect attack likely to fail
Rate of fire spread (km hr^{-1})		
0 – 0.06	Direct	Readily suppressed
0.06 – 0.4	Parallel	Hand tool attack possible only up to 0.14 km h^{-1}, machine attack possible across this range
0.4 – 0.8	Indirect	Building containment lines, backburning, defending properties and focusing on evacuation of people and livestock.
0.8 +	Fail	Indirect attack likely to fail

Data analysis

We analysed fuel properties and fire behaviour predictions of flame height and rate of fire spread in R (RStudio Team 2020). We fitted generalized linear mixed models (GLMM), using the ‘glmmTMB’ function with Gaussian distribution (glmmTMB package, Magnusson et al. 2017), for each response variable from a candidate set of two (small plots) and one (large plots) model. We fitted models using herbivore exclusion treatment (open/partial/closed), and, for small plots the experimental fire treatment (burnt/unburnt) as fixed effects. We also included the experimental block as a fixed effect in all models to account for our study design. We used a separate GLMM to analyse each of the fuel properties of (i) surface litter depth; (ii) plant height and (iii) the cover of plants (hits per 100 points) in both near-surface and elevated strata in each of the exclosure sizes. Similarly, we used a separate GLMM to analyse exclosure treatment effects on fire behaviour predictions of flame height and rate of fire spread from each of the three fire behaviour models (FFDM, Vesta Mk 2 and FRaME) and four different weather scenarios.

For small plots, we used model selection criteria to determine whether to include an interaction between herbivore treatment and fire treatment for each response variable (Murray et al. 2019). We used the ‘model.sel’ function from the MuMIn package to rank each set of models by their Akaike Information Criterion and select the best-performing model, which we defined as the simplest model within 2 AICc of the top-ranked model (Burnham and Anderson 2002).

For all models analysed, we assessed post-hoc analysis of residuals using the ‘simulateresiduals’ function from the ‘DHARMa’ package and were deemed acceptable for all top-performing models (Hartig 2017). We present the results for the best performing models for fuel properties and projected fire behaviour for both small and large plots below.

3.5 Results

Fuel properties

For all fuel properties analysed, the top performing model for the small plots did not include an interaction between herbivore exclusion and the previous experimental burn (Table S3) and the experimental burn conducted in 2012 had no effect on surface litter, plant heights, or the number of plants (Fig. S1, S2). Herbivore activity did not influence surface litter depth in either small or large plots (Fig. 2). Herbivore activity influenced plant heights in small plots but only for the elevated strata (Fig. 3a). In small plots, elevated plant heights were lowest in open plots compared to closed plots. Large herbivores had no impact on near-surface plant height in either small or large plots and no effect on elevated plant heights in large plots (Fig. 3b). In the elevated strata for small plots, there was significantly less plants in open plots compared to closed plots but there was no change in the number of near-surface plants (Fig. 4a). Conversely, in large plots, browsing by large herbivores in open plots reduced the number of plants in near-surface strata compared to the fenced treatment (Fig. 4b). However, in large plots, the number of elevated plants were not impacted by large herbivores.

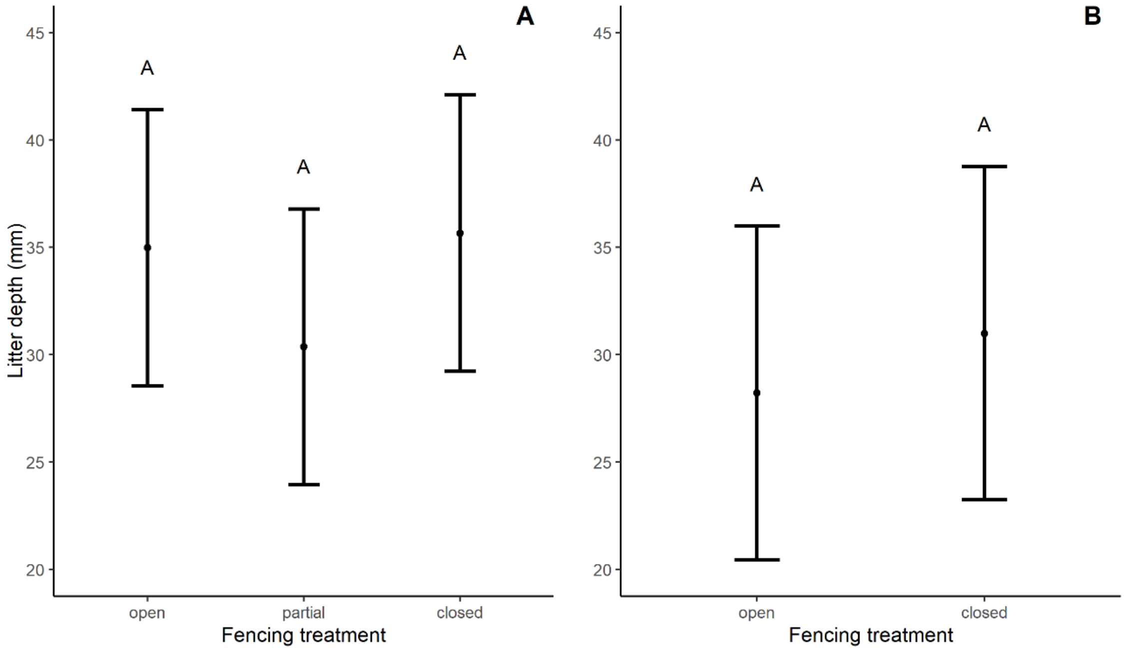

Figure 2: Litter depth measures in small (0.0625 ha) plots (A) and large (4 ha) plots (B) with respect to fencing treatment. Values are model estimated means with 95% credible intervals. Letters above confidence intervals indicate significant differences in surface litter depth.

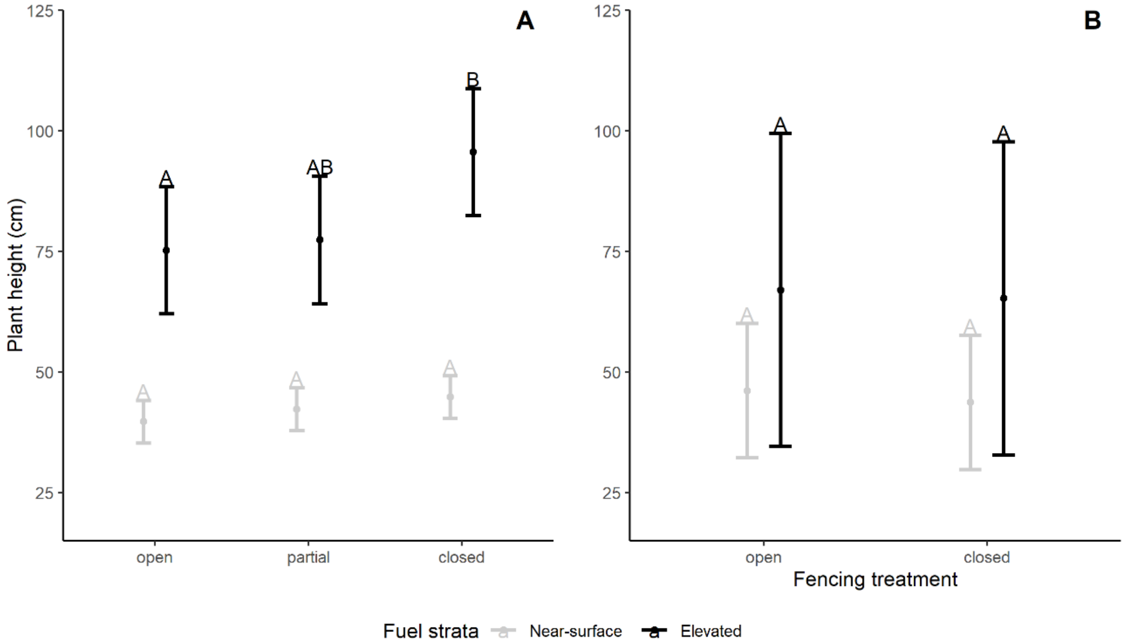

Figure 3: Plant heights at each stratum in small (0.0625 ha) plots (A) and large (4 ha) plots (B) with respect to fencing treatment. Strata levels are near-surface and elevated. Values are model estimated means with 95% credible intervals. Letters above confidence intervals indicate significant differences in plant heights.

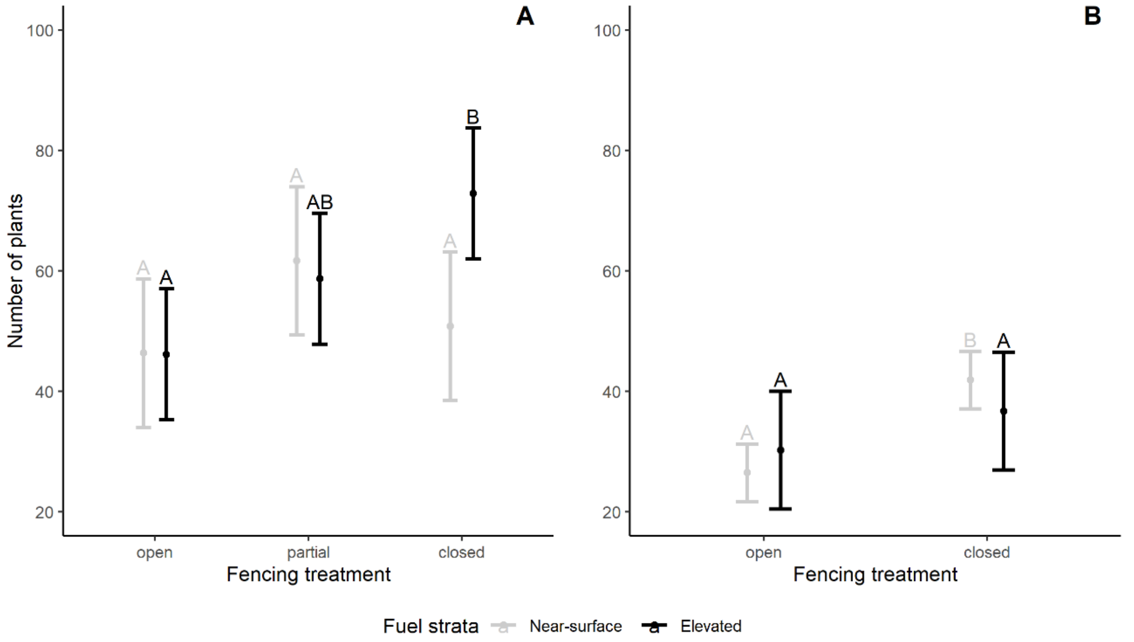

Figure 4: Number of plants (per 100 points) recorded at each stratum in small (0.0625 ha) plots (A) and large (4 ha) plots (B) with respect to fencing treatment. Strata levels are near-surface and elevated. Values are model estimated means with 95% credible intervals. Letters above confidence intervals indicate significant differences in the number of plants.

Fire behaviour predictions

For all three of the fire behaviour models employed, and for each weather scenario, the top model for the small plots did not include an interaction between herbivore exclusion and the previous experimental burn (Table S4). Further, the experimental burn conducted in 2012 had no effect on projected flame height or rate of fire spread for any of the fire models for all weather scenarios (Fig. S3, S4, S5).

For the FFDM, large herbivore activity was not found to influence projected flame height or rate of fire spread in either small or large plots (Fig. 5). In the 2007 wildfire weather scenario (WF07), the maximum threshold levels projected by the FFDM were exceeded for both fire measures in both the small and large plots, indicating firefighting measures were likely to fail (Fig, S6).

For Vesta Mk 2, herbivore activity in small plots influenced both the projected flame height and rate of fire spread in each weather scenario (Fig. S7a, c). In small plots, projected flame height was significantly higher in closed plots compared to the open and partial plots (Fig 5a). Similarly, in the small plots, the projected rate of fire spread was highest in closed treatments compared to the partially-closed plots (Fig. 6c). By contrast, there was no herbivory effect detected in the large plots on fire behaviour predictions using Vesta Mk 2 (Fig. 5b, d). Outputs for the flame heights using Vesta Mk 2 indicated that large herbivores lowered firefighting thresholds under some weather scenarios, with the 2017 wildfire scenario (WF17) revealing a reduced firefighting response required for open and partial plots compared to closed plots (Fig. S7). Further, outputs under the 2007 wildfire weather scenario (WF07) for Vesta Mk 2 were extremely high compared to the other weather scenarios, being above the highest threshold for both small and large indicating a likelihood for failure in controlling a fire (Fig. S7).

For FRaME, large herbivore activity did not significantly alter projected flame height or rate of fire in either small or large plots (Fig. S5). Rate of fire spread predictions using FRaME indicated the potential for the maximum suppression threshold to be exceeded using the 2003 (WF03) and 2007 (WF07) wildfire scenarios in both small and large plots (Fig. S8). The maximum threshold was exceeded across all fencing treatments in the small plots for WF07 and the partial fencing treatment for WF03 (Fig S8c). Similarly, the maximum threshold was exceeded in the large, closed plots for both WF03 and WF07 (Fig. S8d).

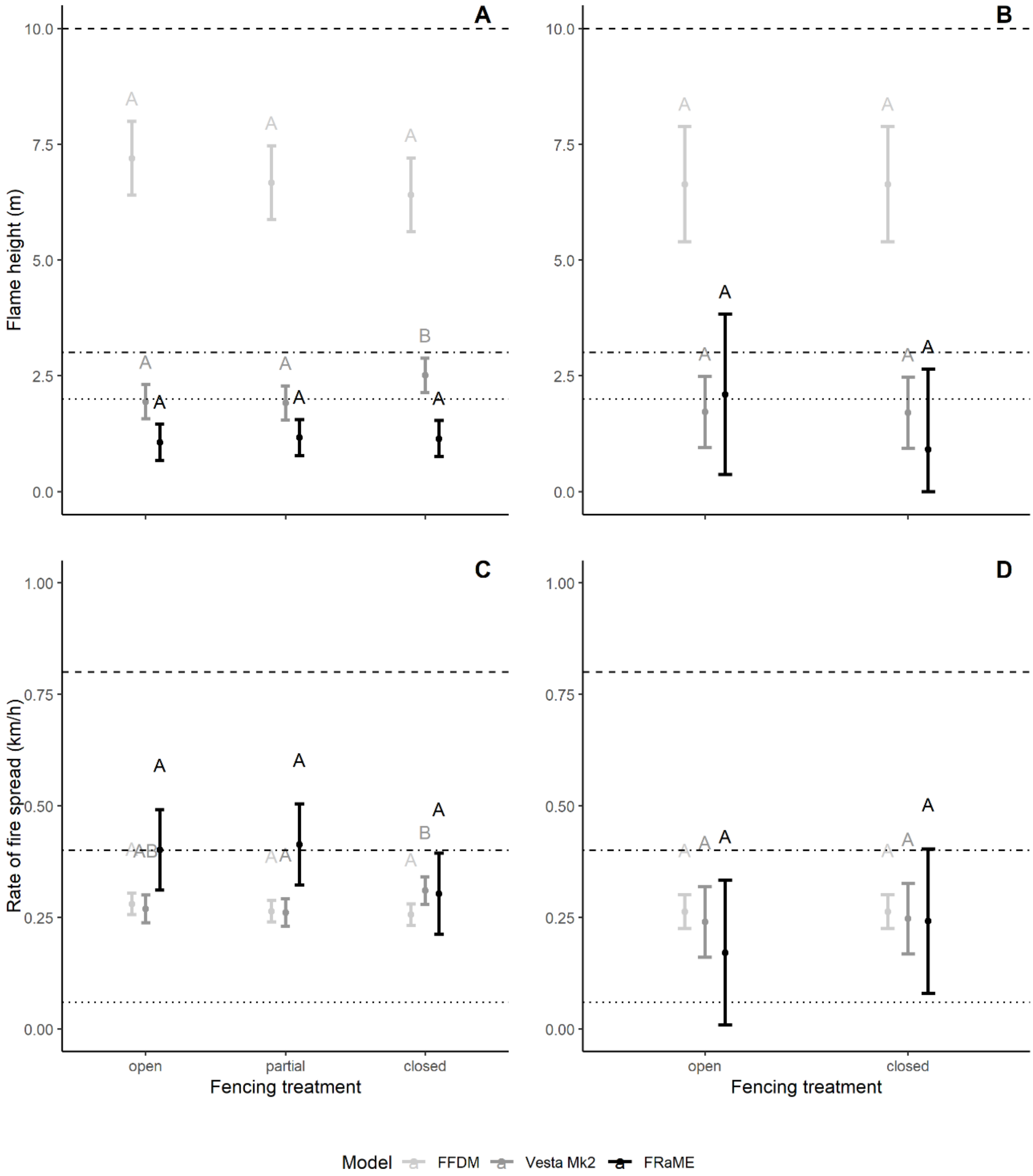

Figure 5: Fire behaviour estimates of flame height (A & B) and rate of fire spread (C & D) produced using three fire modelling methods and equations (see Table S2) in small (0.0625 ha) plots (A & C) and large (4 ha) plots (C & D) with respect to fencing treatment. Models include the Forest Fire Danger Meter (FFDM), Vesta Mk 2 and the Fire Research and Modelling Environment (FRaME). Outputs were produced using the summer average (SuAv) weather conditions (see Table 1). Values are model estimated means with 95% credible intervals. Letters above confidence intervals indicate significant differences of each fire model. Horizontal lines indicate maximum threshold levels of fire management responses employed via direct (dotted), parallel (dot-dash) and indirect (dashed) methods.

3.6 Discussion

Experimental evidence documenting large herbivore influence on fire behaviour in forest ecosystems is limited (Foster et al. 2020). We implemented a manipulative exclosure experiment to address the question: Can post-fire browsing from large herbivores alter projected fire behaviour in coastal eucalypt forests? We found evidence, three years following a wildfire, that herbivore exclusion altered fuel properties and projected fire behaviour. Our key findings were: (1) post-fire herbivory altered some aspects of fuel properties, subsequently producing (2) modified fire behaviour predictions for one fire model; and that (3) large herbivores influenced fire behaviour predictions to a degree that would mitigate the appropriate firefighting responses. Differences in near-surface and elevated plant heights were greater between treatments in the small plots compared to the large plots, suggesting that browsing effects were heterogeneous.

The Vesta Mk 2 model suggested that large herbivore browsing led to lower predictions of fire behaviour in small plots in our study. As Vesta Mk 2 incorporates elevated fuel measures (Cruz et al. 2021), it is likely the reduced average height and number of plants also recorded in small plots subject to herbivore browsing that is driving this reduced fire behaviour. This was expected as large herbivore browsing has been shown to reduce the crown heights of elevated species in the same study area (Chard et al. 2022a). Further, our study found that, when measured across the large plots that incorporated greater heterogeneity, large herbivores did not significantly influence elevated fuels, and no change was predicted in fire behaviour for large plots when using the Vesta Mk 2. If these predictions are reliable, then large herbivores have the capacity to reduce elevated vegetation height and amount in patches of forest ecosystems, thereby calming short-term fire behaviour. If post-fire herbivory is reducing fire behaviour, then fire management practices in forest ecosystems may benefit from measures to support large herbivore populations and encourage browsing in target locations (Rouet-Leduc et al. 2021).

Such expectations may be misleading, however, as pronounced trends were evident in other parameters affected by browsing that were not considered by Vesta Mk 2. While Vesta Mk 2 predicted more severe fire due to the taller elevated fuel stratum evident in small, unbrowsed plots, two other changes occurred to these plants. As reported by Chard et al. (2022a), the base height of the dominant elevated species was higher in unbrowsed plots, and plants were fewer and therefore more widely spaced in unbrowsed plots. Both changes are considered by FRaME - greater base height means that plants are less likely to ignite from below, and greater plant spacing reduces the likelihood of plant ignition by neighbours (Zylstra et al. 2016). If fire is unable to cross these gaps and ignite the plants, then they no longer behave as fuel (increasing fire severity), but instead act as ‘overstorey shelter’, reducing wind speed beneath them and thereby creating a microclimate conducive to less-severe fire (Zylstra et al. 2023).

Despite this, FRaME did not predict a significantly lower suite of fire behaviours, and this reflects the short span of our field data collection. Both parameters describing vertical and horizontal separation between plants continued to increase throughout the three years of survey time (Chard et al. 2022a), therefore we may expect that longer-term monitoring will detect the point at which the effect of the gaps in reducing fire behaviour overwhelms the effect of the taller plants in increasing it.

In addition to these structural changes, previous research in this study area has revealed post-fire browsing by large herbivores altered the vegetation community, resulting in a more depauperate community dominated by unpalatable plants (Foster et al. 2015, Chard et al. 2022a). As FRaME accounts for the flammability of each plant species, and unpalatable plants are (generally) more flammable (Archibald et al. 2019), this may also have contributed to the lower flammability of unbrowsed plots.

The importance of considering all relevant factors may be illustrated by the lack of change in flame height or rate of fire spread predicted using the FFDM fire model. This model utilises only surface fuel load (i.e., litter depth), yet our data indicate that the presence of herbivores had no effect on surface fuel loads, at least during the timeframe of our study.

Considered together then, the comparison between the three models is instructive. The FFDM did not consider any factors affected by (short-term) herbivory, and therefore predicted no effect from it. Vesta Mk 2 considered only those factors that the exclusion of herbivory increased, and therefore predicted increases in flame height and rate of spread due to exclusion. FRaME considered both the factors increased by the exclusion of herbivory (elevated stratum height) and those reduced by it (vertical and horizontal connectivity between fuels), and therefore provided ambiguous results. Given the clear trends in these inputs, it is expected that a definitive answer can only be arrived at using longer-term survey data.

By incorporating the three fire models in our study we provide a greater opportunity for comparison of our study with previous and future studies. Future research should aim to incorporate longer-term fuel monitoring and utilise the appropriate fire models that capture all relevant changes in fuel properties driven by large herbivore browsing, reflecting the current state of wildfire behaviour science.

Under some weather scenarios using the Vesta Mk 2, herbivore activity decreased the projected fire behaviour with respect to fire management thresholds (Penney et al. 2019). Whether this is an accurate prediction, or the opposite occurs due to increasing gap size, such changes are significant as herbivore influence on fire ecology is generally overlooked in fire management decisions in forests (Morgan et al. 2020). Our findings indicate that browsing by large herbivores can potentially modify flame height and rate of fire spread to an extent that is not just statistically significant, but likely practically significant from a firefighting perspective. Until long-term data confirming large herbivore impacts on fire behaviour is available, management practices aiming to address large herbivore populations in forest ecosystems cannot assume their actions will not have important consequences for fire behaviour, and firefighting responses, in these forests.

Our study revealed reduced herbivory effects on both fuel properties and fire behaviour predictions in the large experimental plots. While both plot sizes had the same time since fire, differing results from the two plot sizes may be due to the differences in time since exclosure, the heterogeneity within each plot, as well as the time it took to establish the larger plots following the 2017 wildfire (Chard et al. 2022a). The time that elapsed between the 2017 fire and the completion of the large exclosure fences (10 months) may have allowed herbivores to affect the vegetation community enough to prevent a measured contrast between fenced and unfenced large plots (Chard et al. 2022a). By contrast, small exclosure plots were constructed five years prior to the 2017 wildfire, with measurable differences in vegetation communities (Foster et al. 2016), allowing greater opportunity for ecosystem responses to the herbivory treatment. Herbivore effects on fuel properties and projected fire behaviour in the large plots may become more apparent over a longer study period.

It is important to consider that measured differences between the herbivory treatments of our study may become more distinct 6-12 years post-wildfire when eucalypt forests reach peak flammability (Storey et al. 2016, Dixon et al. 2018) and modifications to plant succession by herbivore browsing are more apparent (Hidding et al. 2013, Silva et al. 2014). Changes in vegetation produce complex, non-linear effects that may confound short-term analyses but demonstrate clear trends over the span of decades (Zylstra 2013, Zylstra et al. 2016). This can lead to flammability dynamics that typically change over the span of multiple decades rather than years, (Zylstra 2018, Lindenmayer et al. 2021, Zylstra et al. 2022).

Despite detecting effects of herbivores on projected fire behaviour, herbivore effects on post-fire vegetation in our study were likely dampened due to the (relatively) large size of the 2017 wildfire. Research has indicated a reduced pyric herbivory response of macropods following large scale fire events (714 ha in Hradsky et al. 2017, ~1,600 ha in Chard et al. 2022a, 2,000 ha in Williamson et al. 2012) compared to studies that reported positive herbivore responses to smaller fires (31 ha in Southwell and Jarman, 1987, 1 ha in Meers and Adams, 2003, 226 ha in Dexter et al. 2013, 0.25 ha in Foster et al. 2015). Smaller fire sizes, coupled with relatively high herbivore densities, may produce more significant changes in fuel properties than observed in this study. As pressure grows for increased implementation of prescribed burning as part of fire management practices for south-east Australia (Morgan et al. 2020), there may be value in considering the impacts of local herbivore populations on flammability. In forests where herbivore browsing produces undesirable outcomes, reducing herbivore browsing density by restricting access to burnt patches, increasing the time since fire of burns or reducing herbivore populations may be appropriate (Forsyth et al. 2012, Read et al. 2021b, Wimpenny et al. 2021). However, if investigations reveal that herbivores are reducing fire behaviour, encouraging large herbivores to browse in locations using frequent, small burns may be an effective way to manage wildfire fuel in these forests (Johnson et al. 2018).

Our experimental design incorporated a previous experimental burn in 2012 as part of related research (Foster et al. 2015, 2016). There was no evidence of a legacy effect from that previous experimental burn in small plots for both fuel properties and fire behaviour. This supports similar findings whereby a previous experimental burn had no influence on vegetation community composition in the same study system (Chard et al. 2022a). Earlier work in these coastal forest ecosystems also revealed a limited influence of fire frequency on plant species richness (Foster et al. 2018). This may indicate the five years between the experimental burn and the 2017 wildfire was sufficient for the regeneration of the understory community and subsequent fuel layer.

A limitation of our study involved how fuel loads were assessed for two of the fire behaviour models. While surface depth was directly measured, other strata were visually estimated as fuel hazard scores. Visual estimations have been shown to overpredict fuel loads at high hazard ratings (Volkava et al. 2016). Fuel hazard scores were incorporated into calculations for the FFDM (near surface and elevated) and Vesta Mk 2 (near-surface). We recommend future research to incorporate destructive sampling to provide objective measures of fuel load in eucalypt forest (Keane 2012).

3.7 Conclusion

Our study highlights an important relationship between fauna, fuel, and fire in eucalypt forests. We demonstrated that potential exists for post-fire herbivory to alter fire behaviour predictions in eucalypt forest communities to a degree that would adjust the appropriate firefighting response, but the nature of that expected change depends largely upon the model in use. Herbivory affected multiple traits in the vegetation, and modelled results differed depending on how many of these traits were accounted for by the models. Critically, if the measured trends in vegetation continued, they would lead to dynamic shifts in behaviour that are only detectable using the most complex of the models (FRaME).

Three contrasting conclusions are therefore possible, depending on the complexity of the model in use and the scale of field data collection. At the simplest level we may not detect any effect of herbivory if we utilise the FFDM, because it does not account for any of the changes in vegetation driven by herbivores. The more complex Vesta Mk 2 accounts for some of these changes and predicts that herbivores may reduce fire risk, but it does not yet consider all parameters affected by herbivores. Pronounced trends in parameters not considered by Vesta Mk 2 are clearly visible in our field data collection, and if these trends continue, we may expect the most complex FRaME modelling to identify critical thresholds in behaviour indicating reduced fire risk where herbivore numbers are lower.

Our study therefore demonstrates that herbivory is likely to be very important to the behaviour of fire, but that accurate detection of its effects requires longer-term monitoring and the use of a model capable of accounting for them.

3.8 Acknowledgements

We acknowledge the Traditional Owners of the land, the Wreck Bay Aboriginal Community, on which our research was conducted. We thank the Wreck Bay Aboriginal Community Council and Parks Australia for supporting this project and assisting with the construction and maintenance of the exclosure fences. We thank the staff of Booderee National Park including (but not limited to) Tyson Simpson-Brown, Phil Brown-Smith, Anthony Roberts, Shane Sturgeon, Nick Dexter, Gavin McLeod and Dion Maple who conducted experimental burns and assisted in the construction of the fences. We would also like to thank those who assisted in the construction of exclosures and data collection: Dylan Cook, Ruth Hollows, Milou Hofman, Sophia Cain, Sean Evans, and Bud Hopkins.

Data availability statement: The data that support the findings of this study are available in Zenodo (zenodo.org/) using the digital object identifier (DOI): 10.5281/zenodo.6855952

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3.10 Supplementary Material

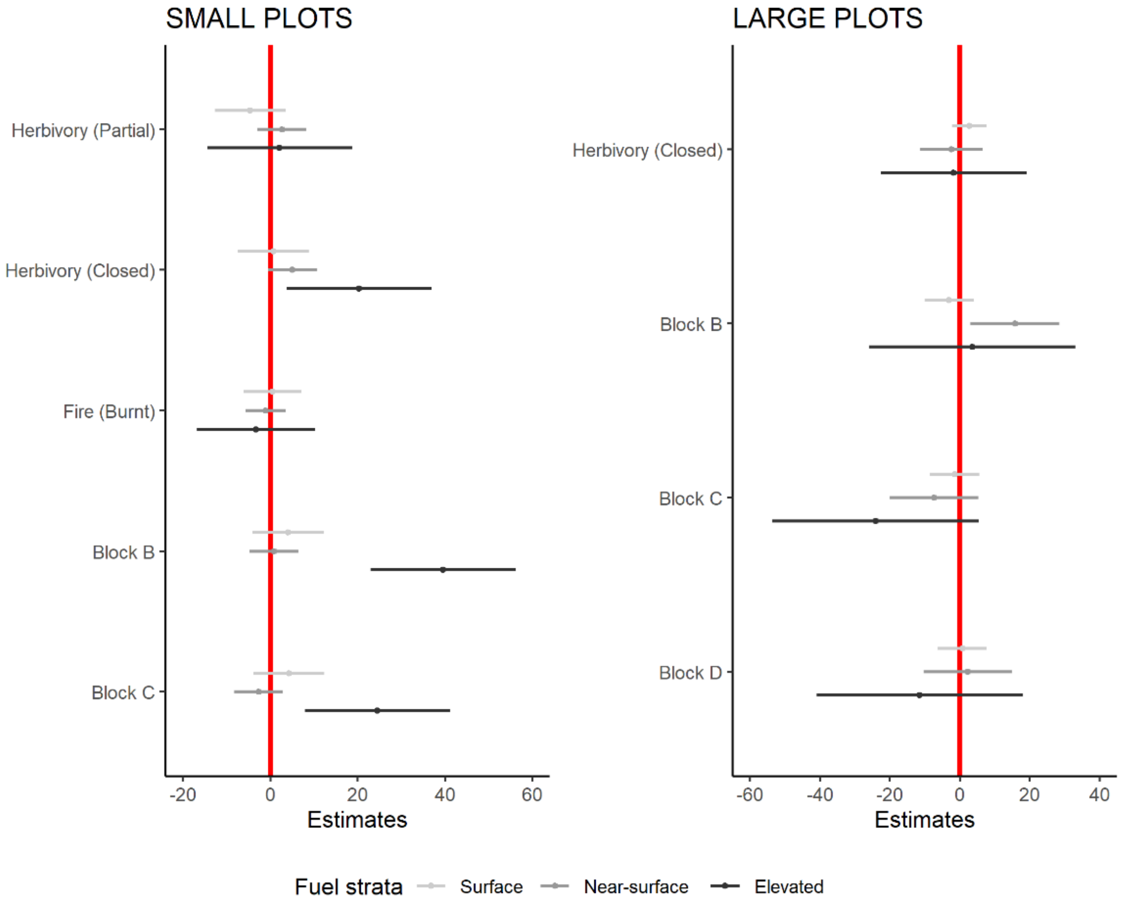

Figure S 1: Effect sizes of the generalized linear mixed model (GLMM) showing estimates of fuel characteristics with 95% confidence intervals from the top performing models. Analysis incorporated surface litter depth and the plants heights at near-surface and elevated strata in small (0.0625 ha) plots and large (4 ha) plots with respect to fencing treatment (open/partial/closed), fire treatment (burnt/unburnt) and block (A/B/C/D). Reference states for comparison were 'Open' plots in 'Block A' (additionally, 'Unburnt' for small plots). Confidence intervals that do not cross the red line denotes statistically significant variables.

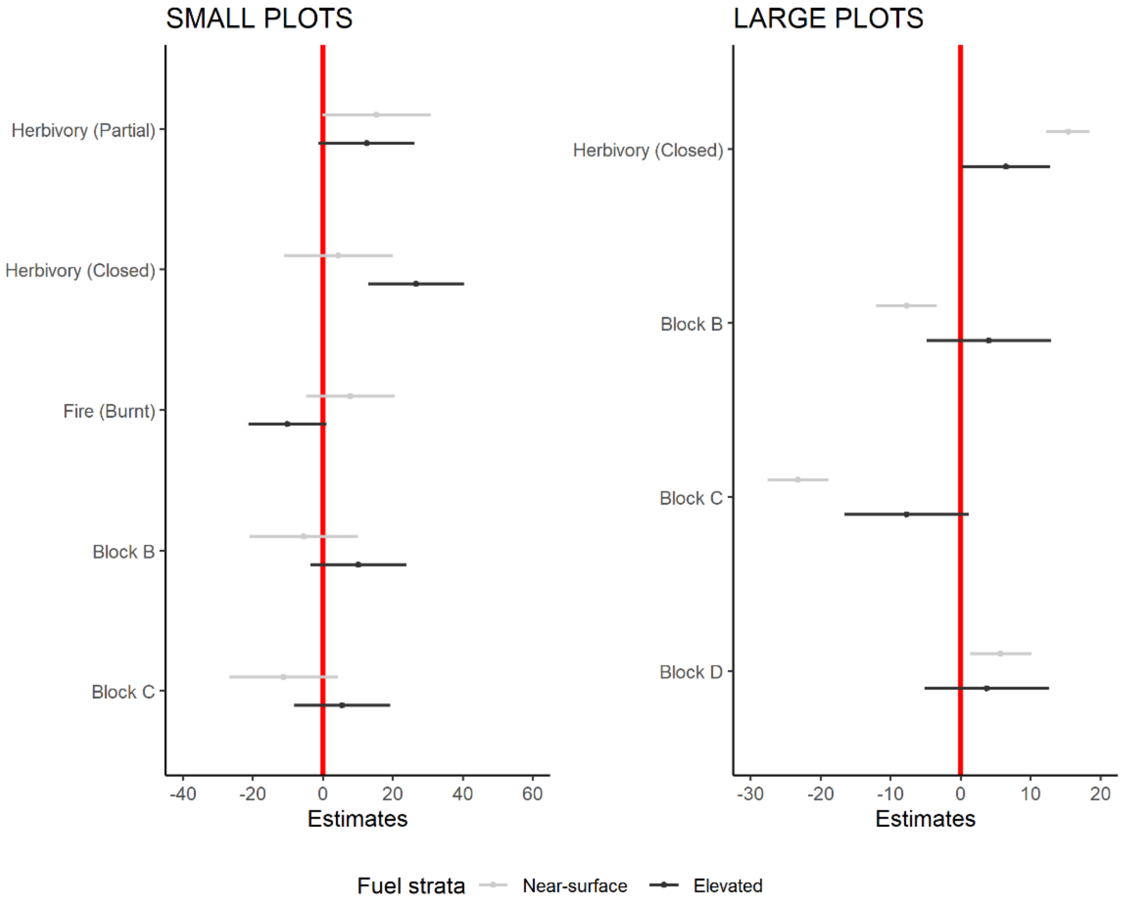

Figure S 2: Effect sizes of the generalized linear mixed model (GLMM) showing estimates of fuel characteristics with 95% confidence intervals from the top performing models. Analysis incorporated the number of plants at near-surface and elevated strata in small (0.0625 ha) plots and large (4 ha) plots with respect to fencing treatment (open/partial/closed), fire treatment (burnt/unburnt) and block (A/B/C/D). Reference states for comparison were 'Open' plots in 'Block A' (additionally, 'Unburnt' for small plots). Confidence intervals that do not cross the red line denotes statistically significant variables.

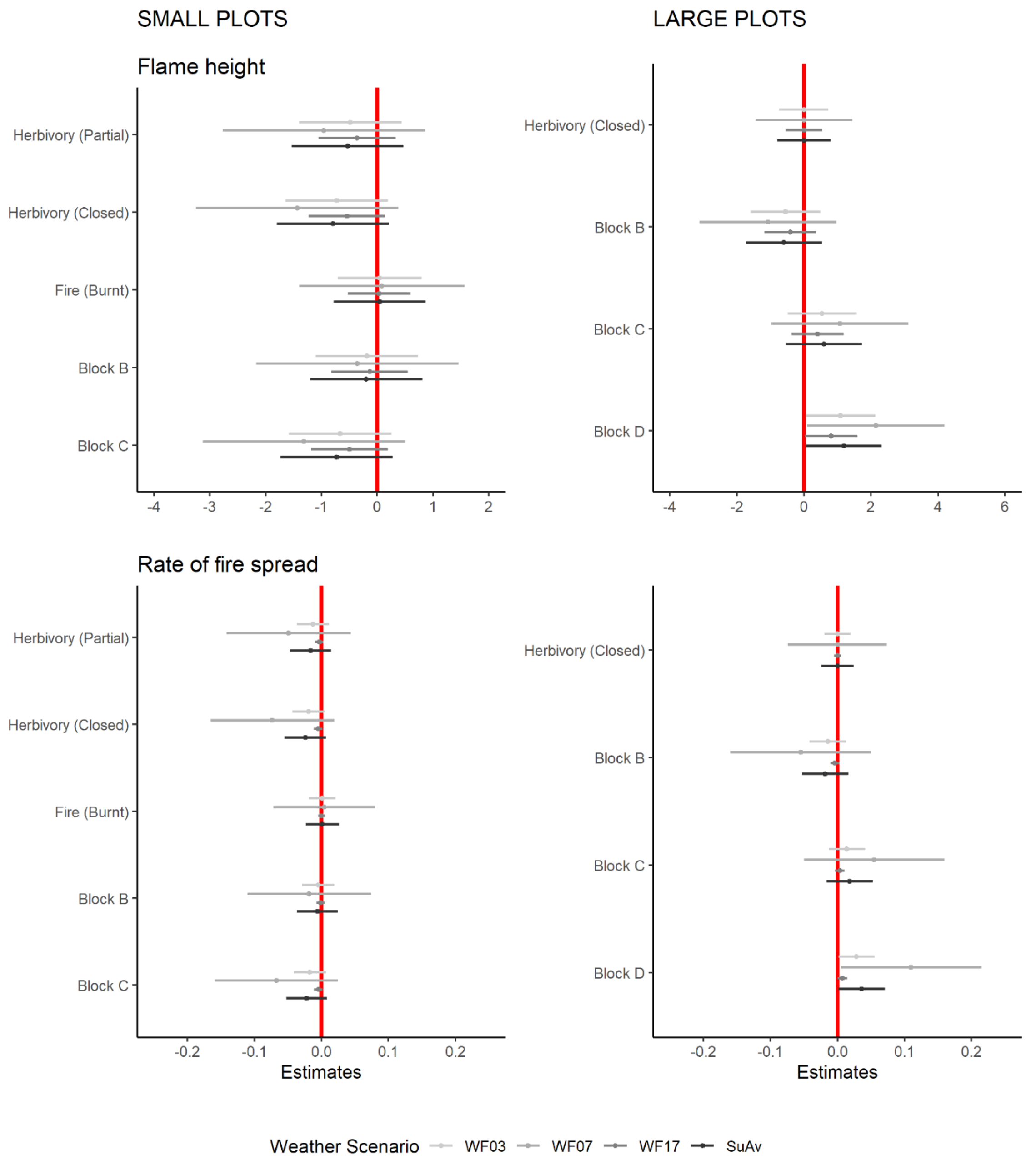

Figure S 3: Effect sizes of the generalized linear mixed model (GLMM) showing estimates of fire behaviour under four differing weather scenarios along with 95% confidence intervals from the top performing models. Analysis incorporated flame height and rate of fire spread calculated using the Forest Fire Danger Meter (FFDM) in small (0.0625 ha) plots and large (4 ha) plots with respect to fencing treatment (open/partial/closed), fire treatment (burnt/unburnt) and block (A/B/C/D). Reference states for comparison were 'Open' plots in 'Block A' (additionally, 'Unburnt' for small plots). Weather scenarios are described in Table 1 of the manuscript. Confidence intervals that do not cross the red line denotes statistically significant variables.

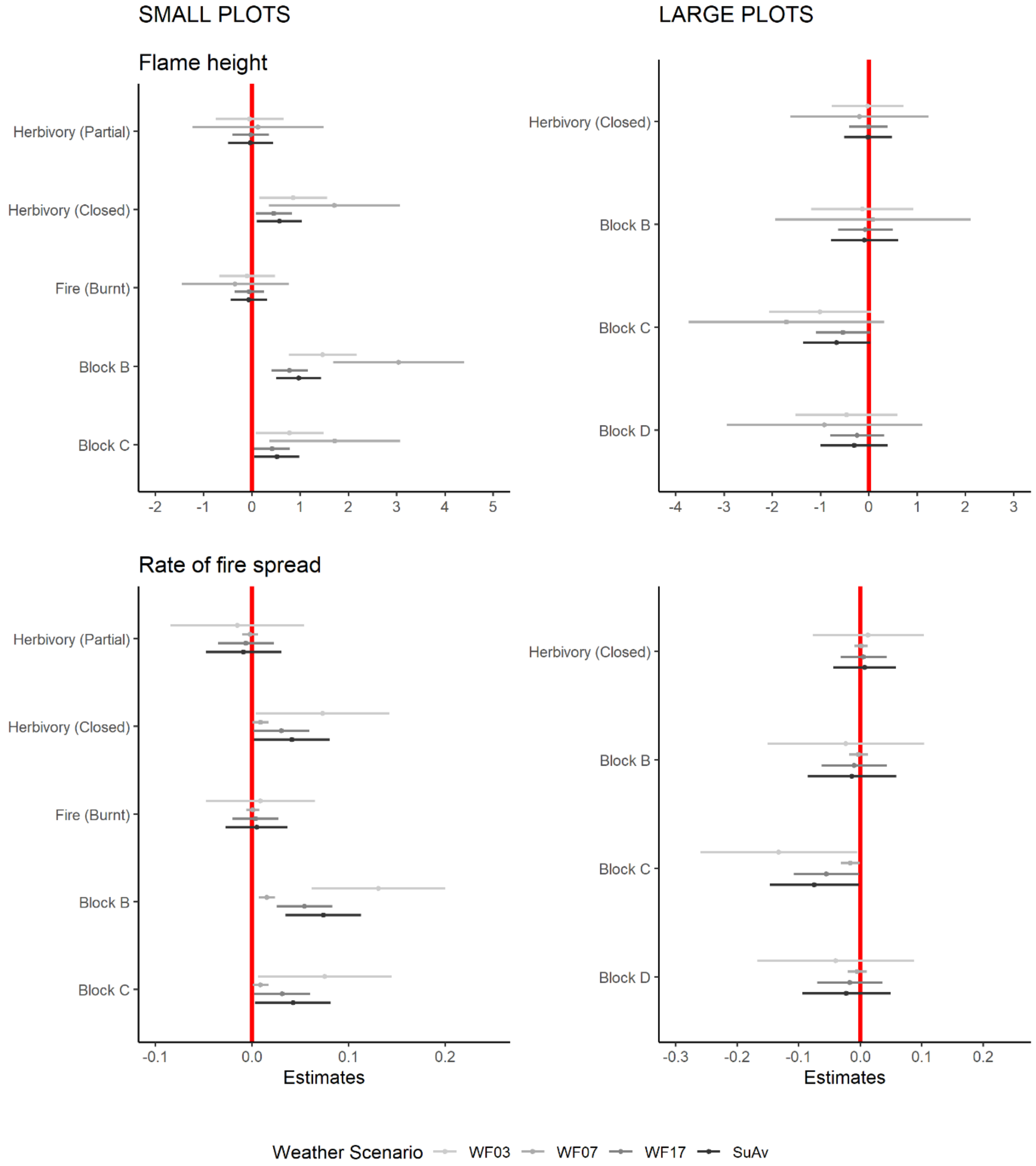

Figure S 4: Effect sizes of the generalized linear mixed model (GLMM) showing estimates of fire behaviour under four differing weather scenarios along with 95% confidence intervals from the top performing models. Analysis incorporated flame height and rate of fire spread calculated using the Vesta Mk 2 in small (0.0625 ha) plots and large (4 ha) plots with respect to fencing treatment (open/partial/closed), fire treatment (burnt/unburnt) and block (A/B/C/D). Reference states for comparison were 'Open' plots in 'Block A' (additionally, 'Unburnt' for small plots). Weather scenarios are described in Table 1 of the manuscript. Confidence intervals that do not cross the red line denotes statistically significant variables.

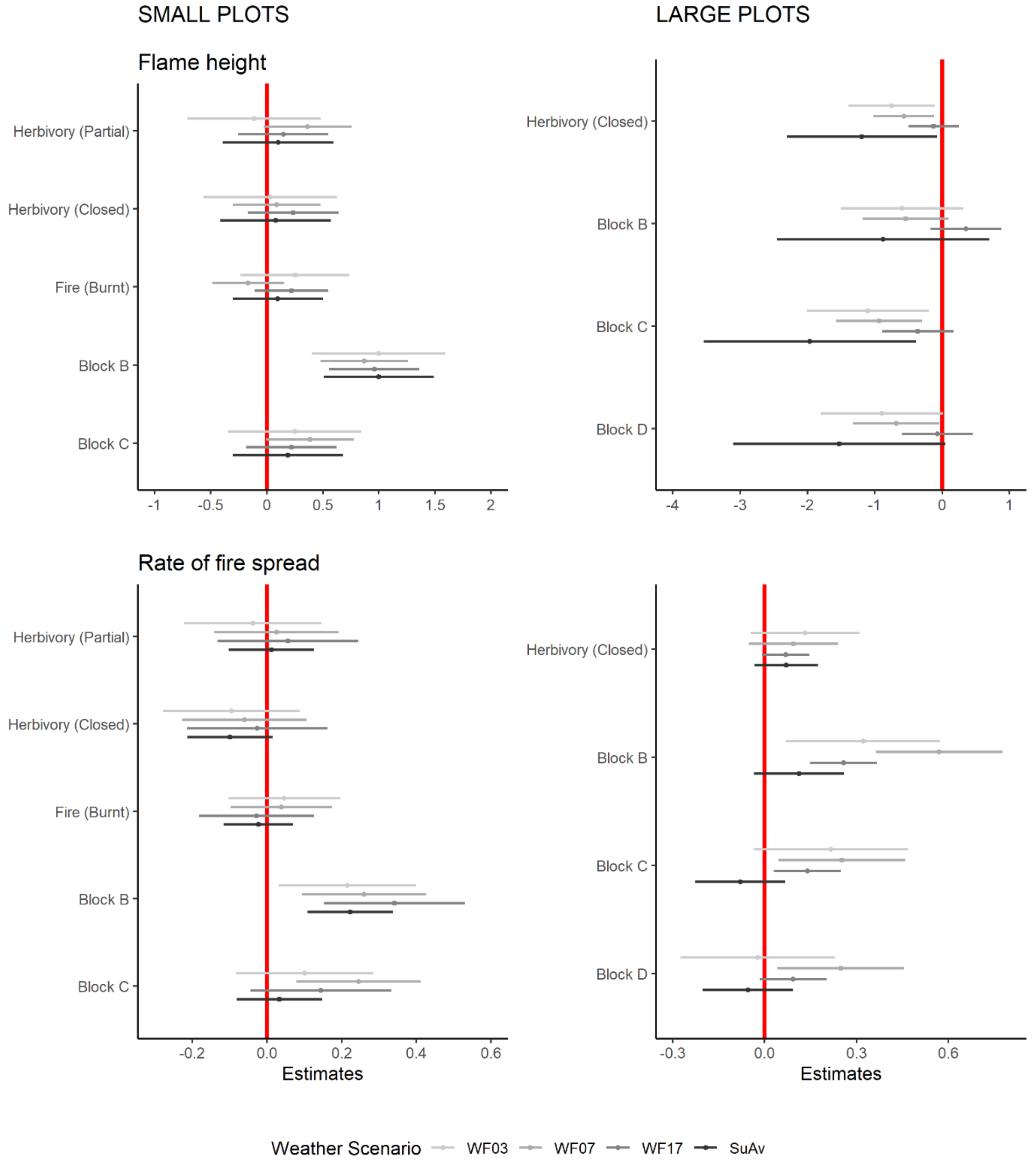

Figure S 5: Effect sizes of the generalized linear mixed model (GLMM) showing estimates of fire behaviour under four differing weather scenarios along with 95% confidence intervals from the top performing models. Analysis incorporated flame height and rate of fire spread calculated using the Fire Research and Modelling Environment (FRaME) in small (0.0625 ha) plots and large (4 ha) plots with respect to fencing treatment (open/partial/closed), fire treatment (burnt/unburnt) and block (A/B/C/D). Reference states for comparison were ‘Open’ plots in ‘Block A’ (additionally, ‘Unburnt’ for small plots). Weather scenarios are described in Table 1 of the manuscript. Confidence intervals that do not cross the red line denotes statistically significant variables.

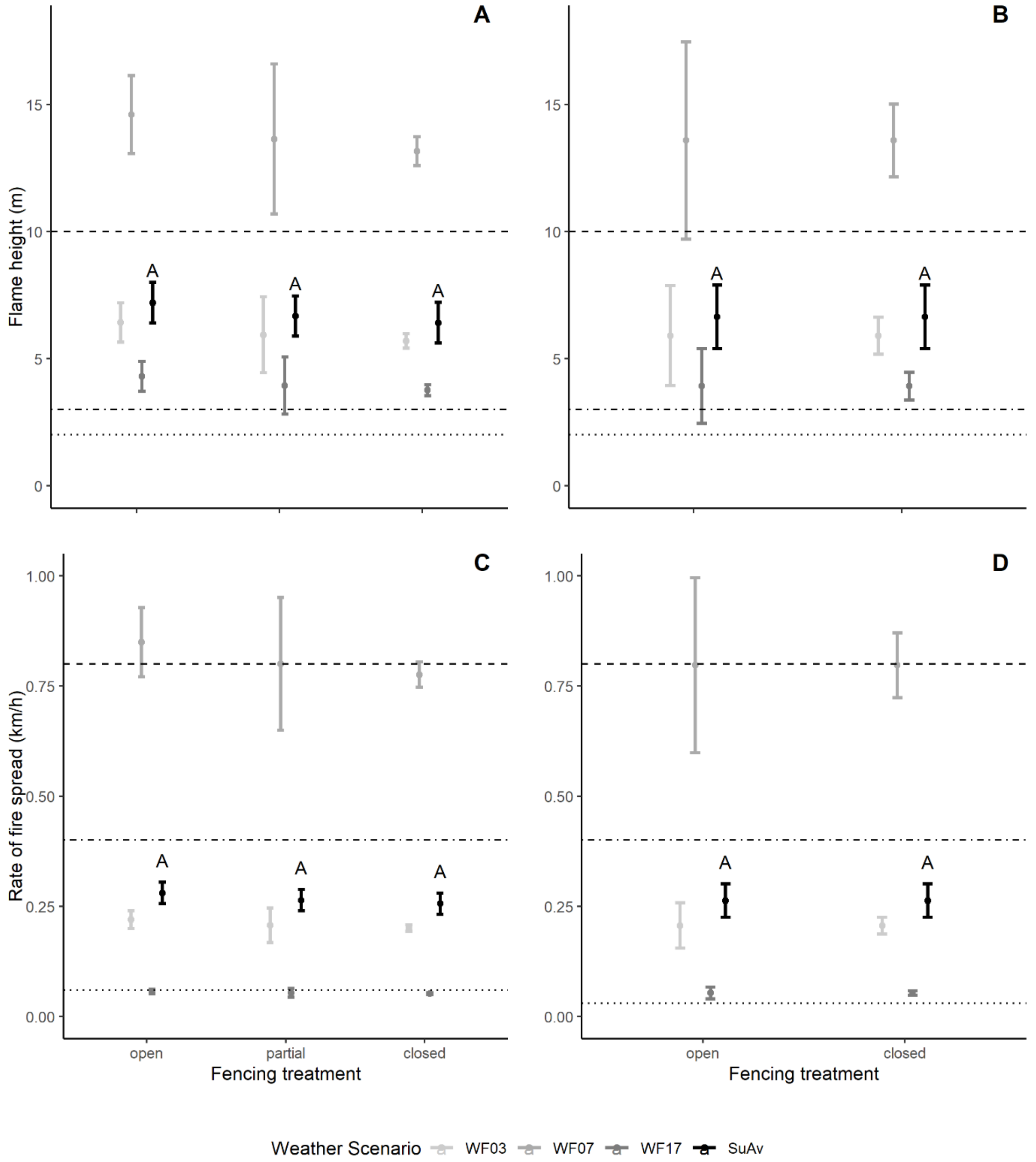

Figure S 6: Effect sizes of the generalized linear mixed model (GLMM) showing estimates of fire behaviour predictions under four differing weather scenarios along with 95% confidence intervals from the top performing models. Analysis incorporated flame height (A & B) and rate of fire spread (C & D) calculated using the Forest Fire Danger Meter (FFDM) in small (0.0625 ha) plots (A & C) and large (4 ha) plots (B & D) with respect to fencing treatment. Weather scenarios are described in Table 1 of the manuscript. Letters above confidence intervals indicate significant differences for the summer average (SuAv) weather conditions. Horizontal lines indicate maximum threshold levels of fire management responses employed via direct (dotted), parallel (dot-dash) and indirect (dashed) methods.

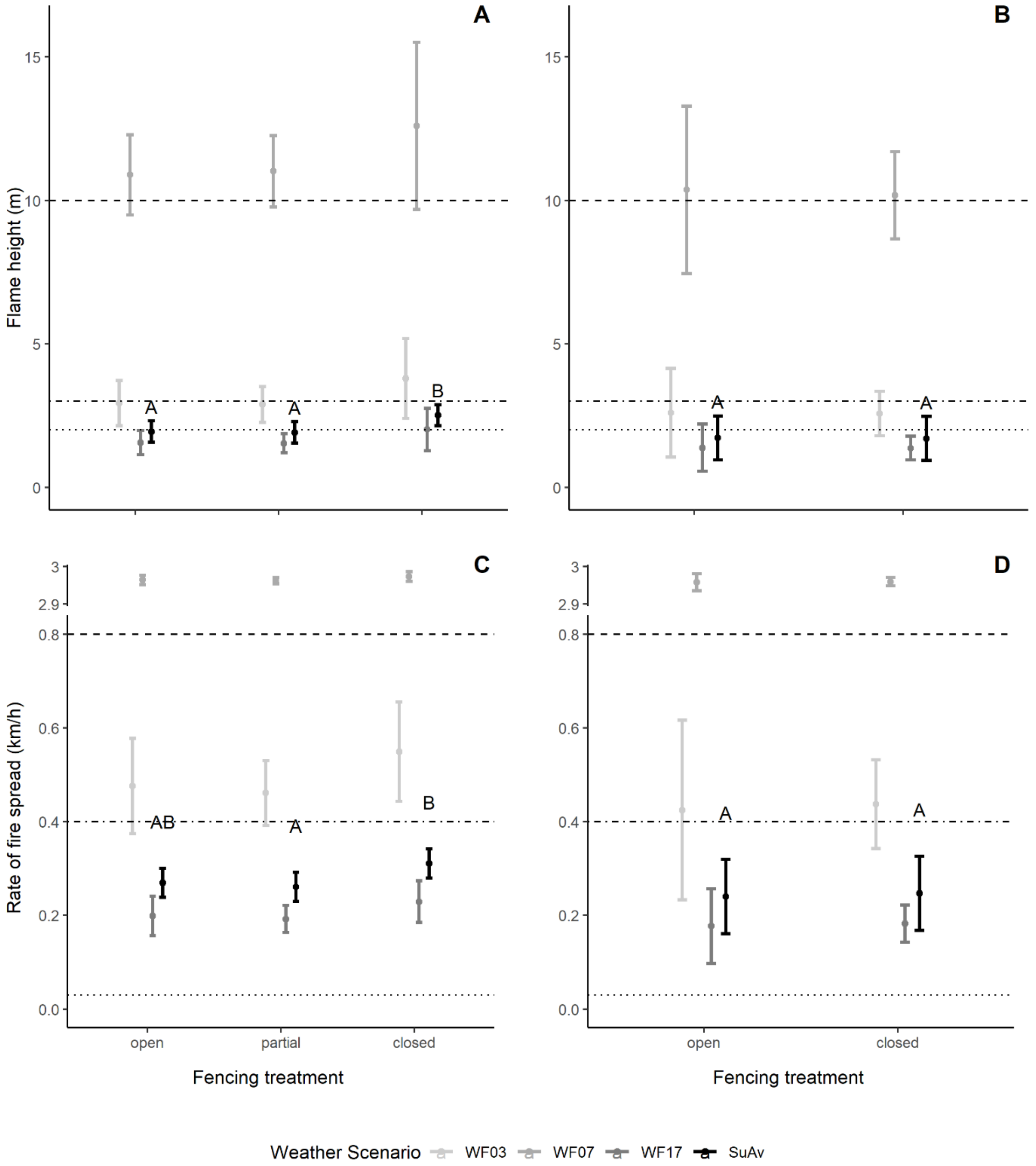

Figure S 7: Effect sizes of the generalized linear mixed model (GLMM) showing estimates of fire behaviour predictions under four differing weather scenarios along with 95% confidence intervals from the top performing models. Analysis incorporated flame height (A & B) and rate of fire spread (C & D) calculated using the Vesta Mk 2 in small (0.0625 ha) plots (A & C) and large (4 ha) plots (B & D) with respect to fencing treatment. Weather scenarios are described in Table 1 of the manuscript. Letters above confidence intervals indicate significant differences for the summer average (SuAv) weather conditions. Horizontal lines indicate maximum threshold levels of fire management responses employed via direct (dotted), parallel (dot-dash) and indirect (dashed) methods.

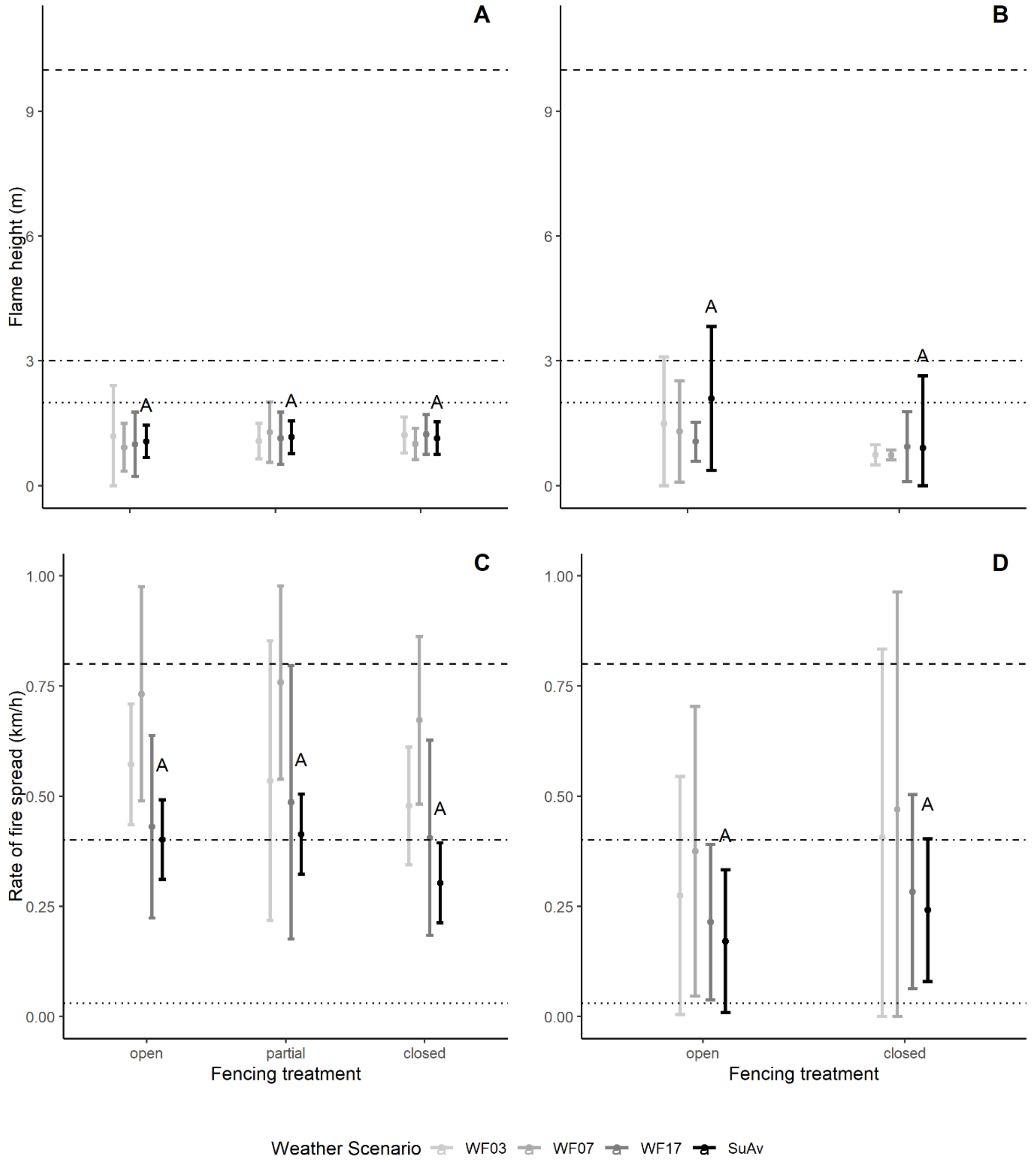

Figure S 8: Effect sizes of the generalized linear mixed model (GLMM) showing estimates of fire behaviour predictions under four differing weather scenarios along with 95% confidence intervals from the top performing models. Analysis incorporated flame height (A & B) and rate of fire spread (C & D) calculated using the Fire Research and Modelling Environment (FRaME) in small (0.0625 ha) plots (A & C) and large (4 ha) plots (B & D) with respect to fencing treatment. Weather scenarios are described in Table 1 of the manuscript. Letters above confidence intervals indicate significant differences for the summer average (SuAv) weather conditions. Horizontal lines indicate maximum threshold levels of fire management responses employed via direct (dotted), parallel (dot-dash) and indirect (dashed) methods.

Table S 1: List of input variables, symbols, units, and source. BOM = Aust Bureau of Meteorology.

Variables	Symbol	Units	Source	Notes
Forest Fire Danger Meter (FFDM) Mk 5				
Temperature	T	°C	BOM	
Humidity	H	%	BOM	
Wind speed	U_{10}	km hr^{-1}	BOM	measured 10 m above ground
Drought factor	DF		BOM	
Slope	θ	°		kept constant at 0°
Total fuel load	W_T	t ha^{-1}	Field	
Vesta Mk 2				
Wind speed	U_{10}	km hr^{-1}	BOM	measured 10 m above ground
Wind adjustment factor	WAF		Cruz (2021)	kept constant at 3.4
Dead fuel moisture content	MC		BOM	
Drought factor	DF		BOM	
Slope	θ	°		kept constant at 0°
Surface fine litter load	W_S	t ha^{-1}	Field	
Elevated fuel height	H_e	m	Field	
Fire Research and Modelling Environment (FRaME)				
Temperature	T	°C	BOM	
Humidity	H	%	BOM	
Wind speed	U_{10}	km hr^{-1}	BOM	measured 10 m above ground
Dead fuel moisture content	MC		BOM	
Slope	θ	°		kept constant at 0°
Fuel load - surface		t ha^{-1}	Field	proportion oven dry weight
Diameter of surface fuel		m	Field	mean value
Fire line		m	Field	
Separation – near-surface		m	Field	distance between plants
Separation – elevated		m	Field	distance between plants
Separation – midstory		m	Field	distance between plants
Separation – canopy		m	Field	distance between plants
Overlap – near-surface/elevated			Field	overlap between strata
Overlap – near-surface/midstory			Field	overlap between strata
Overlap – elevated/midstory			Field	overlap between strata
Overlap – elevated/canopy			Field	overlap between strata
Overlap – midstory/canopy			Field	overlap between strata
Species identification			Field	
Species – moisture of live leaves			Database	proportion oven dry weight
Stratum level			Field	1 (near-surface) to 4 (canopy)
Count of species			Field	
Base height		m	Field	Height to base of crown
Lower edge height		m	Field	Height to lower edge of crown
Upper edge height		m	Field	Height to upper edge of crown
Top height		m	Field	Height to top of crown
Width		m	Field	Width of crown
Openness			Database	Ratio of clumps to clump diameter
Clumping			Database	Ratio of clump to crown volume
Proportion of dead foliage			Field	
Leaf form			Field	flat or round
Leaf thickness		m	Field	
Leaf width		m	Database	
Leaf length		m	Database	
Leaf separation		m	Database	
Stem order			Field	
Ignition temperature		°C	Database	

Table S 2: Equations for predicting fire behaviour for each model and where each equation was sourced. Note that some equations were modified to allow consistency of units across the three fire models.

Models and Equations	Source
Forest Fire Danger Meter (FFDM) Mk 5	**McArthur 1973**
$FFDI = 2 \cdot EXP(-0.450 + 0.987 \cdot \ln D – 0.0345 \cdot H + 0.0234 \cdot U_{10})$	Noble et al. 1980
$R = 0.0012 \cdot FFDI \cdot W$	Noble et al. 1980
$H_f = 13.0 \cdot R + 0.24 \cdot W - 2.0$	Noble et al. 1980
Vesta Mk 2	**Cruz 2021**
$U_2 = U_{10} / WAF$	Cruz 2021
$\Phi M_d = \begin{cases} 1 & \textit{if } MC \leq 4.1\% \\ 0.9082 + 0.1206 \cdot MC – 0.02106 \cdot MC^2 + 0.001853 \cdot MC^3 – 0.00003467 \cdot MC^4, & \textit{if } 4.1\% < MC \leq 24\% \\ 0, & \textit{if } MC > 24\% \end{cases}$	Cruz 2021
$\Phi FA = 1.008 / (1 + 104.9 \cdot EXP(-0.9306 \cdot DF))$	Cruz 2021
$\Phi M = \Phi M_d \cdot \Phi FA$	Cruz 2021
$g(x_1) = -23.9315 + 1.7033 \cdot U_2 + 12.0822 \cdot \Phi M + 0.95236 \cdot (W_s + W_{ns})$	Cruz 2021
$P(II) = \begin{cases} 0, & \textit{if } (W_s + W_{ns}) < 1.0\ t\ ha^{-1} \\ 1 / (1 + EXP(-g(x_1))) & \textit{if } (W_s + W_{ns}) \geq 1.0\ t\ ha^{-1} \end{cases}$	Cruz 2021
$g(x_2) = -32.3074 + 0.2951 \cdot U_{10} + 26.8734 \cdot \Phi M$	Cruz 2021
$P(III) = \begin{cases} 0, & \textit{if } R(II) < 0.3\ km\ h^{-1} \\ 1 / (1 + EXP(-g(x_2))) & \textit{if } R(II) \geq 0.3\ km\ h^{-1} \end{cases}$	Cruz 2021
$R(I) = (0.03 + 0.05024 \cdot (U_2 – 1)^{0.92628} \cdot ((W_s + W_{ns}) / 10)^{0.79928}) \cdot \Phi M$	Cruz 2021
$R(II) = 0.19591 \cdot (U_2)^{0.8257} \cdot ((W_s + W_{ns}) / 10)^{0.4672} \cdot H_e^{0.495} \cdot \Phi M$	Cruz 2021
$R(III) = 0.05235 \cdot (U_{10})^{1.19128} \cdot \Phi M$	Cruz 2021
$R = \begin{cases} R(I) \cdot (1 – P(II)) + R(II) \cdot P(II) & \textit{if } P(II) < 0.5 \\ (R(I) \cdot (1 – P(II)) + R(II) \cdot P(II)) \cdot (1 – P(III)) + R(III) \cdot P(III) & \textit{if } P(II) \geq 0.5 \end{cases}$	Cruz 2021
$H_f = (0.0193 \cdot R^{0.723} \cdot EXP(0.0064 \cdot H_e)) \cdot B$	Cheney *et al*. 2012

B, DEFFM bias correction factor (1.07); D, drought factor; FFDI, Forest Fire Danger Index; ΦFA, fuel availability function; $g(x_{1and2})$, H, humidity (%); H_e, height of elevated fuel (cm); H_f, flame height (m); MC, moisture content (% oven dry weight); M_f, DEFFM fuel moisture function (% oven dry weight); ΦM, fuel moisture effect; ΦM_d, fine dead fuel moisture content effect; P(II & III), probability of a fire spread phase (II and III) to occur; R, forward rate of fire spread (km hr^{-1}); R(I, II & III), rate of fire spread for the respective phase; T, temperature (°C); U_2, 2 m understory windspeed (km hr^{-1}); U_{10}, 10 m open windspeed (km hr^{-1}); W, total fuel load (t ha^{-1}); W_{ns}, near-surface fuel load (t ha^{-1}); W_s, surface fuel load (t ha^{-1}); WAF, wind adjustment factor (3.4). Note: as slope was kept constant across plots, we did not include the slope calculations in the formula.

Table S 3: Model selection and descriptions of the nine generalized linear mixed models (GLMM) analysed for measured fuel characteristics of litter depth, plant height, fuel hazard score (FHS) and number of plants in small (0.0625 ha) plots of differing strata levels. Models in bold indicate the most parsimonious model selected by the least degrees of freedom and delta AICc < 2. Model descriptions relate to the fencing treatment (Herbivory – open, partial, or closed) and previous prescribed burn treatment (Fire – burnt or unburnt).

Strata	***Fuel Property***	***Model No.***	***Model Description***	***DF***	***ΔAICc***
Surface	**Litter Depth**	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	14.55
Near-surface	**Plant height**	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	13.27
	No. plants	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	7.68
Elevated	**Plant height**	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	6.52
	No. plants	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	3.67

Table S 4: Model selection and descriptions of the nine generalized linear mixed models (GLMM) analysed for projected fire behaviour outputs of flame height, rate of spread and fireline intensity in small (0.0625 ha) plots produced from three fire prediction models and four weather scenarios. Fire prediction models include the Forest Fire Danger Meter (FFDM), Vesta Mk 2 and the Fire Research and Modelling Environment (FRaME). Weather scenarios are described in Table 3 of the manuscript. Models in bold indicate the most parsimonious model selected by the least degrees of freedom and delta AICc < 2. Model descriptions relate to the fencing treatment (Herbivory – open, partial, or closed), and previous prescribed burn treatment (Fire – burnt or unburnt).

Fire Model	**Weather Scenario**	**Model No.**	**Model Description**	**DF**	**ΔAICc**
Flame Height					
FFDM	**WF03**	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	15.21
	WF07	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	15.21
	WF17	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	15.21
	SuAv	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	15.21
Vesta Mk 2	**WF03**	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	8.24
	WF07	**1**	***Herbivory+Fire***	**7**	**0.00**

		2	*Herbivory+Fire + Herbivory:Fire*	9	7.34
	WF17	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	8.24
	SuAv	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	8.24
FRaME	**WF03**	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	12.06
	WF07	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	8.74
	WF17	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	12.62
	SuAv	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	9.58
Rate of Fire Spread					
FFDM	**WF03**	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	15.21
	WF07	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	15.21
	WF17	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	15.21
	SuAv	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	15.21
Vesta Mk 2	**WF03**	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	9.32
	WF07	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	9.32
	WF17	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	9.32
	SuAv	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	9.32
FRaME	**WF03**	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	15.20
	WF07	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	15.18
	WF17	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	15.10
	SuAv	**1**	***Herbivory+Fire***	**7**	**0.00**
		2	*Herbivory+Fire + Herbivory:Fire*	9	8.25

Paper IV: Fighting fire with fauna: exploring the potential of using large herbivores to manage bushfire fuel in south-eastern Australia

4.1 Foreword

Following findings that large herbivores have the potential to alter fuel properties (*Paper II*) and fire behaviour (*Paper III*) in forest ecosystems, developing a management plan was the next logical step. However, this synthesis was broadened outside of my study area to encompass the forests of south-eastern Australia. By collating literature on large herbivore effects on vegetation, I viewed these alterations under a fire management lens to determine the potential for using large herbivore populations as a tool for managing bushfire fuel.

Chard, M., Foster, C.N., Lindenmayer, D.B. and Cary, G.J. (2023) 'Fighting fire with fauna: exploring the potential of using large herbivores to manage bushfire fuel in south-east Australia'

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Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with https://policies.anu.edu.au/ppl/document/ANUP_003405

I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multi-author papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

Title: Fighting fire with fauna: exploring the potential of using large herbivores to manage bushfire fuel in south-east Australia

Authors: Chard, M., Foster, C.N., Lindenmayer, D.B., and Cary, G.J.

Publication outlet: Ecological Management and Restoration

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Senior author or collaborating authors endorsement: I, Claire Foster endorse the above contribution statement

Matthew Chard Candidate	MChard Signature	3/15/2023 Date

Endorsed

Claire Foster	C.	15.03.2023
Primary Supervisor – Print Name	Signature	Date
Philip Gibbons	Philip Gibbons	17/3/2023
Delegated Authority – Print Name	Signature	Date

4.2 Abstract

Large herbivores may alter fuel properties in forest communities by modifying vegetation structure and plant communities. While many studies focus on large herbivore effects on vegetation communities, how this may modify future fire behaviour has rarely been examined. We synthesise literature on large herbivore alterations of vegetation, focusing specifically on forest ecosystems in south-eastern Australia. We aimed to assess: (1) how large herbivores impacted forest vegetation, (2) how large herbivores responded to fire in the landscape and (3) the viability of using large herbivore populations in managing bushfires. We found most large herbivores will significantly alter the structure, function, and composition of vegetation communities and they are attracted to recently burnt patches. Evidence suggested that large herbivores may be positively reducing fuel properties in the short-term buy may be contributing to an overall increase in fire risk in the long-term. We discuss options for managing large herbivore populations within forest ecosystems. Future research needs to better understand how large herbivores influence fuel properties and, subsequently, fire behaviour.

Keywords: large herbivores – forest – south-eastern Australia – fuel properties – fire management – bushfire

Implications for Managers:

- Large herbivores can modify aspects of fuel properties that can alter future fire behaviour.

- Modifications to fuel properties by large herbivores may have positive or negative ramifications for fire management practices. Large herbivores that reduce fire behaviour may be a useful tool for reduing future fire risk.
- Resource managers of forests of south-eastern Australia must consider local large herbivore populations in conjunction with fire mitigation efforts.

4.3 Introduction

Vegetation structure and composition is a significant driver of fire behaviour in Australia (Burrows, 1999; Zylstra et al., 2016; Cruz et al., 2021). In the face of increasingly severe fire-weather, due to climate warming, understanding the factors that may modify vegetation communities across Australia will be vital to future fire management (McColl-Gausden & Penman, 2019; Abram et al., 2021). Large herbivores (>2 kg as per Danell, 2006) have the capacity to alter vegetation structure and composition, with research suggesting these modifications may change aspects of fire behaviour (Archibald et al., 2019; Foster et al., 2020; Rouet-Leduc et al., 2021). This warrants investigation of literature that examines whether large herbivore impacts on vegetation communities and, subsequently, fuel properties align with fire management aims.

A major concern in Australian contemporary fire management is the proximity of human habitation with highly flammable forest or woodland (hereafter referred to as forest) ecosystems at the wildland-urban interface (Gibbons et al., 2012; Price & Bradstock, 2014). This is particularly pronounced in south-eastern Australia where human populations are relatively high and built communities often border flammable eucalypt forests (Morgan et al., 2020). Fire management in south-eastern Australian forests is often focused on reducing the loss of human lives and limiting loss and damage of human assets (AFAC, 2012; Royal Commission into Natural Disaster Arrangements, 2020). Current methods to reduce fire risk at the wildlife-urban interface include clearing vegetation (Ximenes et al., 2017) or prescribed burning (Francos & Úbeda, 2021). However, both methods come with significant risk to biodiversity (Driscoll et al., 2010a) and, in the case of prescribed burns, substantial risk of escaped fires (McCaw, 2013), increased air pollution (Broome et al., 2016; Price & Forehead, 2021), and potentially increased future fire activity (Zylstra et al., 2022). Investigating alternative techniques of fuel management may produce lower risk methods of bushfire mitigation.

Understanding the connections between fire, vegetation, and large herbivores may promote more effective fire management in south-eastern Australian forests. In exploring this concept, we posed the overarching question: Could large herbivores be a tool for managing fuel properties in south-eastern Australian forests? We review research that documents how large herbivores influence vegetation communities in south-eastern Australia, as well as how these large herbivores respond to fire. We then explore how the combination of large herbivore effects on vegetation, large herbivore responses to fire, and their potential interactions, may influence fuel properties in a way that could align with (or conversely, be detrimental to) bushfire mitigation.

We review papers from the published literature, using a narrative approach (Pickering & Byrne 2014), limiting our scope to south-eastern Australia. To be included in our review, papers needed to quantify large herbivore effects on vegetation in forest, woodland or tree-dominated ecosystems located in south-eastern Australia (Figure S1). Large herbivores were defined as being >2 kg in weight and primarily forage on vegetation (omnivorous species were excluded; Menkhorst & Knight, 2004). Key findings of large herbivore impacts on vegetation (as described by authors) were extracted and summarised (Table 1). Further searches were conducted on large herbivore behavioural responses to fire in forests of south-eastern Australia. Based on this scope of work, we asked three questions:

1. In what ways do large herbivores alter vegetation?
2. How do large herbivores respond to fire?
3. What is required for large herbivores to be used as a tool for managing bushfires?

Finally, we developed a framework for the management of large herbivores within south-eastern Australian forests with respect to bushfire mitigation.

4.4 Large herbivores of south-eastern Australian forests

Native and introduced large herbivores inhabiting forest ecosystems of south-eastern Australia vary in size, weight, abundance, distribution, home range, foraging strategy, and behaviour, amongst other life history factors (Menkhorst & Knight, 2004; Coulson, 2010). Large native herbivores commonly researched in the context of influencing vegetation are primarily from the *Macropodidae* and include the black (swamp) wallaby (*Wallabia bicolor*), eastern grey kangaroo (*Macropus giganteus*), western grey kangaroo (*M. fuliginosus*), red-necked wallaby (*Notamacropus rufogriseus*), red kangaroo

(*Osphranter rufus*), common wallaroo (*O. robustus*), and Tasmanian pademelon (*Thylogale billardieri*). The two other large native herbivores that impacted forest vegetation were the koala (*Phascolarctos cinereus*) and the common wombat (*Vombatus ursinus*).

Several introduced large herbivores have been shown to influence vegetation communities in south-eastern Australia (Menkhorst & Knight, 2004). These species were either purposefully released for game, escaped captivity, or are agricultural animals (Davis *et al.*, 2016). Non-native species include members of the *Cervidae* such as the sambar deer (*Rusa unicolor*), hog deer (*Axis porcinus*), fallow deer (*Dama dama*), and rusa deer (*R. timorensis*). Other non-native large herbivores include the *Bovidae* - goats (*Capra hircus*), sheep (*Ovis aries*), and cattle (*Bos taurus*) - as well as horses (*Equus caballus*). While other native and introduced large herbivores exist in these systems, studies investigating their impacts on forest vegetation in south-eastern Australia are comparatively lacking (Table S1).

Research investigating herbivore effects on vegetation often also included species below the 2 kg threshold. Where possible, we attempted to extract the specific influence of large herbivores in each study, but this was not always possible with some results reporting the combined effect of all herbivores in the study system. Examples of some native species that did not fall into the large herbivore category, but were investigated, included the common brushtail possum (*Trichosurus vulpecula*); long-nosed bandicoot (*Perameles nasuta*); northern brown bandicoot (*Isoodon macrourus*); and southern brown bandicoot

(*I. obesulus*). Feral rabbits (*Oryctolagus cuniculus*) also were included in several studies.

4.5 In what ways do large herbivores alter vegetation?

Large herbivores may alter vegetation structure, function, and composition through browsing or physical presence in the landscape (Fuhlendorf et al., 2009; Foster et al., 2020). Large herbivore impacts on vegetation communities is driven by the dietary preference, frequency, intensity, and timing of herbivory, as well as the timeframe over which herbivore impacts on vegetation are measured (Morgan, 2021). Further, plant responses to herbivory will also shape vegetation communities (Strauss & Agrawal, 1999).

Large herbivore impacts on vegetation in south-eastern Australian forests include modifications to growth, biomass, composition, structure, diversity, density, survival, damage, dispersal, and soil health (Table 1). Methodologies for quantifying ‘herbivore activity’ included fecal pellet counts (Price & Morgan, 2003; Di Stefano, 2005; Bennett et al., 2020), visual counts (Dexter et al., 2013; Colman et al., 2014), animal tracks (Catling & Burt, 1997; Keith & Pellow, 2005), radio tracking (Di Stefano & Newell, 2008) or through directly assessing herbivore damage to vegetation (Pietrzykowski et al., 2003; Peel et al., 2005; Bilney, 2013). In some cases, manipulative fencing treatments (Allcock & Hik, 2004; Foster et al., 2015; Chard et al., 2022b) or captive trials (Moore, 1994; McArthur et al., 2000) were employed.

Vegetation structure

Changes to plant growth, biomass, and structure by large herbivores is driven primarily by the removal of plant material. Large herbivores have been observed to restrict growth rates of browsed plants in south-eastern Australian forests (Tiver & Andrew, 1997; Di Stefano, 2005). This effect is particularly pronounced on seedlings or regenerating plants, potentially limiting the recruitment capacity for palatable species in the community (Bennett et al., 2020; Bell et al., 2022). Fencing that excluded both native and introduced herbivores has been demonstrated to facilitate seedling growth compared to unfenced areas (Davis & Coulson, 2010; Bennett & Coulson, 2012). Browsing pressure from macropods can reduce overall biomass (Coulson et al., 1990), reduce understory complexity (Colman et al., 2014) and shape the growth of trees and shrubs (Hazeldine & Kirkpatrick, 2015). Conversely, large herbivores in some ecosystems may not impact the vegetation community (Hazeldine & Kirkpatrick, 2015; Mulvaney et al., 2017). However, most studies indicate large herbivores caused a reduction in growth and biomass or a substantial morphological change to the structure of browsed plants.

Large herbivores create trails by moving through the landscape with examples of >10% of the ground surface being covered in animal paths in forest ecosystems in Tasmania (Johnson et al., 2018). The impact of heavier, hard-hooved introduced species such as deer, cattle and horses are likely to cause more damage to plants and compact the soil compared to native herbivores (Atkinson et al., 2019). Further, deer species engage in antler rubbing or thrashing which can significantly damage vegetation communities (Keith &

Pellow, 2005; Peel et al., 2005; Davis et al., 2016). Significant physical damage or browsing pressure from large herbivores may lead to plant mortality (Danell, 2006).

Vegetation function

Plant mortality rates, and subsequent changes in vegetation function, in forests of south-eastern Australia have been experimentally recorded for both native herbivores (Cheal, 1986; Eldridge et al., 2021) and introduced herbivores (Allcock & Hik, 2004; Keith & Pellow, 2005). Fencing experiments have revealed browsing macropod species can reduce the abundance of both introduced and native plant species (Dexter et al., 2013). Similarly, browsing by both macropods and livestock was found to reduce the abundance of seedlings of a native grass *Themeda triandra* (Allcock & Hik, 2004). Large herbivores present a significant threat to regenerative planting efforts whereby planted seedlings need to be protected by physical barriers, such as plant guards, to facilitate plant growth and survival (Bennett et al., 2020). Similarly, manipulative fencing experiments have demonstrated survival rates of plants to be significantly higher when large herbivores are excluded (Allcock & Hik, 2004). Mortality rates of plants can be exacerbated by increases in herbivore populations, unfavorable weather conditions, and disturbances in the landscape (Bell et al., 2022).

Vegetation composition

As large herbivores alter the growth and survivability of palatable plants, this can modify plant succession and shape the composition, diversity, and density of vegetation communities in south-eastern Australian forests (Davis et al., 2016; Morgan, 2021). Fencing experiments revealed browsing reduced species richness, diversity and evenness and promoted the dominance of less palatable plant species (Dexter et al., 2013; Foster et al., 2015; Chard et al., 2022b). Similarly, in mallee woodlands of NSW, the density of *Triodia* species was reduced in browsed plots compared to fenced plots (Bell et al., 2022). Overgrazing by large herbivores threatens the persistence of palatable plants in the understory and may, in extreme cases, cause localized extinctions (Tiver & Andrew, 1997). Grazing by introduced herbivores in arid woodlands of NSW was found to shape vegetation communities, reducing native plant abundance (Eldridge et al., 2018b; Travers et al., 2019). Conversely, grazing by macropods in the same study system had little impact on plant communities (Travers et al., 2019).

Table 1: Large herbivore impacts on forest vegetation communities in south-eastern Australia. Species with a * indicate they are introduced. Methods describe the way in which large herbivore presence/influence was measured whereby: DO, direct observation; En, enclosure; Ex, exclosure; FP, faecal pellet counts; RT, radio tracking; Tr, tracks; V, vegetation analysis. Vegetation responses to large herbivore impacts indicate what aspect was analysed and whether an effect was demonstrated (●), inferred (○), or no effect (—).

	Vegetation											
Species	**Growth**	**Biomass**	**Composition**	**Structure**	**Diversity**	**Density**	**Survival**	**Damage**	**Dispersal**	**Soil Health**	**Method**	**Study**
*Axis porcinus**									●		FP	Davis *et al.* (2010)
	●			●							Ex, Tr	Davis & Coulson (2010)
*Bos taurus**		●			●						Tr, V	Borchard & Eldridge (2012)
										●	FP	Eldridge *et al.* (2017)
		●								●	FP	Vandandorj *et al.* (2017)
					●					●	FP	Eldridge *et al.* (2018a)
										●	FP	Eldridge & Delgado-Barquerizo (2018)
				●	●					●	FP	Eldridge *et al.* (2018b)
					●	●					FP	Travers *et al.* (2019)
					●		●				FP	Travers *et al.* (2018)

					●					●	FP	Eldridge *et al.* (2020a)
										●	FP	Eldridge *et al.* (2020b)
*Capra hircus**	●	○		○		○					FP	Tiver & Andrew (1997)
	●					●					V	Bell *et al.* (2022)
					—			●			Ex, V	Pisanu *et al. (*2005)
					●					●	FP	Soliveres & Eldridge (2014)
										●	FP	Eldridge *et al.* (2015)
										●	FP	Eldridge *et al.* (2017)
		●								●	FP	Vandandorj *et al.* (2017)
					●					●	FP	Eldridge *et al.* (2018a)
										●	FP	Eldridge & Delgado-Barquerizo (2018)
				●	●					●	FP	Eldridge *et al.* (2018b)
					●	●					FP	Travers *et al.* (2019)
					●		●				FP	Travers *et al.* (2018)
					●					●	FP	Eldridge *et al.* (2020a)
										●	FP	Eldridge *et al.* (2020b)
*Dama dama**							●	●			V	Bailey *et al.* (2021)
*Equus caballus**						●		●		●	V, DO	Whinam & Comfort (1996)
								●	○	●	V	Landsberg *et al.* (2001)

	Vegetation											
Species	**Growth**	**Biomass**	**Composition**	**Structure**	**Diversity**	**Density**	**Survival**	**Damage**	**Dispersal**	**Soil Health**	**Method**	**Study**
*Lepus europaeus**										●	FP	Eldridge *et al.* (2017)
		●								●	FP	Vandandorj *et al.* (2017)
					●					●	FP	Eldridge *et al.* (2018a)
				●	●					●	FP	Eldridge *et al.* (2018b)
					○	○					FP	Travers *et al.* (2019)
					●		●				FP	Travers *et al.* (2018)
					●					●	FP	Eldridge *et al.* (2020a)
Macropod sp.	●					●					V	Bell *et al.* (2022)
					●					●	FP	Soliveres & Eldridge (2014)
										●	FP	Eldridge *et al.* (2015)
										—	FP	Eldridge *et al.* (2017)
		—								—	FP	Vandandorj *et al.* (2017)
					—					—	FP	Eldridge *et al.* (2018a)
										●	FP	Eldridge & Delgado-Barquerizo (2018)
				●	●					●	FP	Eldridge *et al.* (2018b)
					—	—					FP	Travers *et al.* (2019)
					—		—				FP	Travers *et al.* (2018)

					●					●	FP	Eldridge *et al.* (2020a)
										●	FP	Eldridge *et al.* (2020b)
Macropus fuliginosus	●						●				FP	Bennett *et al.* (2020)
		●									DO	Coulson *et al.* (1990)
			○	○			●				DO	Cheal (1986)
		●		●		●				●	Ex, FP	Eldridge *et al.* (2021)
Macropus giganteus			●		●		●				Ex, DO	Dexter *et al.* (2013)
			●		●						Ex, FP	Foster *et al.* (2015)
			●	●	●						Ex, FP	Chard *et al.* (2022a)
		●		●		○					FP	Hazeldine & Kirkpatrick (2015)
							●				Ex, FP	Allcock & Hik (2004)
				●		●					DO, FP	Colman *et al.* (2014)
		●		●			●			●	Ex, FP	Eldridge *et al.* (2021)
Notamacropus rufogriseus			○		○		○				Ex, DO	Dexter *et al.* (2013)
			○		○						Ex, FP	Foster *et al.* (2015)
			○	○	○						Ex, FP	Chard *et al.* (2022a)
		○		●		○					FP	Hazeldine & Kirkpatrick (2015)
	○		○				○				FP	Di Stefano (2005)
				●		●					DO, FP	Colman *et al.* (2014)
		●		●							V	Pietrzykowski *et al.* (2003)

	Vegetation											
Species	**Growth**	**Biomass**	**Composition**	**Structure**	**Diversity**	**Density**	**Survival**	**Damage**	**Dispersal**	**Soil Health**	**Method**	**Study**
Osphranter robustus							●				Ex, FP	Allcock & Hik (2004)
Osphranter rufus	○	○		○		●					FP	Tiver & Andrew (1997)
*Ovis aries**	●	●		○		●					FP	Tiver & Andrew (1997)
							●				Ex, FP	Allcock & Hik (2004)
					●		●				DO, V	Moore & Walker (1972)
					●					●	FP	Soliveres & Eldridge (2014)
										●	FP	Eldridge *et al.* (2015)
										●	FP	Eldridge *et al.* (2017)
		●								●	FP	Vandandorj *et al.* (2017)
					●					●	FP	Eldridge *et al.* (2018a)
										●	FP	Eldridge & Delgado-Barquerizo (2018)
				●	●					●	FP	Eldridge *et al.* (2018b)
					●	●					FP	Travers *et al.* (2019)
					●		●				FP	Travers *et al.* (2018)
					●					●	FP	Eldridge *et al.* (2020a)
										●	FP	Eldridge *et al.* (2020b)

Species	Vegetation										Method	Study
	Growth	Biomass	Composition	Structure	Diversity	Density	Survival	Damage	Dispersal	Soil Health		
Phascolarctos cinereus			●	○			●	○			V	Whisson & Shimmin (2006)
		○									FP	Rhind *et al.* (2014)
*Rusa timorensis**				●				●			Ex, FP, Tr	Keith & Pellow (2005)
	●	●	●			●		●			DO, FP, Tr	Hamilton (1982)
					●						Ex	Moriarty (2004)
*Rusa unicolor**				●							Ex, FP	Bennett & Coulson (2012)
			–	–	–						Ex, FP	Mulvaney *et al.* (2017)
		●		●				●			Ex, FP	Bennett (2008)
			●		○						En	Moore (1994)
							●	○			V	Bilney (2013)
									●		V	Eyles (2002)
		●						●			V	Peel *et al.* (2005)
Thylogale billardierii		○		○		○					FP	Hazeldine & Kirkpatrick (2015)
		●						●			En	McArthur *et al.* (2000)
		●		●							V	Pietrzykowski *et al.* (2003)
Vombatus ursinus		–		–		–					FP	Hazeldine & Kirkpatrick (2015)
				●							Ex, FP	Bennett & Coulson (2012)
	○			○							Ex	Davis & Coulson (2010)
		●			●						Tr, V	Borchard & Eldridge (2012)
Wallabia bicolor			●		●		●				Ex, DO	Dexter *et al.* (2013)
			●		●						Ex, FP	Foster *et al.* (2015)
			●	●	●						Ex, FP	Chard *et al.* (2022a)
							●				FP	Price and Morgan (2003)
	●		○				●				FP	Di Stefano (2005)
			●			●					RT	Di Stefano & Newell (2008)
							●				Ex, FP	Allcock & Hik (2004)
				●		●					DO, FP	Colman *et al.* (2014)
				●							Ex, FP	Bennett & Coulson (2012)
	○			○							Ex	Davis & Coulson (2010)

Less evidence exists for large herbivores exerting beneficial influences on vegetation communities in south-eastern Australian forests. Deer have been shown to facilitate seed dispersal of native and weed species in forest communities (Eyles, 2002; Davis et al., 2010). Similarly, browsing by macropods has been shown to improve overall soil health in forest communities, increasing plant species richness and improving soil health via increased litter incorporation and stability (Eldridge et al., 2021). However, grazing by livestock and hares is associated with poorer soil health in arid woodland ecosystems (Eldridge et al., 2015; 2017). More research is required to identify optimal browsing pressure from large herbivores that improves or maintains healthy ecosystem functioning and soil quality (Morgan, 2021).

4.6 How do large herbivores respond to fire?

Before determining how the modification of forest vegetation communities by large herbivores may impact fuel properties, we need to understand how fire drives large herbivore behaviour in these ecosystems. The capacity for alterations to plant communities by herbivores can be compounded by disturbances in the landscape such as fire and land clearing (Archibald et al., 2019). Therefore, how large herbivores respond to fire may dictate herbivore-driven impacts on forest vegetation communities.

Studies of fire-herbivore relationships (often under the banner of pyric herbivory; Fuhlendorf et al., 2009) have revealed that burnt areas may deter some species, likely due to the heightened predation risk from the reduced vegetation cover (Williamson et al. 2012). However, more studies show large herbivores to be attracted to burnt areas, driven by the increased accessibility of nutritious and easily digestible plant matter often referred to as ‘green pick’ (Fuhlendorf et al., 2010; Allred et al., 2011; Matthews et al., 2015; Bielski et al., 2018). Increased large herbivore presence in burnt patches further exacerbates impacts on regenerating vegetation potentially transforming entire vegetation communities (Blackhall et al., 2008; Foster et al., 2015; Bowman et al., 2021; Chard et al., 2022b).

Post-fire herbivore occurrence in forests of south-eastern Australia can be viewed in the context of pyric herbivory (Fuhlendorf et al., 2009). Most findings relate to time since fire responses of large native herbivores (Table 2). Herbivore activity (encompassing presence, abundance, browsing pressure, etc.) has been measured via fecal pellet counts (Meers & Adams, 2003; Styger et al., 2010; Foster et al., 2015; Chard et al., 2022b), camera traps (Hradsky et al., 2017; Geary et al., 2020; Bowman et al., 2021), direct observations (Southwell & Jarman, 1987; Chard et al., 2022a), and tracks (Catling et al., 2001). Generally, large herbivores in south-eastern Australian forests increased in occurrence following fire. This increased occurrence in burnt patches ranged from post-fire timeframes of 14 days (Meers & Adams, 2003), 1 month (Hradsky et al., 2017); 9 months (Foster et al., 2015) and 2 years (Parkins et al., 2019). Further, most insights are focused on macropods and, more specifically, the response of the eastern grey kangaroo, red-necked wallaby, and swamp wallaby (Catling et al., 2001; Foster et al., 2015; Geary et al., 2020; Hradsky et al., 2017a; Chard et al., 2022a). As with other pyric herbivory studies, the main driver for increases in occurrence in post-fire environments was the increased green pick in the understory (Bowman et al., 2021). Only two species were not found to be influenced by fire; the western grey kangaroo (Geary et al., 2020; Senior et al., 2021) and the whiptail wallaby (*M. parryi*; Southwell & Jarman, 1987).

Large fire events (determined by comparative fire size from studies) did not elicit any pyric herbivory responses of large herbivores (Williamson et al., 2012). Conversely, smaller fires attracted large herbivores to burnt areas in the landscape (Foster et al., 2015; Meers & Adams, 2003). This phenomenon appeared to be the case for fires less than ~700 ha and may indicate that larger fires result in less focused foraging pressure in burnt patches, possibly as the impacted area is too large for changes in herbivore behaviour to be noticeable (Chard et al., 2022b). However, analysis of several forest fires in Tasmania, ranging up to 30,000 ha in size, found that fire incidence, not fire size, was the determining factor for macropod occurrence in the landscape (Styger et al., 2010). We encourage future studies to analyse fire size as a response for large herbivore occurrence and provide information on the size of the fire/s being investigated.

Table 2: Large herbivore responses to fire in forest vegetation communities in south-eastern Australia. Methods describe the way in which large herbivore activity/presence was measured whereby: CT, camera trap; DO, direct observation; Ex, exclosure; FP, faecal pellet counts; Tr, tracks. Fire size indicates the size of the fire that analysed, with ranges indicating multiple fires were incorporated or a specific fire event was not selected. Fire response of large herbivores indicate whether herbivore activity increased (▲), decreased (▼), or remained the same (—) post-fire.

Large herbivores	Method	Fire size (ha)	Fire response	Source
Macropus fuliginosus	CT	NA	—	Geary *et al.* (2020)
	DO	<1 – 100,000	—	Senior *et al.* (2021)
Macropus giganteus	Tr	NA	▼	Catling *et al.* (2001)
	CT	NA	—	Geary *et al.* (2020)
	CT	NA	—	Hradsky *et al.* (2017a)
	DO	<1 – 3,000	▲	Chard *et al.* (2022a)
	Ex, FP	0.25	▲	Foster *et al.* (2015)
	Ex, FP	2	▲	Meers and Adams (2003)
	FP, CT	28	▲	Bowman *et al.* (2021)
	DO	31	▲	Southwell and Jarman (1987)
	Ex, FP	1,600	—	Chard *et al.* (2022b)
	FP	2,000	—	Williamson *et al.* (2012)

Notamacropus parryi	DO	31		—		Southwell and Jarman (1987)
Notamacropus rufogriseus	Tr	NA	▲			Catling *et al.* (2001)
	CT	NA		—		Geary *et al.* (2020)
	FP	<1 – 30,719	▲			Styger *et al.* (2010)
	FP, CT	28	▲			Bowman *et al.* (2021)
	DO	31	▲			Southwell and Jarman (1987)
Thylogale billardierii	FP	<1 – 30,719	▲			Styger *et al.* (2010)
	FP, CT	28	▲			Bowman *et al.* (2021)
Vombatus ursinus	CT	<1 – 40,000	▲			Parkins *et al.* (2019)
Wallabia bicolour	Tr	NA	▲			Catling *et al.* (2001)
	CT	NA		—		Geary *et al.* (2020)
	CT	NA		—		Hradsky *et al.* (2017a)
	DO	<1 – 3,000	▲			Chard *et al.* (2022a)
	CT	<1 – 40,000	▲			Parkins *et al.* (2019)
	Ex, FP	0.25	▲			Foster *et al.* (2015)
	CT	714		—		Hradsky *et al.* (2017b)
	Ex, FP	1,600		—		Chard *et al.* (2022b)
	FP	2,000			▼	Williamson *et al.* (2012)

While large, native herbivore species appear to preferentially select for burnt patches within south-eastern Australian forests, data on introduced species are lacking. More generally, deer species in Poland and Portugal have been found to utilise burnt forest patches (Fattebert et al., 2019; Silva et al., 2014) but whether the same behavioural response occurs in south-eastern Australia is unclear. Research on how introduced large herbivores respond to fire in Australian forests is vital to comprehensively understanding fire-herbivore interactions.

4.7 What is required for large herbivores to be used as a tool for managing bushfires?

Large herbivores have been suggested as a tool for altering fuel properties across several ecosystems, including forests, to mitigate bushfire risk (Rouet-Leduc et al., 2021). However, the effectiveness of this approach is dependent on many factors, and undesired outcomes are possible if herbivore impacts, ecosystem properties, and long-term (as well as short-term) repercussions on fuel properties are not carefully considered (Driscoll et al., 2010b; Foster et al., 2020). For large herbivores to alter fire behaviour in forest ecosystems, they must significantly modify fuel properties. This can be in the form of: (1) altering fuel amount, (2) modifying fuel structure, and (3) changing fuel condition (Foster et al., 2020). The impact of large herbivores on aspects of fuel properties will vary with each species (Table 3).

Fuel amount

Fuel amount is the live and dead plant material available to burn (Gould et al., 2008). Reducing fuel amount should reduce the rate of spread and intensity of a wildfire in the short-term (Sullivan et al., 2012). Large herbivores have been considered as a tool to reduce fuel amount under the banner ‘grazing reduces blazing’ (Whittaker & Mercer, 2004), although this notion has been rigorously challenged proving not to be applicable across all landscapes (Williams et al., 2006) and perhaps having the opposite effect in the long-term (Archibald et al., 2019). Most large herbivores present in forests of south-eastern Australia have demonstrated a capacity to reduce vegetation growth or biomass of dominant plant species (Rouet-Leduc et al., 2021). In radiata pine plantations, Tasmanian pademelons and red-necked wallabies suppressed the growth of dominant pine seedlings (Pietrzykowshi et al., 2003). Goats and macropods can reduce the abundance of the dominant grass species, *Triodia scariosa*, in mallee woodlands which readily contributes to fuel amount (Bell et al., 2022). Similarly, browsing by western grey kangaroos showed reduced growth of the dominant buloke (*Allocasuarina luehmannii*) seedlings in semi-arid forest communities (Bennet et al, 2020). Community-wide influences have also been demonstrated to reduce fuel amount with goats, sheep and red kangaroos limiting plant growth and recruitment of more than 50% of plant species in forest ecosystems in South Australia (Tiver & Andrew, 1997). It is likely that diverse understory communities may be more impacted (i.e. reduced fuel amount) by the presence of generalist browsing species such as wallabies or deer (Davis & Coulson, 2010) whereas grazing herbivores like kangaroos, cattle and sheep may be more adept at reducing fuel amount in grass-dominated forest communities (Bell et al., 2022). Nevertheless, large herbivores appear to have the capacity to reduce short-term fuel amount in forest communities of south-eastern Australia.

Fuel structure

Fuel structure refers to the horizontal and vertical connectivity of fuel (Kitzberger et al., 2012). It has been suggested that fuel structure may have a more important role in fire behaviour than fuel amount (Zylstra, 2021). Fuel structure is complex as the spatial arrangement of fuel determines how heat and air flow through vegetation strata, meaning a reduction in fuel connectivity may not result in reduced fire behaviour but, for example, allow for increased air flow subsequently increasing rate of fire spread (Gould et al., 2011; Schwilk, 2015; Cruz et al., 2015, 2021). In forests of south-eastern Australia, trampling by large herbivores disrupts the horizontal connectivity of fuel potentially creating fuel breaks and reducing fire spread (Lovreglio et al., 2014; Chen et al., 2016). In montane vegetation, wombats and macropods have been shown to cover more than 10% of the ground surface in animal trails (Johnson et al., 2018). While detailed investigations have not been conducted, it is likely that most large herbivores in south-eastern Australia will contribute to animal trails in some capacity and that larger, heavier, and hooved herbivores may cause more intense impacts (Phillips & Newsome, 2001; 2002). Altering the vertical connectivity of fuels may reduce the likelihood for fire to 'ladder' into the canopy creating a crown fire (Scott, 2001). Hog deer, swamp wallabies and common wombats can significantly reduce the plant height of several shrub species seedlings, reducing vertical connectivity in coastal forests (Davis & Coulson, 2010). Similarly, the modification of vegetation into 'umbrella-shaped trees' by red-necked wallabies may reduce the likelihood of wildfires reaching the canopy (Hazeldine & Kirkpatrick, 2015). Koalas have also been shown to reduce canopy cover of manna gum trees (*Eucalyptus viminalis*) by half, reducing crown fire potential (Scott, 2001; Whisson & Shimmin, 2006). For comprehensive assessments on fuel structure, analysis using wildfire modelling that incorporates the spatial arrangement of fuel within forest ecosystems is required (Zylstra, 2021).

Fuel condition

The last fuel property large herbivores may influence is fuel condition, which is the chemical composition of fuel encompassing moisture content, Carbon:Nitrogen ratio, Carbon:Phosphorus ratio and concentration of volatile oils (Keane, 2012). Alterations in fuel condition will influence the ignition potential, rate of fire spread, and fireline intensity (Nelson, 2001). Generally, plants that are more flammable tend to have lower moisture content, higher C:N and C:P ratios, and higher concentrations of volatile oils (Archibald et al., 2019). Consequently, more flammable plants are less palatable, with large herbivores in south-eastern Australian forests preferentially selecting plants with higher moisture, lower C:N and C:P ratios and less volatile oils (Archibald et al., 2019; Morgan, 2021). While foraging impact will depend on the abundance and resilience of plant species, as well as the palatability of neighbouring plants, large herbivores have been shown to promote the dominance of unpalatable species in the understory (Dexter et al., 2013). Browsing by koalas on Kangaroo Island reduced canopy cover which subsequently transformed the understory to be dominated by the unpalatable, and highly flammable, bracken fern *Pteridium esculantum* (Whisson & Shimmin, 2006). Further, as fire activity can drive the increased dominance of flammable plants (Pausas et al., 2017), large herbivores that forage in burnt patches may be contributing to an understory dominated by flammable plant species as palatable plants are removed (Chard et al., 2022a). Swamp wallabies can also promote the dominance of bracken fern following fire in coastal forests (Foster et al., 2015, 2016; Chard et al., 2022b). Long-term investigation into large herbivore influence on plant diversity of forest communities is required to determine how herbivory influences fuel condition and whether fire behaviour is modified.

The timeframe of large herbivore influence on fuel properties is crucial. Large herbivore effects on fuel properties should be assessed both between fire seasons (short-term), and over multiple fire seasons (long-term). For example, it is likely that large herbivore browsing will reduce fuel amount and fuel structure between fire seasons, however continued browsing pressure over multiple fire seasons may alter plant community succession leading to the dominance of more flammable species in the long-term and increased fire risk (Archibald et al., 2019). Browsing by macropods in coastal eucalypt forests of south-eastern Australia has revealed short-term reductions in plant height but, over 3-8 years transformed the understory community to be less diverse and dominated by flammable plant species such as bracken (Chard et al., 2022b). Long-term research on this topic is generally lacking and extending the time frames of studies may provide more insight into temporal shifts in fuel properties caused by large herbivores.

Table 3: Assumed influence of large herbivore species on fuel properties in forest vegetation communities in south-eastern Australia. Species with a * indicate they are an introduced species. Assumptions are based upon relevant literature pertaining to herbivore impacts on vegetation communities and responses to fire. Mechanisms that large herbivores may influence include: (1) fuel amount; the amount fine fuel available at surface, near-surface, elevated and bark stratum; (2) fuel structure; the density and vertical/horizontal continuity of fuel; and (3) fuel condition; the chemical composition or flammability of understory plants in relation to C:N ratio, volatile oils, and moisture content. Fuel alterations by large herbivores indicate whether herbivore species may increase (▲), decrease (▼), or not effect (—) that aspect of fuel with respect to the resulting fire behaviour. Blank spaces indicate that sufficient data is not available to estimate influence on fuel properties.

Large herbivores	**Fuel**		
	Amount	Structure	Condition
*Axis porcinus**	▼	▼	
*Bos taurus**	▼	▼	
*Capra hircus**	▼	▼	
*Dama dama**			
*Equus caballus**	▼	▼	

*Lepus europaeus**	▼		
Macropus fuliginosus	▼	▼	▲
Macropus giganteus	▼	▼	▲
Notamacropus rufogriseus	▼	▬	
Osphranter robustus			▲
Osphranter rufus			
*Ovis aries**	▼	▼	▲
Phascolarctos cinereus	▼	▼	
*Rusa timorensis**	▼	▼	▲
*Rusa unicolor**	▼	▼	▲
Thylogale billardierii	▼	▼	
Vombatus ursinus	▼	▼	
Wallabia bicolor	▼	▼	▲

4.8 Management plans for large herbivores

We developed a framework to assist management decisions about large herbivore influence on fuel properties in south-eastern Australian forests (Table 4). Depending on the immediate and historical relationship between fire, vegetation and large herbivores, resource managers may apply multiple strategies to utilise large herbivores to achieve management aims (Figure 1). We further detail management options for facilitating or reducing large herbivore populations within south-eastern Australian forests.

Promoting large herbivores

For large herbivores to be utilised as a fuel management tool, steps need to be taken to benefit the presence and persistence of large herbivore populations. For example, the removal of feral predators is one method that can promote large herbivore abundance. The removal of the invasive red fox (*Vulpes vulpes*) increased macropod populations in a coastal forest (Dexter et al., 2013). Alternatively, if large herbivores engage in pyric herbivory, undertaking prescribed burns may not only reduce (short-term) fuel amount but provide a secondary reduction in fuel properties by attracting large herbivores to burnt areas (Rouet-Leduc et al., 2021). As large herbivore impacts are less evident following larger burns (Chard et al., 2022b), employing smaller burns may encourage focused foraging in target areas, maintaining reduced fuel in these locations than through burning alone. Conversely, if the large herbivores present prefer to forage in unburnt areas, then reducing prescribed burn effort or increasing the time between burns may (counterintuitively) reduce fuel in forest communities.

Table 4: How to determine if large herbivores can be used as a tool for fuel management in south-eastern Australian forests.

Step	*Explanation*
1. Develop management aims with respect to fire management	Establish fire management aims within the area whether that be asset protection, fire severity reduction, biodiversity conservation or a combination of these. What are the methods that are being employed, or could be employed, within the area? This may include prescribed burns, land clearing for fire breaks or regenerative planting. If prescribed burning is a possibility, compile the limiting factors for undertaking this action (optimal weather, season, timing, location, etc.). Prescribed burns may be undertaken to reduce available fuel in conjunction with healthy ecosystem functioning by breaking up the landscape with mosaic burns (Bradstock *et al.*, 2005).
2. Consider historical context of the landscape	Understand the fire history and vegetation community within the management zone. Map aspects of the local fire regime such as frequency, size, severity, type (wildfire or management). Are fire trends changing in frequency or severity? Similarly, map vegetation across the management zone. Compare with historical records to identify any shifts in vegetation communities. Ascertain critical areas that are biologically significant (e.g. threatened communities) or are on the wildland-urban interface posing the greatest threat to humans/assets.
3. Determine large herbivore presence	Identify which, if any, large herbivores are present within the management area. This may be achieved through one or more of the following methodologies: direct observation, faecal scat surveys or camera traps. Seek expert help if unsure about species identification. Again, consider the historical context of the herbivores present in the

	system. Are there any species that are now locally extinct and are any species recent colonisers? Estimate the relative density of each of the large herbivore species. Faecal accumulation rate surveys are often the most appropriate methodology to determine this in forest ecosystems (Coulson *et al.*, 2021). Compare density estimates with historical records to understand population dynamics. Are large herbivore populations increasing, decreasing, fluctuating, or remaining constant?
4. *Determine how large herbivores will impact fuel characteristics*	After collating the large herbivores present, and their relative densities, determine how they may impact fuel properties. This may be achieved by assessing their foraging strategies including, but not limited to: - Browser or grazer - Native or introduced - Forage in groups or individually - Behaviour responses to fire (attracted or deterred by burnt patches) This should be considered in conjunction with the vegetation community of the management area. For each species, assess how they may impact fuel amount, fuel structure and fuel condition. Further, consider the short- and long-term implications of large herbivore impacts as short-term benefits may have negative repercussions in the long-term. Employing fire behaviour modelling may provide a clearer understanding of large herbivore impacts. Fire behaviour modelling may require control sites in which large herbivore access is restricted.
5. *Assess management aims and apply appropriate measures*	Consider how each large herbivore species may be influencing fuel properties and whether this aligns with fire management aims (see Figure 1). If large herbivores are assisting, then populations may need to be encouraged in the landscape. Removing feral predators may facilitate increased populations of large herbivores. This also needs to be

	considered alongside feral herbivore control as introduced large herbivores may have other detrimental influences on ecosystem health. If large herbivores engage in pyric herbivory, conducting small, intermittent burns may exacerbate large herbivore impacts as they focus their foraging effort in burnt patches. Further, where appropriate, other large herbivore species may be encouraged into the area if they are perceived to benefit both fire management and biodiversity. Conversely, if large herbivores are detrimental to fire management aims, actions may need to be taken to reduce or remove their impact. This may be achieved through culling, fencing, or introducing biological controls (e.g. predators). If the large herbivores engage in pyric herbivory, reducing the frequency of prescribed burns may reduce herbivore impacts. If a large herbivore species is not expected to influence fuel properties, then no immediate action is necessary though it is recommended to continue to monitor the species. Action may be required in the future if populations fluctuate.

Deterring large herbivores

Large herbivores may be significantly contributing to bushfire risk if they are found to increase fuel amount, negatively alter fuel structure, and promote more flammable plant species both in the short- and long-term (Foster et al., 2020; Rouet-Leduc et al., 2021). Resource managers may need to explore options of reducing or removing the influence of large herbivores within south-eastern Australian forests. Physically restricting access via fencing to prevent foraging is possible but is often feasible and effective only for small areas. Managers must weigh the cost-benefit of constructing fences in forests that require regular maintenance as canopy trees may fall or drop large branches on the fence (Chard *pers. obs.*).

If restricting access of large herbivores is not feasible, culling large herbivores may be considered. Culling of western grey kangaroos and red kangaroos has been conducted in mallee communities to reduce overgrazing (Morris et al., 2019). Similarly, culling of sambar deer in the Yarra Ranges of Victoria has been suggested as the only practical option to reduce their impacts on vegetation communities (Bennett, 2008). In some cases, harvesting of large herbivore populations may be explored and is considered the preferrable control method over culling (Read et al., 2021). However, appropriate ethical and legislative issues must be accounted for when dealing with both native and introduced species (Davis et al., 2016; Morris et al., 2019). Removal of large herbivores via harvesting/culling methods have been shown to assist in plant regeneration of palatable, less-flammable species (Sluiter et al., 1997).

Alternatively, reducing large herbivore densities may be achieved by encouraging predator populations within the landscape. Introducing or promoting native predator populations may create a ‘landscape of fear’ that can be used to influence the spatial distribution of large herbivore species (Allen et al., 2019). In south-eastern Australia, dingoes (Canis lupus dingo) have been proposed as a native biocontrol method for targeting introduced herbivores as well as overabundant native herbivores (Allen et al., 2019; Geary et al., 2020). The presence of dingoes in forest ecosystems has been linked to significant modifications in vegetation structure by the subsequent reduction in herbivory (Catling et al., 2001). Such an action must be considered carefully as introducing predators may have other adverse implications for ecosystem functioning and wider land uses (Côté et al., 2004).

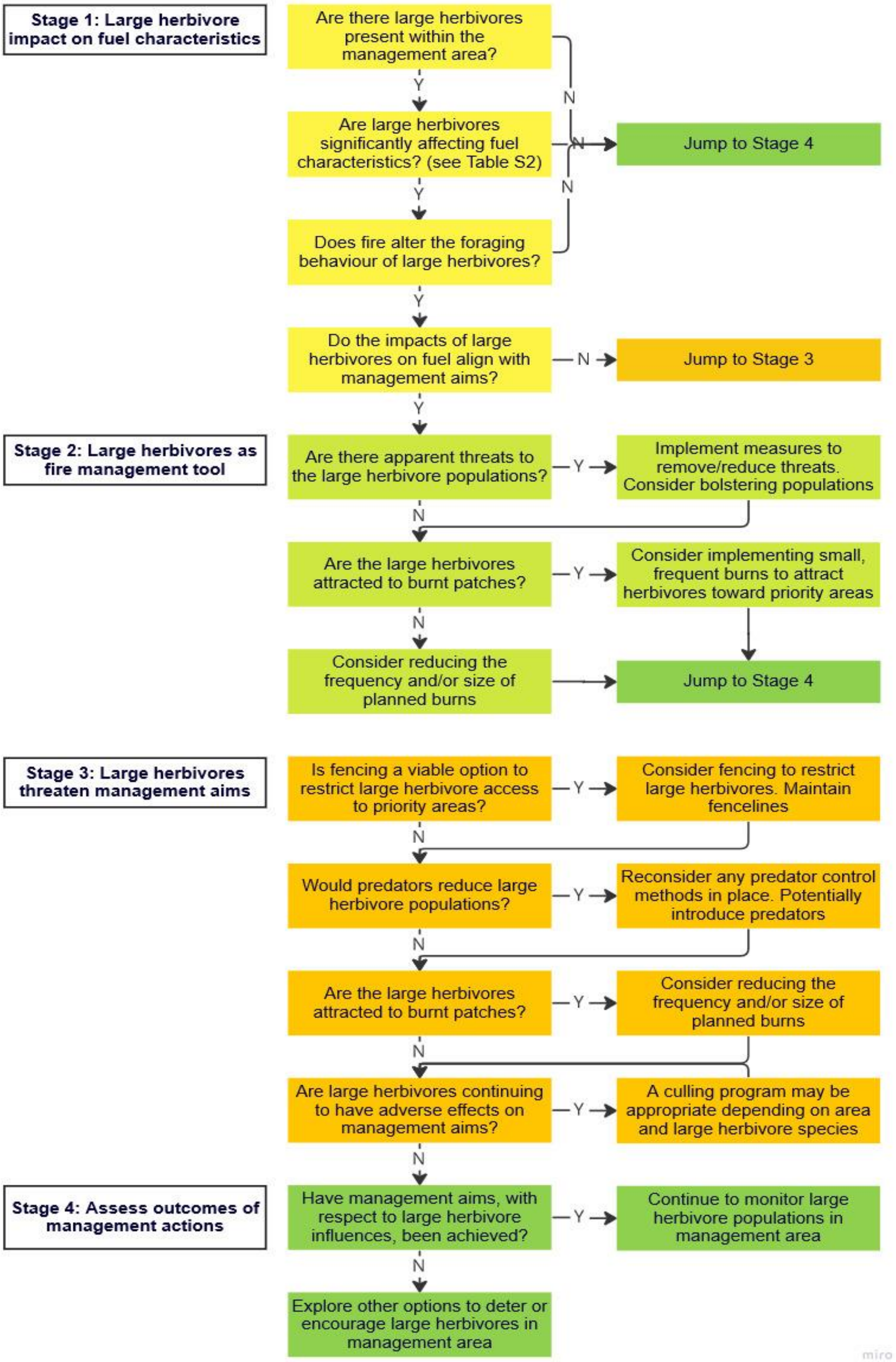

Figure 1: Decision tree to identify appropriate strategies for managing large herbivores in forest ecosystems of south-eastern Australia with respect to management aims.

If the herbivores present within a landscape engage in pyric herbivory, then prescribed burning practices may be useful in managing large herbivore impacts on vegetation. Aggregating planned burns either spatially or temporally may reduce vegetation modification as foraging pressure is spread over a larger area (Chard et al., 2022b). Reducing the frequency of prescribed burning may limit browsing pressure from large herbivores, however this must be balanced with fire management goals (Morgan et al., 2020). Employing this technique may reduce the dominance of flammable species in the understory as less flammable (and more palatable) plants have a greater chance of survival (Allcock & Hik, 2004).

Limitations of fire-herbivore research

A major limitation of fire-herbivore research in south-eastern Australian forests is quantifying large herbivore densities. Of the studies documenting large herbivores in south-eastern Australian forests, only one provided a quantitative estimation of large herbivore density (Meers & Adams, 2003). Other studies provided relative densities, activity levels between treatments, or changes in herbivore occurrence (Foster et al., 2015; Chard et al., 2022a), yet without accurate density estimates it is difficult to holistically assess and predict large herbivore impacts on forest communities by certain species. A comprehensive review of assessing macropod populations in various landscapes suggests that faecal pellet counts (and subsequently faecal accumulation rates) are the optimal method for estimating large macropod densities in forest ecosystems (Coulson et al., 2021). This methodology may be the most suitable for accurately determining densities of most large herbivore species within forested areas and should be implemented in future studies investigating fire-herbivore interactions.

Further challenges exist in landscapes wherein multiple large herbivore species coexist but have different foraging strategies (Davis et al., 2008; Bennett & Coulson, 2012). While fencing may exclude large herbivores within an ecosystem, disentangling the influence of individual species on fuel characteristics is difficult as browsing impacts on vegetation is difficult to attribute to each species (Davis et al., 2016; Morgan, 2021). Fencing has been used to effectively separate and analyse the influence of native (swamp wallaby and wombat) and introduced (deer) species in forest ecosystems (Bennett & Coulson, 2012). Similarly, fencing has been used to separate small herbivores (rabbits) from large herbivores (kangaroos and goats) and assess vegetation damage of each (Bennett et al., 2020). The cost-benefit of such experiments need to be considered, as well as the challenges of fencing forest landscapes, with the potential findings of such research.

Increasing both the spatial and temporal scale of large herbivore research is imperative to identifying landscape-scale modifications to forest communities and fuel properties (Foster et al. 2020; Morgan 2021). Additionally, research that directly quantifies such changes to fuel properties by large herbivores and subsequently models projected fire behaviour is required (Chard et al., 2022b). While the influence of large herbivore species within south-eastern Australian forests can be estimated, vegetation modification needs to be viewed through a bushfire modelling lens to better understand impacts on fuel properties. Increasing study duration will provide a more accurate assessment of fuel dynamics, especially regarding the short- and long-term impacts of large herbivores. Consequently, this will guide more effective strategies to manage large herbivores within forests of south-eastern Australia.

4.9 Conclusion

We explored the potential for large herbivores to be used as a tool to reduce bushfire fuel in south-eastern Australian forests. We postulated the following questions, investigated each within the current literature, and summarise our key findings:

(1) In what ways do large herbivores alter vegetation? Most large herbivores in forest communities will significantly alter the structure, function, and composition of vegetation through their browsing or physical presence.

(2) How do large herbivores respond to fire? Evidence suggests that most large herbivore species in south-eastern Australia (or comparable study systems) should be attracted to recently burnt patches due to the prevalence of palatable food in the recovering understory.

(3) What is required for large herbivores to be used as a tool for managing bushfires? Our findings indicate that large herbivores may be positively reducing fuel properties in the short-term by reducing fuel amount and causing breaks in fuel structure. However, this could ultimately contribute to an overall increase in fire risk in the long-term as fuel condition changes to a more flammable landscape.

4.10 Once large herbivore impacts are quantified within a system, and over an appropriate timeframe, resource managers must select the most appropriate management options for large herbivores in forest ecosystems.

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4.12 Supplementary Material

Table S1: The number of studies conducted on large herbivores found in forests of south-eastern Australia that document some aspect of vegetation change. Species with a * indicate they are an introduced species. Weight ranges were sourced from Menkhorst & Knight (2004).

Family	Species	Common name(s)	Weight (kg)	Studies
Bovidae	*Bos taurus**	Cattle, Cow	720-1100	11
	*Capra hircus**	Goat	20-80	14
	*Ovis aries**	Sheep	45-160	15
Cervidae	*Axis porcinus**	Hog Deer	25-45	2
	*Cervus elaphus**	Red Deer	90-160	0
	*Dama dama**	Fallow Deer	35-90	1
	*Rusa timorensis**	Javan Rusa, Sunda Sambar, Rusa Deer	50-120	3
	*Rusa unicolor**	Sambar Deer	110-240	6
Equidae	*Equus ferus caballus**	Horse, Brumby	380-600	2
Leporidae	*Lepus europapeus**	European Hare	2.5-6.5	7
Macropodidae	*Macropod sp.*	NA	3-85	13
	Aepyprymnus rufescens	Rufous Bettong, Rufous Rat-kangaroo	2.5-3.5	0
	Macropus eugenii	Tammar Wallaby	4-10	0

	Macropus fuliginosus	Western Grey Kangaroo	28-54	1
	Macropus giganteus	Eastern Grey Kangaroo	37-66	7
	Notamacropus dorsalis	Black-striped Wallaby, Scrub Wallaby	7.5-20	0
	Notamacropus parma	Parma Wallaby	3.2-5.8	0
	Notamacropus parryi	Whiptail Wallaby, Pretty-faced Wallaby	15-26	0
	Notamacropus rufogriseus	Red-necked Wallaby, Bennett's Wallaby	16-27	7
	Onychogalea fraenata	Bridled Nail-tail Wallaby	3-6	0
	Osphranter robustus	Common Wallaroo, Euro	25-55	1
	Osphranter rufus	Red Kangaroo	35-85	1
	Petrogale penicillata	Brush-tailed Rock-wallaby	5-8	0
	Thylogale billardierii	Tasmanian Pademelon, Rufous-bellied Pademelon	5.8-9	3
	Thylogale stigmatica	Red-legged Pademelon	4.2-6.5	0
	Thylogale thetis	Red-necked Pademelon	4-7	0
	Wallabia bicolor	Swamp Wallaby, Black Wallaby	15-20	10
Phalangeridae	*Trichosurus caninus*	Short-eared Brushtail Possum	2.5-4.5	0
	Trichosurus cunninghami	Mountain Brushtail Possum	2.5-4.5	0
Phascolarctidae	*Phascolarctos cinereus*	Koala	9-14	2
Vombatidae	*Lasiorhinus latifrons*	Southern Hairy-nosed Wombat	20-32	0
	Vombatus ursinus	Common Wombat	20-35	4

Table S2: Considerations for determining whether large herbivores are altering fuel properties in forest ecosystems of south-eastern Australia. Alterations to fuel properties may occur between fire seasons (short term) or over a period of many fire seasons (long term).

	Short term	**Long term**
Fuel amount	Will large herbivores increase or reduce the fuel biomass for the next fire season?	Will long-term herbivory alter plant species that readily contribute to fuel biomass?
Fuel structure	Will large herbivores reduce the vertical or horizontal continuity of fuel for the next fire season?	Will long-term herbivory alter fuel structure that can modify fire pathways through a vegetation community?
Fuel condition	Will large herbivores alter the flammability of available fuel for the next fire season?	Will long-term herbivory promote palatable or unpalatable plants in the vegetation community?

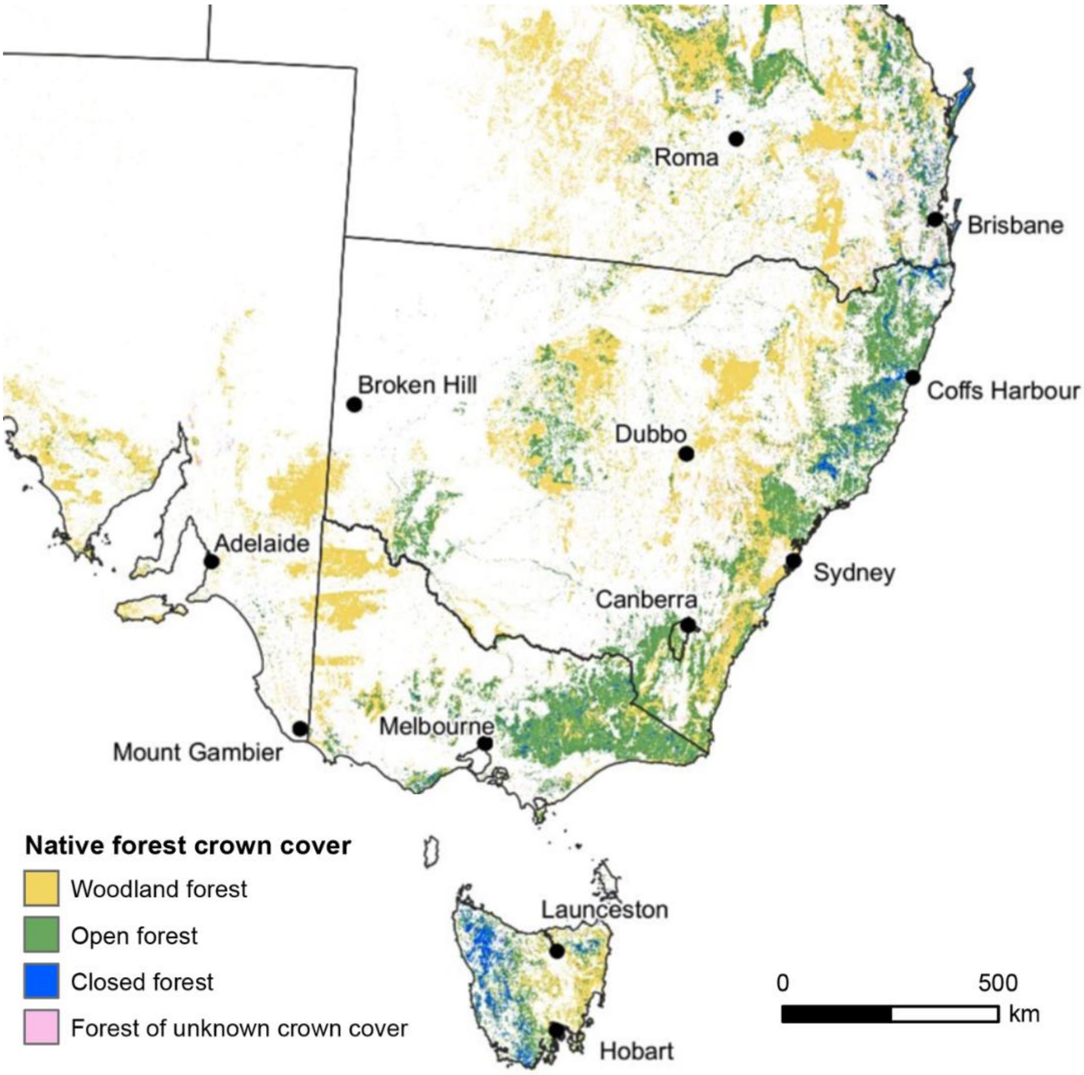

Figure S1: Map of south-eastern Australia displaying native forest crown cover (map adapted from Australian Bureau of Agricultural and Resource Economics and Sciences; MPIGA, 2018)

Conclusions

My research aimed to explore the relationship between fire, fuel, and fauna, with the central aim of determining herbivore-mediated influences on fire behaviour. Prior to my research, there had been no work quantifying large herbivore impacts on future fire behaviour in Australian forest ecosystems.

Summary of Outcomes

Paper I: Time since fire influences macropod occurrence in a fire-prone coastal ecosystem

In *Paper I*, I used a long-term spotlighting dataset to investigate how patterns of occurrence of large herbivores were influenced by fire and vegetation type. The dataset allowed for the study of two large herbivore species, the eastern grey kangaroo (*Macropus giganteus*), and the swamp wallaby (*Wallabia bicolor*). I found the occurrence of both macropods declined strongly with time since fire. The number of fires was found to influence the occurrence of only the eastern grey kangaroo, with increased fires reducing its occurrence across the Park. I also found that both macropod species were more likely to occur in forest vegetation relative to woodland, shrubland and heathland communities. My results indicated that both fire and vegetation influenced the occurrence of large herbivores in the study area. Macropods likely preferred forest communities due to the abundance of palatable plants present in the understory. As time since fire increased, macropod occurrence decreased, indicating that both species were selecting recently burnt patches in the landscape and were less likely to occur in long unburnt patches. A likely mechanism underpinning this behaviour is the increased availability of green pick in the understory following a fire, due to the vegetation regrowing or resprouting. My findings highlighted the need for management to consider large herbivores when conducting management burns as such practices may focus herbivore browsing in recently burnt areas, potentially altering the understory vegetation.

Paper II: Post-fire pickings: Large herbivores alter understory vegetation communities in a coastal eucalypt forest

In *Paper II*, I quantified how browsing pressure from large herbivores can alter forest vegetation communities following a wildfire. Browsing from macropods was found to reduce vegetation community richness, diversity and evenness. Post-fire herbivory produced a depauperate vegetation community dominated by bracken (*Pteridium esculentum*) and other unpalatable plant species. Interestingly, there appeared to be no effect of time since fire on macropod occurrence which was contrary to our findings in *Paper I*. I proposed that the size of the 2017 wildfire was large enough to dissipate the increased browsing pressure of macropods across the study area. These results demonstrate the impact of post-fire herbivory on the composition of regenerating vegetation communities. If such changes to vegetation communities are inconsistent with management objectives, measures may need to be taken to reduce browsing pressure by large herbivores following fire events. Restricting herbivore access to forest patches following a fire (planned or otherwise) could encourage a more diverse and species-rich understory of plants in forest communities.

Paper III: Fencing foragers fuels fires: Can large herbivores alter fire behaviour in coastal eucalypt forests?

In *Paper III*, I quantified the impact of large herbivore browsing on projected fire behaviour. My findings demonstrated the potential for large herbivores to alter fire behaviour. However, the magnitude of such changes was dependent on the fire model employed. These findings highlighted the risk of possibly drawing misleading conclusions if just one of the fire models had been considered. Future studies of herbivore effects on fire risk in forest ecosystems must ensure that they account for herbivore-mediated effects on a range of fuel properties (not just fuel amount). This study also emphasised the need for long-term datasets to provide a better understanding of large herbivore impacts on fire behaviour.

Paper IV: Fighting fire with fauna: exploring the potential of using large herbivores to manage bushfire fuel in south-east Australia

In *Paper IV*, I conducted a synthesis of published studies of large herbivore impacts on forest vegetation, interpreting reported effects on vegetation from the perspective of modifications to fuel properties. This paper aimed to explore the potential for large herbivores to be used as an additional tool in the management of bushfire fuel in forest ecosystems of south-eastern Australia. I found that large herbivore impacts on fuel properties were varied and complex, and inferring possible consequences for fire behaviour was further complicated by the fact that changes to fuel are not always directly proportional to changes in fire behaviour (e.g. simplified vegetation structure does not always produce reduced fire severity). Drawing conclusions regarding the likely effects of herbivory on fire is further compounded by the time frames over which large herbivore effects are considered, with conflicting effects being common when comparing short- and long-term impacts. To help resolve some of these complexities I developed a framework to assist resource managers in accounting for large herbivore populations when conducting fire management practices.

Synthesis and Management Implications

My thesis explored the interaction of fire, fuel, and fauna in a forest ecosystem. The findings of my empirical papers (*Papers I*, *II*, and *III*) demonstrated the need to view this relationship holistically, and as a dynamic feedback system. My results demonstrated that large herbivores may alter fire behaviour in forests. Subsequently, fire management in forest ecosystems needs to account for large herbivore populations present in a landscape (*Paper IV*).

Macropods were found to display pyric herbivory behaviour, being more likely to occur in burnt patches than long unburnt sites (*Paper I*). This was expected as previous research in the same study area recorded a similar result, with increased herbivore activity following a fire (Foster *et al.*, 2015). However, a similar effect was not apparent following the 2017 wildfire, where large herbivore activity did not decline with increasing time since fire (*Paper II*). This may have been a result of the large size of the 2017 fire, as larger fires often produce weaker or no evidence of large herbivores selecting for burnt patches (Williamson *et al.*, 2012). A review of other studies in south-eastern Australia investigating this phenomenon appeared to confirm the fire size hypothesis as studies of macropod responses to small fires were more likely to detect a pyric herbivory response (*Paper IV*). This suggests that while some herbivores may be attracted to recently burnt patches, the size of a burn will influence the browsing pressure that a given patch will experience (Styger *et al.*, 2010). This is important to consider when conducting hazard reduction burns. Future management may need to account for large herbivore populations, and how they may influence vegetation communities, and varying burn sizes may be one way to achieve this (Driscoll *et al.*, 2010). Future research should further investigate the influence of fire size on large herbivore occurrence within a study system and all studies should report the size of the fire/s being investigated to allow for cross-study synthesis.

An interesting finding from my research was the effect of both fire and herbivory on bracken (*Paper II*). Comparisons between fencing treatments revealed no significant changes to bracken morphology in a post-fire landscape. This was surprising as it was expected that the unpalatable bracken would benefit in plots subject to browsing due to reduced competition from palatable species and increased space. However, my findings indicate that it is possible that bracken is positively responding to any form of disturbance and is benefitting from current fire regimes and large herbivore browsing. As bracken can disproportionately contribute to bushfire fuel, as it produces large amounts of highly flammable material (Mason *et al.*, 2016), documenting the dominance of bracken in the understory is critical to our understanding of future fire behaviour in eucalypt forests.

While large herbivores were shown to strongly affect post-fire vegetation communities (*Paper II*), the influence on fire behaviour was less clear (*Paper III*). This was due to the differing effects of herbivores on different aspects of vegetation, and the different aspects of fuel considered in each fire model (Cruz *et al.*, 2015; Zylstra *et al.*, 2016; Cruz, 2021). Future research on herbivore-mediated changes to fire behaviour must select the appropriate model that captures the range of likely changes to vegetation driven by large herbivores. Models that incorporate measures of near-surface and elevated fuel, as well as plant species-specific information, should better reflect changes to understory vegetation and fire behaviour caused by large herbivores (Zylstra, 2021). Given the clear trends we observed in the vegetation dynamics post-fire, future studies should employ longer-term monitoring of herbivore effects to allow for more definitive conclusions regarding herbivore effects on fire behaviour.

A critical finding of this thesis was the evidence that large herbivores may alter fire behaviour to such a degree that would change the appropriate firefighting response (*Paper III*). The ramifications for such changes, in the face of increasing future fire severity (Andela *et al.*, 2019), may become important for fuel management practices. Currently, herbivore influences on fire ecology are largely overlooked in fire management decisions for forest ecosystems (Morgan *et al.*, 2020). While long-term studies are required to fully understand the importance of herbivores in forest fire ecology, and each large herbivore species may have differing effects on fire behaviour (*Paper IV*), this thesis shows that accounting for possible impacts of large herbivores on future fire management practices would appropriate, and beneficial.

National and global applications

It is likely that the experimental results (*Paper I, II, and III*) and the synthesis on large herbivore effects in south-eastern Australia (*Paper IV*) are applicable at both a national and global scale. While outcomes will vary depending on the herbivore species, vegetation communities, landscapes and fire regime's, similar themes should persist when large herbivores are present in an ecosystem. Large herbivores are likely to influence vegetation communities in such a way to alter in situ fuel properties and subsequent fire behaviour. It is likely that large herbivores will reduce short-term fire risk but may promote a more flammable understory (Archibald *et al.,* 2019). Examples of large herbivores reducing long-term fire risk, while not compromising species diversity and ecosystems functioning, is currently lacking and requires further investigation.

This raises the question as to whether the function of large herbivores in an ecosystem is to (unintentionally) increase fire risk, literally fuelling future fire to promote nutrient recycling and balance vegetation communities. Increased fire frequency would produce more burnt patches and areas of green pick, which are areas favoured by large herbivores (Parkins *et al.,* 2019). Or perhaps these recorded outcomes are a result of anthropogenic modifications to natural landscapes leading to altered ecosystems. This imbalance has resulted in increased populations of both native and feral large herbivores in the landscape and perhaps caused adverse effects to ecosystem functioning. These effects may be more pronounced within Australian systems as top order predators have been historically suppressed and feral herbivore populations are prevalent (Fisher *et al.*, 2021).

It should be noted that the study system for the empirical chapters of this thesis is unique. Booderee National Park is a coastal eucalypt forest with no large feral herbivore populations and few predators present (Dexter *et al.*, 2013). Populations of large exotic herbivores are likely to have an increased influence on plant communities in Australia due to their morphology, abundance, and dietary preferences. The presence of top order predators, such as dingoes, in Australian landscapes has been shown to reduce herbivore modification to vegetation communities (Fisher *et al.*, 2021), likely reducing long-term fire risk. The combination of native and feral large herbivores, in conjunction with the presence of native and feral predators, within an ecosystem may provide a better representation of the Australian landscape. This is an aspect of ecosystem functionality that merits further research.

Future research

Future research on fire-herbivore interactions in vegetation communities should focus on the investigation of impacts at both larger spatial and temporal scales (Foster *et al.*, 2020). Further, investigations into large herbivore impacts on vegetation communities must account for the potentially nuanced effects of herbivores on fuel properties, and how this may shape future fire behaviour. Long-term studies will provide a more accurate assessment of herbivore effects on fuel dynamics, which will subsequently guide more reliable fire management strategies.

Conclusion

My research explored the feedback cycle between herbivores and fire in forest ecosystems and demonstrated the potential for post-fire herbivory to influence future fire behaviour. Future research that investigates large herbivore influences on fire behaviour over a longer timeframe should be prioritised. Overall, this thesis has demonstrated the connections of fire, fuel, and fauna in forest ecosystems and provided a basis for future investigations into pyric herbivory in forests.

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