The Superb Lyrebird *Menura novaehollandiae* as an Ecosystem Engineer

Submitted by

Alex C. Maisey

Dip. Cons. Land Mgt., Dip. Sust., B. Env. Sc. (Hons)

A thesis submitted in total fulfillment of the requirements for the degree of Doctor of Philosophy

Research Centre for Future Landscapes

Department of Ecology, Environment and Evolution

College of Science, Health and Engineering

La Trobe University

Victoria, Australia

August 2020

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Abstract

Ecosystem engineers regulate the resources available to other species by the physical changes they make to habitats. The superb lyrebird *Menura novaehollandiae* has been described as an ecosystem engineer in wet forests of south-eastern Australia due to the large volume of soil it displaces when foraging on the forest floor. This results in changes to soil and litter structure, which potentially affect a range of other organisms. A two-year field-based study was carried out, using experimental exclusion plots to test the engineering role that lyrebirds play in wet forests in Victoria's Central Highlands. The effects of foraging on the abiotic habitat structure and composition of litter and soil was tested, and the influence this has on invertebrate, plant, and soil fungal communities. An experimental approach was used with three treatments: lyrebird exclusion, lyrebird exclusion with simulated foraging, and non-exclusion reference plots. Treatments were replicated in three forest types in each of three forest blocks. Lyrebirds foraged extensively throughout all seasons, displacing litter and soil at a rate of approximately 156 t/ha per annum. Litter depth and soil compaction increased where lyrebirds were excluded, with litter layer approximately three times deeper and a 37% increase in soil compaction (top 7.5 cm) after two years of exclusion. Habitat modification by lyrebirds increased the germination rate of seedlings, but seedling density, when considered with the effect of mortality due to physical destruction by foraging lyrebirds, showed no net difference between treatments. There was a strong response to engineering seen in the invertebrate community, with increased richness and biomass in simulated plots (i.e. lyrebird engineering, no predation), representing an intriguing 'farming' effect exerted by lyrebirds on their invertebrate prey. Sequencing of soil fungal DNA revealed little change in this community due to lyrebird foraging, but strong variation in fungal composition was associated with different forest types. The superb lyrebird is a geographically widespread and important ecosystem engineer that profoundly shapes the structure and function of litter environments and hence forest ecosystems. Given the extent of the recent bushfires in eastern Australia, these outcomes have pertinent implications for management of forest ecosystems and indeed the lyrebird, throughout its range.

Statement of Authorship

Plate 1. Light filters through the canopy in a cool temperate rainforest gully in Sherbrooke Forest.

I, Alex Maisey, performed this research under the supervision of Prof. Andrew Bennett (principal supervisor), Dr. Angie Haslem (co-supervisor) and Dr. Steve Leonard (co-supervisor).

Except where reference is made in the text, this thesis contains no material published elsewhere or extracted in whole or in part from a thesis accepted for the award of any other degree or diploma. No other person's work has been used without due acknowledgment in the main text of the thesis. This thesis has not been submitted for the award of any degree or diploma in any other tertiary institution.

I wrote this thesis with the intention to publish each chapter containing original data and analysis (Chapters 2 to 5, see my contribution outlined below). The first data chapter (Chapter 2) has been published in the international journal *Ecological Applications*, while the other three data chapters have been prepared for publication for peer-reviewed scientific journals. As such, I use the term 'we' to refer to my co-authors collectively within Chapter 2, while for unpublished chapters I write in passive voice.

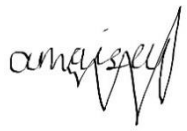
The first chapter of this thesis outlines key concepts relating to ecosystem engineers and provides introduction to the study species, the superb lyrebird *Menura novaehollandiae*. A series of four data chapters follow. Each data chapter has been prepared as a stand-alone manuscript, addressing the role of the superb lyrebird as an ecosystem engineer. I investigate ecosystem engineering influences on abiotic habitat structure and the implications for major groups of taxa spanning three kingdoms. Some repetition of methods between chapters is accordingly inevitable. The final chapter (Chapter 6) provides a synthesis of this body of work.

Within the appendices I have included four published papers on various ecological aspects of the superb lyrebird (Appendix 1) that I have authored or co-authored while undertaking this PhD project. Two of these publications include data collected during my Honours year, while the other two were undertaken opportunistically and in addition to my main thesis research, and as such, have not been included therein. A complete list of cited references from all chapters is included at the end of the thesis.

Candidate's contribution to each data chapter:

Chapter title	**Publication status**	**Candidate's contribution**
(Ch 2) Foraging by an avian ecosystem engineer extensively modifies litter and soil layer in forest ecosystems	Published	I conceived the study, performed all fieldwork and 90% of the statistical analysis and was primary author of the manuscript.
(Ch 3) Farming by engineering: interactions between the superb lyrebird *Menura novaehollandiae* and litter and soil invertebrates	To be submitted	I conceived the study, performed all fieldwork and 90% of the statistical analysis and was primary author of the manuscript.
(Ch 4) An avian ecosystem engineer facilitates seedling germination in wet forests	To be submitted	I conceived the study, performed all fieldwork and the statistical analysis and was primary author of the manuscript.
(Ch 5) Soil fungal communities differ between forest types but show little evidence of change associated with large-scale soil turnover by an ecosystem engineer	To be submitted	I conceived the study, performed all fieldwork and 90% of the statistical analysis and was primary author of the manuscript.

This research was undertaken with approval from the La Trobe University Animal Ethics Committee (permit AEC15-65 and 16-80), Forests Act 1958 (permit FS/14/3694/1/7) and National Parks Act 1975 (permit 10007664).



Alex C Maisey

22 August 2020

Acknowledgements

This work was supported by an Australian Government Research Training Program Scholarship and a La Trobe University Postgraduate Research Scholarship.

My first thanks must be to my supervisor, Andrew Bennett. Andrew is a truly wonderful mentor, and the opportunity to undertake my postgraduate studies with Andrew has been a privilege. Thank you Andrew for sharing your wisdom, logic, and clear thought during the research process, as well as your kind and supportive feedback on my work. I am surely the envy of all those undertaking a PhD project supervised by anyone else!

Angie Haslem joined my supervisory team part-way through this research, and has made an enormous contribution to the project. Ange, thank you for your careful reading of the many edits I have sent your way, your statistical knowledge, and your warm and thoughtful manner.

I thank Steve Leonard for his supervision during the early days of this project. Steve's calm and collected advice helped me establish the study design, while not panicking in the face my analyses. Thank you Steve!

I thank Richard Peters for his support and encouragement from day one (including the informal orientation and warm welcome we received on arrival at La Trobe on our first day!), including his support in the role of Research Progress Panel Chair.

Much of my statistical knowledge I owe to Greg Holland – Thanks Greg for building my confidence with R and for your good humour and generosity in so willingly giving time to all of us (including 'geeking-out' with us in 'R club').

I gratefully acknowledge the support from Alan Lill - a source of inspiration and many enjoyable conversations reminiscing on days trudging through the forests in the depths of winter – as a pioneer of lyrebird research in Sherbrooke Forest and elsewhere, Alan understands the challenges of lyrebird fieldwork!

At the age of 11 I became acquainted with these charismatic birds, under the guidance of Jan Incoll, the 'Lyrebird Lady' of Sherbrooke Forest. We learned much about lyrebirds together, uncovering countless fragments of unknown natural history. I am forever grateful to Jan for 'taking me under her wing' in those early years.

I thank the members of the Sherbrooke Lyrebird Survey Group. Here I learned to handle and band lyrebirds, and with the example of Norm Carter I have learned the value of careful measurement and consistency in method. John Lloyd has also been an inspiration in his devotion to the forest over many decades.

I thank Sally Bewsher for her careful reading of drafts, her company on many field trips and her friendship over many years.

I acknowledge the late Sydney Curtis, pioneering Albert's Lyrebird expert and self-confessed lyrebird addict. Throughout his conservation-oriented life Syd spent many decades researching the elusive Albert's Lyrebird in the sub-tropical rainforests of SE Queensland. Syd is single-handedly responsible for much of what we know of this species today. Many pre-dawn recordings were made from rainforest hides with parabolic microphones attached to long cables, placed at the male lyrebirds' tangled vine platforms (one of Syd's scientific discoveries). As a 12-year old budding lyrebird fanatic, I was encouraged by Syd to pursue my love of lyrebirds. I have fond memories of taking Syd to an Albert's Lyrebird nest some years ago - one of the few he had seen.

I thank Owen Bassett for introducing me to his excellent lyrebird work (under the guidance of the late David Ashton). David Ashton's legacy, in the form of his insightful research papers, has also given me much inspiration while working in the magnificent ecosystem of Victoria's tall forests.

I thank all of the Bennett and Clarke lab members, fellow students and colleagues in the Department of Ecology, Environment and Evolution and Research Centre for Future Landscapes, especially Nicole Coggan, Margreet Drijfhout, Orsi Decker, Dan Nugent, Fred Rainsford, Erika Zaid, Simon Verdon, Jacinta Humphrey, Simon Watson, Ursula Ellenberg, Pete Green, Mike Clarke, May Gu, Chunya Zhu, Patricia Woolley, Christine Forster, Jim Radford – all have contributed to making the experience of undertaking this PhD at La Trobe greatly enjoyable, and I have learnt something (and often many things) from each of you.

I wish to warmly thank my PhD buddies Jess Lawton, Cara Sambell and Josh Grubb, for the ongoing support and friendship through our shared experiences of PhD life. I enjoyed our many hallway conversations, lunchtime discussions and sharing of the inevitable doubts and woes that life as a PhD student entails.

I thank my good friend Victoria Austin for sharing her passion for lyrebirds (albeit biased toward females). I am so glad there is someone on Earth who can talk lyrebirds for as long as I can!

Life during any PhD project is rarely linear and (from what I can tell) never goes to plan, and I could not have done this without the varied support of many individuals along the way. Asha Billing, her family Noel, Lynne and Brenna Billing, Jane Hollands, Don Petty and Sue Robertson, Roger Shaw, Annette Anderson, Franciscus Scheelings, Lucie Semenec, Eleonora Egidi, Ashley Franks and Anastasia Dalziell. Thank you for all you have given.

I gratefully acknowledge the invaluable support from Bill Holsworth, with the Holsworth Wildlife Research Endowment allowing this project to be generously funded for three years.

I thank my entire family for their support over the years of my somewhat prolonged studies. Particularly my parents Gary Maisey and Tania Vick, as well as their lovely partners Rose Dyson and Greg Donoghue (a special thanks to Greg for his expert proof-reading of my work); my clever sisters, Samantha and Lauren, for humouring me during my many conservation rants, and my partner Meghan Lindsay for her love and strength as a conservationist.

Finally, I wish to dedicate this thesis to my dear grandmother Marcelle Maisey, for being my greatest supporter in my natural history pursuits, from as far back as I can remember. Your encouragement and belief in my abilities has given me confidence and led me to follow my passion. Thank you!

Chapter One

Ecosystem engineers in Australia and the role of the superb lyrebird *Menura novaehollandiae*

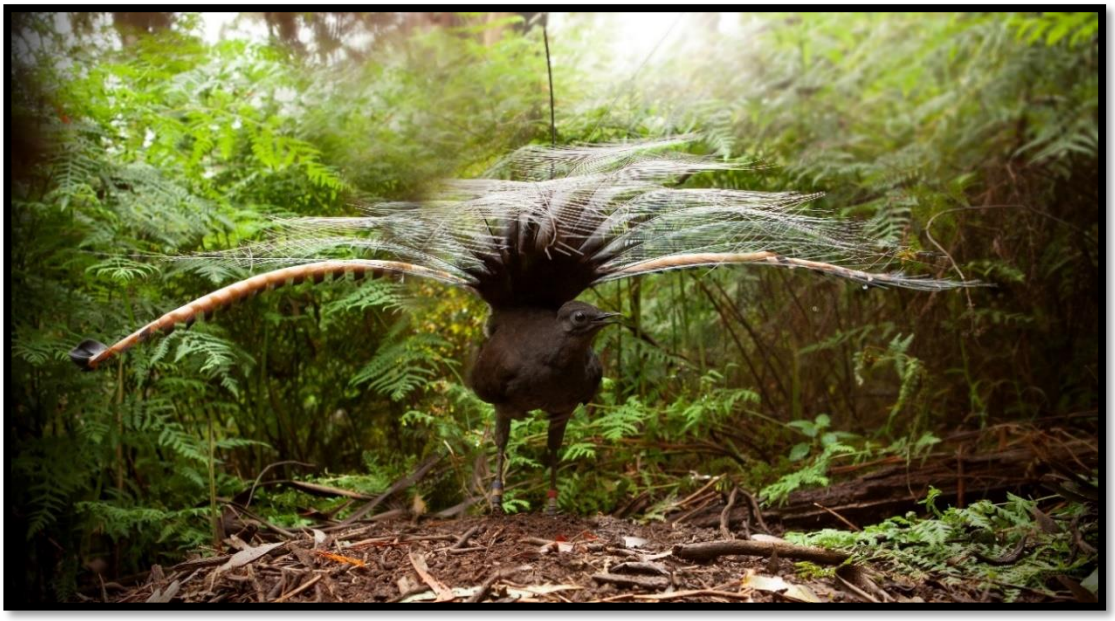


Plate 2. Male lyrebird on its display mound in partial tail display.

1.1 INTRODUCTION

1.1.1 Ecosystem engineers: a definition and introduction

Ecosystem engineers are an important, yet sometimes overlooked, component of ecosystem function (Coleman and Williams 2002, Byers et al. 2006, Wright and Jones 2006). Since the inception of the term 'ecosystem engineer' in 1994 (Jones et al. 1994), the definition of what constitutes 'engineering' has caused much debate (Cuddington et al. 2011), due both to the ubiquity of this process in ecosystems and confusion with similar concepts such as keystone species (Cuddington et al. 2011). Jones et al. (1994) argued that the role of engineering had been neglected in ecological theory, especially given that engineers occur in many ecosystems and interact with many species. Indeed, many important ecological functions now considered to be the result of engineering have existed in the literature spanning back as far as Charles Darwin's writings on the soil-changing activities of the earthworm (Wright and Jones 2006).

Jones et al. (1994) proposed that an organism may be classified as an ecosystem engineer if it modulates the availability of resources to other species, excluding the provision of itself as the resource. This definition presented ambiguity, as some self-moderated changes by organisms fall outside described processes of trophic, parasitic or competitive relationships, yet still may have population-level impacts on other species (e.g., provision of avian nest sites by hemi-parasitic mistletoe plants (Watson 2001)). The definition of engineering was subsequently extended to include the provision of all physical resources in non-trophic relationships (Jones et al. 1997), such that the provision of surface area (and thus living space) by the growth of an organism is considered a form of engineering. A key feature separating engineering from non-engineering is that engineering does not include assimilatory or dissimilatory processes, nor competition (Jones et al. 1997).

The ecosystem engineering concept has been criticised on the basis that all organisms interact with their abiotic environment and thus change resource availability. Cuddington et al. (2011) specified more precisely that for an organism to be considered an engineer: a) it must cause structural change to the abiotic environment larger than that of background variation introduced by other processes; b) other biota must be sensitive to the degree or type of abiotic change; and c) the biotic response must be greater than that caused by other background processes affecting the same response variable. These criteria allow for a clear delineation between engineers and non-engineers, and provide a conceptual framework upon which studies can be based.

1.1.2 Autogenic and allogenic engineering

Engineering interactions may be further separated into two categories. Engineers may be considered to be 'autogenic' when the physical growth of the organism moderates the environment in which other species live (e.g., canopy trees altering the light regime in a forest (Hastings et al. 2007)); or 'allogenic', when a species mechanically or chemically alters the biotic or abiotic environment. Such activities create resources used by other species (e.g., beaver *Castor canadensis* building dams, providing resources for herbs otherwise excluded from the riparian plant community (Wright et al. 2002)).

1.1.3 Engineer vs. keystone species

The term 'keystone' species has often, incorrectly, been used synonymously with ecosystem engineer. Many keystone species exert trophic pressures on other species, moderating food webs and changing community structure (Paine 1966). The removal of such species from a system will alter a species assemblage and cause changes disproportionate to its relative biomass (Krebs et al. 1994). If engineering is recognised and separated from keystone processes, the mechanisms underlying the function of species in an ecosystem may be understood, and therefore better applied to conservation problems.

The coupling of trophic effects of keystone species with the effects of engineers can result in the most profound consequences on ecosystems. A notable example is the prominent loss of kelp forests in areas such as the Aleutian Islands, associated with increased grazing pressures from sea urchins, the result of a trophic cascade caused by the extirpation of the urchin-feeding sea otter *Enhydra lutris* (Estes and Palmisano 1974). Changes caused by the loss of the keystone role played by the otter is far-reaching, although the change in habitat due to the loss of the ecosystem engineering kelp may have effects of similar magnitude. Kelp forests significantly reduce wave action, allowing sediment to accumulate and inhibit the growth of sessile intertidal invertebrates, while providing a complex structure harbouring a suite of motile species that rely on the kelp as habitat (Estes and Palmisano 1974). The presence of sea otters has even been linked to the abundance of higher trophic level vertebrates, such as the harbor seal *Phoca vitulina* (Estes and Palmisano 1974) and bald eagle *Haliaeetus leucocephalus* (Anthony et al. 2008), giving strong credence to its keystone status.

1.1.4 Types of ecosystem engineers

Engineering may occur as the result of a range of organismal activities and can be classified into groups based on habitat type and mode of action (Table 1.1). Jones et al. (1994), in their seminal paper, described six conceptual models of types of engineering (cases 1-6; Fig. 1.1).

Case 1: The simplest form of engineering is autogenic habitat provision (Fig. 1.1). This occurs when an organism is modified from one state to another, generally through growth or senescence, thereby creating a non-trophic resource that other organisms may exploit. Trees are a ubiquitous example; as they grow and mature, they become suitable for colonisation by epiphytes (e.g., ferns, orchids), in many cases only becoming suitable at specific age and size classes.

Case 2: Allogenic engineering (Fig. 1.1) occurs when an organism directly modifies a physical structure, thereby providing a resource for another organism. For example, in North America, the red-naped sapsucker *Sphyrapicus nuchalis* changes the state of tree trunks by excavating large hollows for nesting (Cockle et al. 2011). Once disused, the hollows are exploited by two species of swallow, both obligatory hollow-nesters that rely entirely on the woodpeckers (Daily et al. 1993).

Case 3: In addition to autogenic provision of living space, trees also engineer habitat by modulating resource flows with their living and dead tissues (Fig. 1.1). For example, through the abscission of leaves and branches, forest trees form debris dams in first-order streams. Debris dams significantly change the flow regime, capture organic material and facilitate *in situ* breakdown, sustaining the energy source for in-stream communities (Bilby and Likens 1980). The debris is not the resource; rather the dam caused by the debris interacts with sediments and flow of water, creating the resource – the pond habitat.

Case 4: An allogenic analogue to trees forming debris dams is the beaver, represented by Case 4 (Fig. 1.1). Beaver modify the state of trees to form a dam, which in turn interacts with the stream and associated resource flows to create a floodplain. The altered hydrology supports herbaceous plants that would otherwise not occur along the stream banks (Wright et al. 2002).

Case 5: An extension of Case 3, whereby a complex interaction emerges between an engineer and a large abiotic force, such as climate-driven impacts of fires, floods, or hurricanes (Fig. 1.1). For example, floristic diversity gives rise to vegetative materials that vary in chemical and structural composition. With successional growth stages, vegetation communities represent varying degrees of flammability (Zylstra 2018). When fires do occur, the qualities of a plant species may determine the extent or severity of fire. Rainforest trees, with their high moisture content and dense canopies, cool the air, slow wind speed and lower fire intensity. Moderation of resource flows continues in the post-fire environment as described by Case 3.

Case 6: In coastal ecosystems, mangroves may function as described by Case 6 (Fig. 1.1), when interacting with cyclones and tsunamis, to protect the coastline from erosion (Marois and Mitsch 2015). The mangroves stabilise sediment, that under the effects of tsunamis and cyclones interact with resource flows to retard erosive forces of the abiotic disturbance.

1.2 STRUCTURAL CHANGES BY ENGINEERS AFFECT ECOLOGICAL PROCESSES AND FUNCTION

Ecosystem engineers cause structural change to habitats through many pathways. Below are examples of some of the most ubiquitous and important pathways for habitat alteration caused by ecosystem engineers.

1.2.1 Fire

In many treed landscapes throughout the world, fire is a strong force in shaping habitats (Cary et al. 2003, Bowman et al. 2009). Large-scale disturbance processes such as fire are also likely to strongly interact with ecosystem engineers to profoundly shape ecosystems. There are multiple ways in which engineers might interact with fire. Plants, as autogenic engineers, may mediate fire via the provision of living or dead tissue as fuel, with different species possessing different levels of flammability (Jones et al. 1994, Zylstra et al. 2016, Stoof et al. 2017).

Animals can modulate fire behaviour, resulting in increased patchiness within the boundaries of burnt areas (Foster et al. 2020). The malleefowl *Leipoa ocellata* of semi-arid Australia interacts with fire on a local scale through extensive scraping and burial of litter into large, heat-producing mounds of organic matter, in which they lay their eggs (Fig. 1.2). This activity lowers the severity of fire around mounds, even during high intensity fires, although completely unburnt refuges are more likely to occur under milder fire conditions. An examination of the behaviour of a large, natural fire revealed that malleefowl mounds suppressed fire intensity for up to two years after a mound had been abandoned (Smith et al. 2017). This spatial pattern is proposed to give rise to unburnt refuges, that aid recolonisation by fire-sensitive plants and animals (Smith et al. 2017).

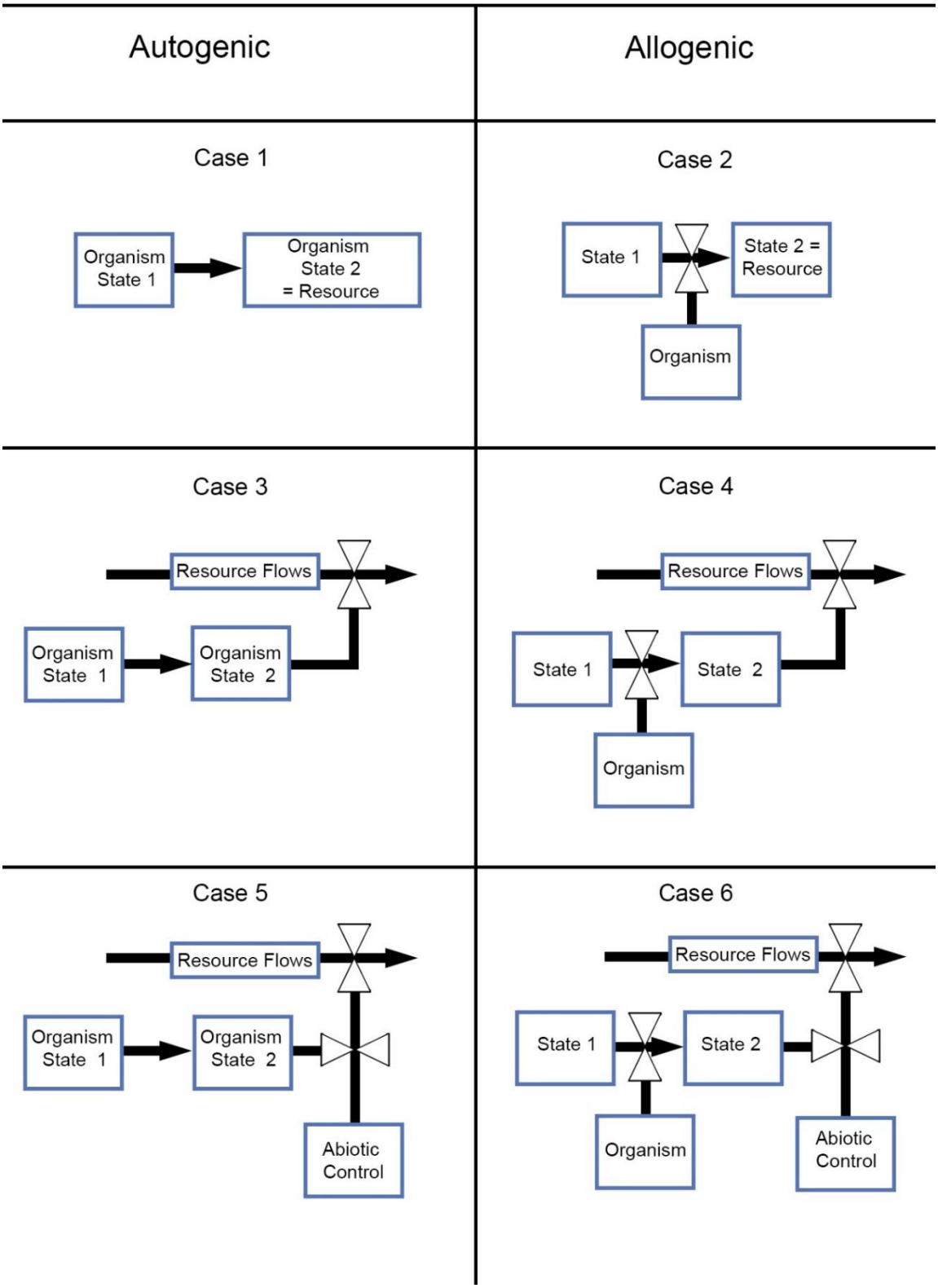


Figure 1. 1 Conceptual models (after Jones et al. 1994) outlining six ways in which a species may serve as an ecosystem engineer. The symbol '⧖' denotes a point of modulation.

Table 1. 1 Summary of major engineering modes and illustrative examples of engineers and their interacting taxa.

Mode of engineering	**Example organism/s**	**Function**	**Organism/s affected**	**References**
Marine bio-accretion	Scleractinian corals *Case 3*	Calcification and subsequent accretion of coral reefs, causing significant change in the physical and chemical marine environment. Structures support a rich marine biota that use the coral substratum upon which to settle.	Marine bacteria, fish	Coleman and Williams (2002),Wild et al. (2004) Wild et al. (2011)
	Crustose coralline algae *Cases 3 & 5*	Modulate currents by means of its own cellular structure and providing a structural base to reefs through cement-like secretions.	*Haliotis Sp.* (abalone)	Shepherd and Turner (1985), Andersen (1992)
	Tubeworm *Lanice conchilega* *Case 3*	Though not as permanent in structure as coral reefs, the biogenic reefs built by tubeworms may persist for decades, functioning in similar ways to boost species richness through processes comparable to those of hard corals.	Other polychaetes, Amphipods	Callaway (2006), Callaway et al. (2010)
Autogenic habitat provision	Trees *Case 1*	Provision of habitat through growth or senescence, thereby creating a non-trophic resource that other organisms may exploit. Fallen litter and logs provide habitat after death.	Diverse suites of epiphytes, invertebrates, vertebrates	Bilby and Likens (1980), Bennett (1987), Bultman and Uetz (1982), Langellotto and Denno (2006),
	Trees *Case 3*	Tree canopies may alter light regime, temperature, wind speed and humidity. Roots may stabilise (or destabilise) soils, interact with nutrient cycling and alter small-scale hydrology.	Diverse suites of epiphytes, invertebrates, vertebrates	Bennett (1987), Lawton (1994), Nieder et al. (2000)

Table 1.1. continued

Mode of engineering	**Example organism/s**	**Function**	**Organism/s affected**	**References**
Allogenic habitat provision	Termites *Case 4*	Modification through feeding that causes wood rot in trees, eventually forming tree hollows and thereby den/nest sites for nocturnal or diurnal animals; provides a containing structure for eggs or young to be nurtured and raised.	Amphibians, reptiles, birds, mammals	Gibbons and Lindenmayer (2002)
	Red-naped sapsucker *Sphyrapicus nuchalis* *Case 4*	Bores hollows in trees, providing nest sites for other animals; creates feeding wells in spruce, aspen and willows, granting access to a nutritional sap resource.	Chipmunks, hummingbirds, swallows, invertebrates	Daily et al. (1993), Martin and Eadie (1999), Aitken and Martin (2007)
Allogenic habitat provision	Gopher tortoise *Gopherus polyphemus* *Case 4*	Burrowing creates thermally stable shelters for various other taxa.	Gopher frogs *Rana capito*	Kent et al. (1997), Pike and Mitchell (2013)
Allogenic habitat removal	Large herbivores *Case 4*	Trampling by ungulates may compact soils into pans or crusts, cause gully erosion and create areas devoid of litter and vegetation.	Arthropods, herbaceous plants	Hole (1981)

Table 1.1. continued

Mode of engineering	Example organism/s	Function	Organism/s affected	References
	Plateau pika *Ochotona curzoniae* and Himalayan marmot *Marmota himalayana* *Case 4*	Alteration of habitat through grazing results in the loss or gain of species separate from those that are browsed, through manipulation of living space and light resources.	Herbaceous plants	Qu et al. (2016)
	Elephants *Loxodonta sp.* *Case 6*	Alteration of habitat by pushing over trees; modulating resources such as soil moisture, nutrient availability and micro-climate. Vegetation change interacts with fire cycles to alter the successional trajectory.	Shrubs	Shannon et al. (2008), Sankaran et al. (2008)
Terrestrial bioturbation	Worms *Case 4*	The biological reworking of soil and sediments. The creation of burrows, the incorporation and mixing of leaf litter into soils and the production of casts. Facilitate soil, gas and water exchange as well as the redistribution of minerals and organic matter through the soil horizon.	Plants, nematodes, bacteria, arthropods	Lavelle et al. (2001), Jouquet et al. (2006), Meysman et al. (2006), Kooch and Jalilvand (2008), Eisenhauer (2010)
	Digging mammals *Case 4*	Tunnelling, construction of burrows and warrens, foraging pits, scrapes and scratchings interact with the substrate to affect resource availability and landscape heterogeneity. Increased soil turnover alters soil-water relations (e.g., moisture, infiltration, porosity) and nutrient cycling.	Plants, fungi, arthropods, reptiles, other mammals	Desbiez and Kluyber (2013), Fleming et al. (2014), Eldridge et al. (2015), Valentine et al. (2018), Coggan et al. (2018),
	Trees *Case 4*	Growth and decay of roots, creating macro-pores within the soil that facilitate higher infiltration and gas exchange; promote soil creep, and when the tree falls, displace soil downhill by tree-throw.	Bryophytes	Gabet et al. (2003), Osterkamp et al. (2012), Jonsson and Esseen (1990)

Table 1.1. continued

Mode of engineering	**Example organism/s**	**Function**	**Organism/s affected**	**References**
Aquatic bioturbation	Greater flamingo *Phoenicopterus roseus* and fiddler crab *Uca tangeri* *Case 4*	Sediment re-working and bio-irrigation activities interact with tidal wetting and drying cycles and nutrient capture on mudflats.	Biofilms	El-Hacen et al. (2019)
	Bivalves, isopods, polychaetes *Case 4*	Construction of extensive networks of galleries alter habitat in deeper sediment layers. Moderates resource flux at the water and sediment interface.	Arthropods, bacteria	Berkenbusch and Rowden (2003), Mermillod-Blondin and Rosenberg (2006)
Hydrology modification	Trees *Case 5*	Shed branches, twigs and leaves create debris dams that modify resource flows in freshwater environments by slowing hydrodynamics.	Arthropods	Bilby and Likens (1980)
	Beaver *Castor canadensis* *Cases 4 and 6*	Builds 'lodges' and dams that increases ephemeral wetland edge habitats.	Sedges, herbaceous plants	Wright et al. (2004), Nummi and Holopainen (2014)
	Common chordgrass *Spartina anglica* *Cases 4 and 6*	Manipulates sediment accretion through retardation of hydrodynamic energy flows.	Crustaceans, bivalves, gastropods, annelids	Bouma et al. (2009), Luiting et al. (1997)
Behaviour modification	Trematode flatworm *Case 4*	Parasitic effects cause gigantism in bivalves, inhibiting burial in sediment. The structure is therefore exposed above the sediment layer and available for colonisation.	Marine invertebrates	Thomas et al. (1999)
	Gastrointestinal nematodes *Case 4*	Alters food consumption in Reindeer *Rangifer tarandus.*	Herbaceous plants	Arneberg et al. (1996)

Figure 1. 2 Images of mallee vegetation depicting the ground layer a) with typical distribution of litter and b) adjacent to a malleefowl mound. (Source: Smith et al. (2017))

1.2.2. Climate

Many large-bodied organisms modify the local micro-climate through autogenic engineering roles in ecosystems, the most ubiquitous in forest landscapes being trees themselves. Trees moderate the micro-climate by altering the light regime with their canopy vegetation, reflecting much of the sun's energy while evaporatively cooling the air. Trees slow the wind speed and thus retain humidity, while providing thermal mass that may resist extreme cooling. They create a more mesic environment that many or most inhabitants rely upon (Didham and Lawton 1999). The ability of trees to interact with the abiotic environment differs depending on species, geography and underlying substrate. Trees differ in their size, leaf-shape and growth form, all of which substantially affect a tree's ability and effectiveness as an autogenic ecosystem engineer (Paz-Kagan et al. 2016).

Trees do not cease to be engineers at death. Tree-fall is a major contributor to forest heterogeneity, the process supporting an array of colonists and even vertebrates that capitalise on the altered light regime. In tropical rainforests, tree-fall sites support increased species richness. Up to 75% of rainforest plant species are thought to rely upon gaps for establishment (Wong and Whitmore 1970, Webb and Tracey 1994).

1.2.3 Hydrology

Hydrological cycles represent some of the most extensively studied systems influenced by ecosystem engineers, both in terrestrial and aquatic ecosystems. In Australia, much attention has been given to arid woodlands and deserts due to their sensitivity to long-term hydrological cycles in driving primary production (Lake 2000, Tongway and Ludwig 2005). Engineering impacts in

such systems are often pronounced. Fossorial mammals have taken centre stage as ecosystem engineers, stemming from their ability to create widespread foraging pits that alter infiltration (Mallen-Cooper et al. 2019). For example, Eldridge et al. (2010) proposed that the short-beaked echidna *Tachyglossus aculeatus*, through its foraging diggings, provides a mechanism for coupling critical resources such as seeds, water and sediments in arid environments.

1.2.4 Nutrient cycling

Perhaps the most widely recognised ecosystem engineers in temperate terrestrial ecosystems are earthworms. While their assimilatory contribution to soil fertility is widely acknowledged, earthworms may also moderate mineralization through physical and chemical alteration of soils. Anecic species redistribute surface litter to subterranean 'middens', in which bacterial and fungal communities form that are unique from that of surrounding soil (Aira et al. 2009). Further, the incorporation of the organic layer with mineral soil in a microbially-rich environment increases the mineralization rate and the bioavailability of nutrients for plant growth. As castings and burrows dry out, the mucous-coated structures stabilise soil, thereby conserving soil organic matter from decomposing over the long-term (Brown et al. 2000).

In xeric regions where earthworms are sparse, the activities of termites take prominence. Termites maintain diverse mechanisms that alter nutrient composition and availability over immense spatial and temporal scales (Dangerfield et al. 1998). Mounds built by termites in the genus *Macrotermes* amass concentrations of clays in landscapes where the aeolian-derived sediments are generally nutrient poor (McAuliffe et al. 2014). The clays comprising the mounds have high cation exchange and are therefore important zones of nutrient flux. When mounds are impacted by heavy rainfall in combination with periodic disturbance from mammals (e.g., aardvarks, anteaters), rich deposits form in outwash pediments, extending radially from mounds (Dangerfield et al. 1998). When a colony dies, the outwash pediment may cover large areas of ground (e.g., ~40 m^2), enriching plant growth on the pediment fringe by providing increased nutrient and water runoff. In Kenyan savannas, provision of such resources alters species composition and biomass of nutrient-demanding grasses (Arshad 1982).

1.3. SCALE AND PATTERN OF ECOSYSTEM ENGINEERING

1.3.1 Geographic scale

The spatial scale at which the effects of an engineer can be detected may vary. For example, at a fine spatial scale the effects of a mistletoe plant may alter nutrient dynamics directly beneath the

host tree, while at a meso-scale these impacts may be less detectable but, importantly, at the population level, mistletoes increase landscape heterogeneity at vast landscape scales (Aukema 2004).

1.3.2 Spatial pattern

Most ecosystem engineers function by increasing habitat heterogeneity, that in turn promotes species richness (MacArthur and MacArthur 1961). The scale at which habitat heterogeneity is influenced by animal engineers may, however, vary greatly (Hastings et al. 2007). On a fine scale, engineered structures may be clustered around spatially discrete activity centres, while at broader scales the occurrence of structures may be highly uniform. For example, the central-place foraging pattern of termites creates nutrient gradients within tens of metres of mounds, causing 'hot-spots' of vegetative growth (Pringle et al. 2010). At the broader scale, a highly uniform pattern of mounds is revealed. This regular pattern of mounds has been linked to the ability of such landscapes to support a greater abundance, biomass and reproductive output of arthropods that would not occur if termite mounds were randomly distributed (Pringle et al. 2010).

In some ecosystems, the engineering role of a species may be spatially restricted owing to topography or underlying geology. In riparian zones along rivers, trees shed living and dead limbs that, under appropriate hydraulic conditions, form debris islands. In turn, these islands provide substrate for seedling germination. The pattern of island formation differs between headwaters and lower reaches of the river, and may structure populations of other plant species (Gurnell and Petts 2006). Inherent in understanding spatial pattern is the consideration of the scale of engineering effects.

1.3.3. Temporal span and pattern

The temporal persistence of engineered structures varies widely between taxa: for example, ephemeral alteration of the physico-chemical properties of the water column by bubble nets cast by the humpback whale *Megaptera novaeangliae* has the potential to interact with marine microorganisms, but only persists a matter of seconds (Hastings et al. 2007); while the fissured bark of the rainforest hoop pine *Araucaria cunninghamii* provides living space used by unique communities of Oribatid mites over centuries (Proctor et al. 2002). Clearly, the impacts of a whales' bubble net to other species (excluding the prey they surround) are trivial; however, some short-lived engineered structures may influence communities simply by their ubiquity in a system. For example, feeding depressions left in shallow sand and mudflats of Western Australia by stingrays (e.g., *Pastinachus atrus*, *Himantura* spp. *Taeniura lymma* and *Urogymnus asperrimus*) only persist for days, yet their effects on micro and macro-invertebrates are evident, owing to the sheer number of depressions made by the feeding rays (O'Shea et al. 2012).

Engineering may be cyclic or episodic. Insect populations, such as leaf-tie caterpillars in the genus *Pseudotelphusa*, moderate the availability of habitat to leaf-chewing invertebrate herbivores (by tying leaves together with silk) on a cyclic seasonal basis. Infestations may occur with episodically varying severity; the effects of leaf-tie caterpillars may function as engineers only when infestations are particularly severe (Lill and Marquis 2003).

Other engineers maintain ecosystems in stasis. Volkenborn et al. (2007) proposed that lugworms *Arenicola marina*, a widespread deposit-feeding marine worm, delayed successional change from sand to mudflats along Germany's northern coastline.

1.3.4 Abiotic legacies

The temporal span of an engineer's impact on a system may be determined by the permanency and resilience of engineered structures. Engineers may function on relatively small timescales, such as the burrowing activity of New Zealand Callianassid shrimps (small decapods that form large colonies), constituting an important marine engineering process in intertidal and shallow subtidal soft-sediments (Gibson et al. 2011). Given the dynamic physical structure of soft sediment marine habitats, the engineered structures would be rapidly lost from the system in the event of extinction of the engineer. On the other hand, the physico-chemical legacy left by termites in the genus *Microhodotermes* in the Cape Province of South Africa is estimated to persist for ~4000 years (Moore and Picker 1991).

1.4. REGULATORY FORCES ON ECOSYSTEM ENGINEERS

1.4.1 Feedbacks

Many engineering activities incorporate feedbacks on the engineers themselves. Engineered structures may have positive or negative consequences for their creators, and as such have the potential to become an 'extended phenotype' (Dawkins 1978). The extended phenotype hypothesis proposes that selection may act upon the engineer through its propensity to create the physical structure, which in turn directly influences survivorship. Dams built by beaver are an archetypal example of an extended phenotype; their creation increases survivorship by allowing animals to access the forest along flooded pathways in relative safety from predators when undertaking further dam-building activities. Similarly, the semi-aquatic reed *Spartina anglica* plays an important role in creating habitat that is suitable for both itself and other species, by reducing hydrodynamic energy and trapping sediment and nutrients in the harsh inter-tidal zone of saltmarsh habitats (Balke et al.

2012). Its ability to raise the elevation of the saltmarsh over years of sediment accretion may result in improved survivorship during environmental change (van Hulzen et al. 2007).

Some allogenic engineers, through their activity, directly moderate their own food resources resulting in a 'farming' effect, although these relationships have rarely been documented. For example, the greater flamingo *Phoenicopterus roseus* in Mauritania, Northwest Africa, creates bowl-shaped feeding depressions in extensive coastal mudflats. Fiddler crabs *Uca tangeri* collect and transport sediment from these low-lying depressions to their burrows, which are constructed upon plateaus in the surrounding matrix. This directional movement and reworking of sediment produces and accentuates a complex irrigation mosaic that connects flamingo feeding depressions in mudflats. As such, tidal hydrodynamic energy is slowed; bowls and connecting gullies remain wetter for longer, capturing nutrients and promoting growth of microalgae, the shared food source of flamingos and crabs (El-Hacen et al. 2019).

1.4.2 Interacting engineers

When engineers interact with each other, significant changes may occur in their environment, thus affecting other species. Lobry de Bruyn and Conacher (1995) suggest that the availability of nutrients held within the mounds of termites (a well-recognised engineer), may be released to plants at a higher rate, stemming from the physical destruction of mounds by another engineer, the short-beaked echidna, when foraging for termites. While this is an example of an additive effect, interactions between engineers may also change the direction of interactive effects. Bailey and Whitham (2002) reported complex interactions between two engineers, elk *Cervus canadensis* and aspen *Populus tremuloides*, together with the influence of fire, affecting arthropod communities in Arizona, USA. In the absence of browsing by elk, fire severity did not influence arthropod abundance; but when browsing was present, sites with high fire severity showed significantly lower arthropod abundance. In contrast, at sites with browsing present and intermediate fire severity, arthropod abundance was significantly higher (Bailey and Whitham 2002). These observations point to a facilitatory effect of the browsers under these fire conditions. Further, the loss of arthropod abundance was disproportionate to the reduction in aspen biomass. Bailey and Whitham (2002) attributed the observed changes in the arthropod community to resource quality (e.g., chemical composition, physical configuration of leaves) rather than purely the availability of physical space provided by the aspen.

1.5. TROPHIC INTERACTIONS WITH ENGINEERING

1.5.1 Herbivory interacts with engineering

The distinction between trophic and herbivory interactions has been an area of some confusion since the inception of the ecosystem engineer concept (see Chapman et al. 2013). Complexity is introduced when the trophic impact of a herbivore on plant species modulates resources for other plants. For example, Gálvez et al. (2008) detailed the effects of rabbit warrens on plant composition and richness. In addition to their bioturbation activities surrounding a warren, rabbits grazed on large herbs and tall grasses, thereby modulating light availability and providing suitable living space for small prostrate and rosette-forming herbs that would otherwise fail to compete with the more palatable species. Moreover, rabbit latrines concentrate soil nutrients and therefore alter plant growth (Willott et al. 2000); however, this process is primarily assimilatory, so while sometimes included as engineering (e.g., Gálvez et al. 2008) this interaction is better characterised within a food web framework.

1.5.2 Predation interacts with engineering

Worldwide, the biological group most studied for their engineering activities are fossorial mammals (Coggan et al. 2018): their impacts can be large and noticeable in terrestrial ecosystems (Mallen-Cooper et al. 2019). Many of the most abundant (and potentially most important) of these mammalian engineers have been lost from landscapes, likely due to predation by introduced predators. In Australia, for example, the formerly widespread burrowing bettong *Bettongia lesueur* is now extinct in the wild (except for fenced sanctuaries and predator-free islands), yet was once considered to be common 'vermin' by European colonists (Noble et al. 2007). The engineering effects of this species may have been important in maintaining floristic diversity and plant recruitment in arid environments, due to the mesic conditions created by extensive foraging pits and disused warrens left by the animals (James et al. 2010). The widespread decline of this species through the 1800s has been attributed to the red fox *Vulpes vulpes* and feral cat *Felis catus*, making it difficult to now establish the true nature and magnitude of engineering by the burrowing bettong, and understand the implications of its loss (Noble et al. 2007).

In contrast, apex predators may function as keystone species to restore populations of engineers. In the widely-publicised reintroduction of the gray wolf *Canis lupus* into Yellowstone National Park, a remarkable trophic cascade was facilitated, extending to the beaver, a major ecosystem engineer of floodplains (Wolf et al. 2007). Wolves had been absent from the park for 70 years, during which elk populations had undergone enormous growth. Over-browsing by elk had removed woody vegetation from riparian zones in valleys, lowering the recruitment of aspen, cottonwoods *Populus*

spp., and willows *Salix* spp. (Ripple and Beschta 2006). With little riparian wooded vegetation, beaver populations declined. Streams had become incised and the water table lowered (Wolf et al. 2007). Following reintroduction of the wolf, elk feeding behaviour changed, shifting away from exposed riparian zones toward higher altitude wooded vegetation. The elk population declined and recruitment of riparian woody vegetation increased, allowing for the recovery of beaver populations (Ripple and Beschta 2012). In turn, hydrological function may be slowly restored by the ecosystem engineering activities of beaver (Wolf et al. 2007).

1.6. EFFECTS OF INTRODUCED ENGINEERS

There is a growing literature on the pressures that exotic ecosystem engineers exert on habitats and their consequences (Crooks 2002). Exotic engineers represent a significant hazard to ecosystems and potentially disrupt a range of ecosystem processes. In this context, examining organisms in their role as engineers may be critical in conservation planning. Instructive studies have sought to identify whether engineering activities by introduced species may differ from seemingly similar activities by native species. For example, James et al. (2011) measured the qualities of foraging pits by the introduced European rabbit *Oryctolagus cuniculus* and compared these with analogous activities by the native burrowing bettong and greater bilby *Macrotis lagotis* in semi-arid Australia. While all three mammal species create shallow foraging pits, those of the two natives supported a near-two-fold increase in seedling abundance when compared with rabbit forage pits. This was attributed to the more effective coupling of plant-available nutrients, porosity, soil moisture and ameliorated temperature extremes within pits dug by the bettong and bilby (James et al. 2011).

1.7. CHALLENGES TO RESEARCH ON ECOSYSTEM ENGINEERS

Challenges to understanding ecosystem engineering include difficulties relating to scaling up manipulation and measurement of engineering effects to the landscape scale, issues arising from pseudoreplication, lack of baseline data, and the temporal constraints of most research projects. Most studies conducted to date have focused on the microhabitat scale (e.g., foraging pit *c.f.* adjacent non-pit, generally on a spatial scale of <5 m) with landscape-scale studies being rare (Coggan et al. 2018). This is partly owing to the difficulty in upscaling measurements and the implicit need to manipulate or measure engineer densities on a landscape scale. Much research on Australian digging mammals has been conducted in predator-free sanctuaries, which of course severely constrains the spatial limits of such studies (but see Decker et al. (2019a) for an example of a broad-scale, multi-sanctuary study). A further complication arising from sanctuary-scale studies is that of pseudoreplication. When mensurative studies are undertaken within small areas and sanctuaries, there is a high risk that external macrogeographic factors will affect interactions and thus confound results. As such, Coggan et al. (2018) advocate for practitioners to implement

manipulative study designs, where possible, and thus avoid using 'natural controls' (where engineering effects do not occur), thereby limiting the likelihood of pseudoreplication.

1.8. ECOSYSTEM ENGINEERS: AN AUSTRALIAN CONTEXT

In Australia, the ecosystem engineering concept has been embraced by many practitioners, especially in arid environments (Coggan et al. 2018) where engineering effects are generally more prominent than in mesic environments (Romero et al. 2014, Decker et al. 2019b, Mallen-Cooper et al. 2019). Most studies conducted in arid zones have focused on engineering of soils by mammals (Martin 2003), particularly those that dig foraging pits (Garkaklis et al. 1998, 2004, Murphy et al. 2005, Eldridge and Mensinga 2007, James and Eldridge 2007, James et al. 2010, Eldridge et al. 2015) or create dens, warrens and burrows (Dickman 2003, Noble et al. 2007, Dawson et al. 2019). Digging mammals have been recognised for their important role in maintaining healthy soils, including the incorporation of organic matter, aeration, improvement in infiltration and the provision of suitable sites for seed germination and seedling establishment (Martin 2003). In turn, these flow on to affect soil microbial communities (Eldridge et al. 2015), vegetation dynamics (Gordon and Letnic 2019, Ross et al. 2020) and invertebrates (Coggan et al. 2016, Grossman et al. 2019). More generally, the deterioration of function in a range of Australian ecosystems has been attributed to the loss of digging mammalian engineers (Fleming et al. 2014).

Global bias in research effort toward mammalian engineers holds true in Australia (Coggan et al. 2018, Mallen-Cooper et al. 2019), possibly reflecting concern with the significant rate of decline in mammals during the past ~200 years (Johnson 2006, Fleming et al. 2014). Many studies have focused on nutrient cycling and seedling establishment facilitated by mammals; however, the potentially deleterious effects on vegetation communities attributable to over browsing and habitat modification by the same species has received relatively little attention (but see Verdon et al. 2016). In a comprehensive meta-analysis, Romero et al. (2014) identified that engineering effects are greater in lower latitudes, owing to the availability of a greater pool of interacting species; yet in Australia there has been little work on engineers in tropical regions (Coggan et al. 2018). Furthermore, avian engineers have been largely overlooked in Australia (but see Song et al. 2012, Nugent et al. 2014, Smith et al. 2017, Mallen-Cooper et al. 2019), especially in mesic ecosystems (Coggan et al. 2018). The diverse engineering functions of varied taxa across multiple environments suggests many animal engineers remain unidentified (Appendix 2.1).

Evaluating effects of engineering in Australian is sensitive to limited baseline data. With the rapid decline in range and abundance of many mammal species (Hobbs and Mooney 1998), much of the ecosystem function maintained by these species has long been lost from the landscape. Fleming et al. (2014) point out that of the 29 species of terrestrial mammals in Australia that dig, ~70% have a

conservation listing (other than of 'Least Concern') by the International Union for Conservation of Nature, including ~20% which are extinct. The loss of function from mammalian extinctions and range contractions may take decades to be fully realised, presenting the problem of 'shifting baselines' (*sensu* Pauly 1995). Finally, the short lifespan of most research projects limits the ability of practitioners to fully appreciate the temporal trends of engineering processes.

1.8.1 Current and future direction of research on ecosystem engineering in Australia

The vast scale and unique biota of Australian ecosystems offers a rich landscape for research on ecosystem engineers. While most literature to date is underpinned by mensurative studies (Coggan et al. 2018), manipulative studies are likely to gain in popularity as practitioners look to extend inference to greater spatial and temporal scales. Increasing societal interest in 'wildness' and 'rewilding' of landscapes (Corlett 2016) suggests that reintroductions of species are likely to continue, thereby providing valuable research opportunities. Such conservation actions will also allow for improved multi-scale studies on ecosystem engineering, a development that will pay homage to the original intention of the ecosystem engineering concept. Finally, recent literature has called for consideration of the separate and combined effects of trophic and engineering contributions of engineers (Sanders et al. 2014, Coggan et al. 2018). Manipulative experiments are likely to play an integral role in answering these pertinent questions.

1.9. STUDY SPECIES - THE SUPERB LYREBIRD

The superb lyrebird *Menura novaehollandiae* is an international icon of the Australian avifauna. It has attracted significant public interest owing to its mimetic abilities and ornate tail (Fig. 1.3), used for sexual displays in which males choreograph species-specific calls with dance-like movements (Dalziell et al. 2013). Lyrebirds are large (~1 kg), ground-foraging passerines, that spend much of their life on the forest floor, turning over leaf litter and topsoil with powerful claws in the search for invertebrate prey.

Figure 1. 3 Male superb lyrebird in partial tail display.

1.9.1 Distribution

The natural distribution of the superb lyrebird generally follows the Great Dividing Range from Stanthorpe, Queensland (Robinson and Frith 1981) to Gippsland in southern Victoria (Fig. 1.4). Kinglake National Park, north of Melbourne, is the western limit of the species (Zann and Dunstan 2008). It can occur from sea level to ~1500 m in altitude (Robinson and Frith 1981, Higgins et al. 2001).

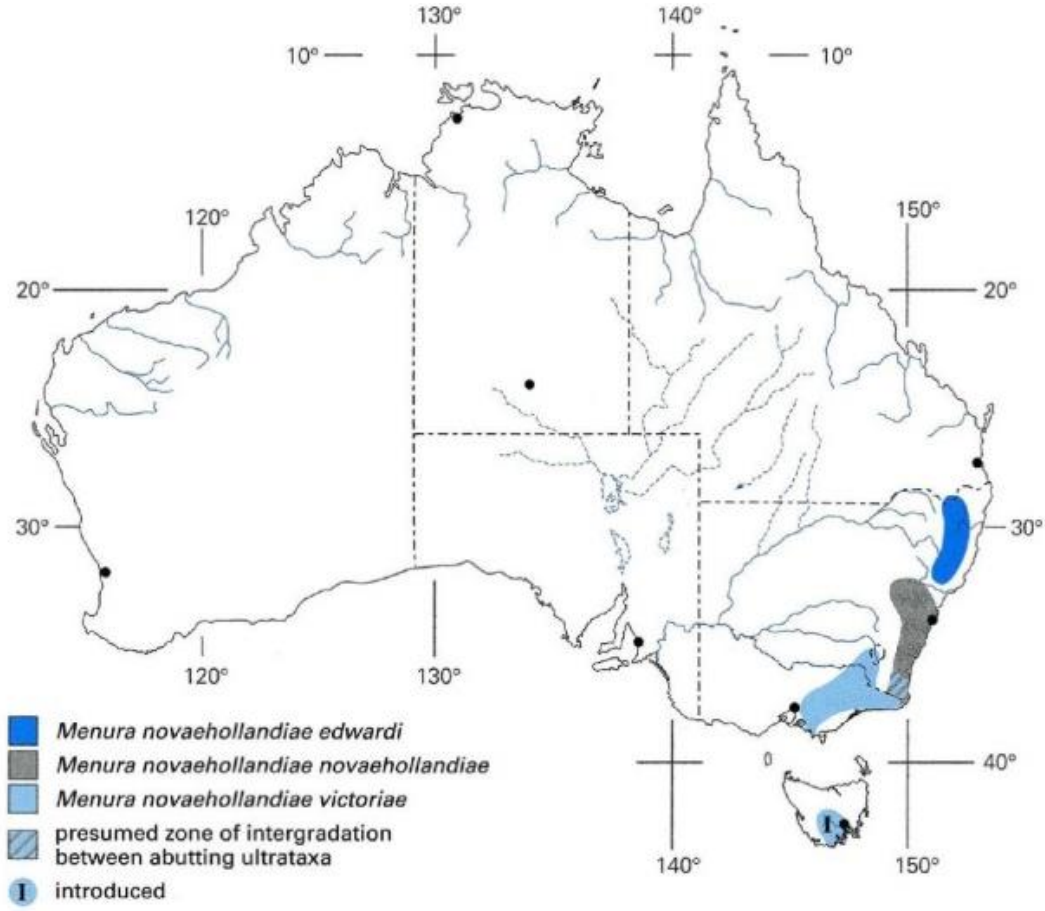


Figure 1. 4 Distribution map of the superb lyrebird (Higgins et al. 2001).

The superb lyrebird is currently considered polytypic, with three named races (Fig. 1.4). *M. novaehollandiae victoriae* occurs in eastern Victoria and is the source of a population introduced into Tasmania in the 1930s, motivated by concern that the species was being over-hunted for the male's tail feathers used to decorate hats (Robinson and Curtis 1996).

1.9.2 Habitat

The superb lyrebird has been recorded in a wide variety of moist forest types in south-eastern Australia (Higgins et al. 2001). While the Albert's lyrebird *Menura alberti*, the sole congener, is found exclusively in sub-tropical rainforest (Robinson and Curtis 1996), the superb lyrebird is more general in its habitat requirements. In the northern extent of its range, populations occur throughout the Queensland and New South Wales granite belt, on the western watershed of the Great Dividing Range (Chisholm 1921, Marshall 1950). In this region, lyrebirds persist in atypically xeric habitats, including shrubby woodland and open forest, where dry rainforest thickets may be important (Watson and Wardell-Johnson 2004). In the sandstone country of the Blue Mountains near Bathurst,

lyrebirds inhabit dry sclerophyll forest characterised by diverse heathland and acacia understory (Powys 1995); however, breeding activity may still be concentrated in resource-rich tall wet forest and warm temperate rainforest (Dalziell and Welbergen 2016). Primary sub-tropical rainforest is less commonly inhabited by superb lyrebirds (Robinson and Curtis 1996). Tall wet, mountain ash forests of Victoria's Central Highlands represent optimal habitat for the superb lyrebird (Loyn 1985), and the habitat in which the species has been studied most extensively over the past 50 years - particularly in Sherbrooke Forest in the Dandenong Ranges National Park, east of Melbourne (e.g., Watson 1965, Reilly 1970, Kenyon 1972, Smith 1982, Lill 1986, Smith 1988, Zann and Dunstan 2008, Dalziell et al. 2013, Maisey et al. 2016, Maisey et al. 2018).

1.9.3 Breeding

The superb lyrebird conforms to a classic k-selection strategy, with slow life-history traits (Lill 1986). Individuals are long-lived, with uniparental female care; a single egg clutch results in a maximum of one chick each year, and juveniles mature slowly (four years to breeding for females and up to eight years for males to attain full breeding plumage (Smith 1988)). Females begin to construct the large, domed nest in late autumn (Fig. 1.5). Nests may be built at ground level, usually placed against a solid backing such as a tree or embankment, or in excess of 16 m high, in the bow of a large eucalypt (Maisey et al. 2016). A new nest is constructed each year. In the south of the species range, nest sites are more likely to be located in rainforest vegetation and near streams or gullies, where litter is deep and overstorey vegetation is tall (hypothesised to provide concealment from predators (Maisey et al. 2018)). In northern parts of the lyrebirds' range, nests are often built on rock faces or boulders (Smith 1988).

From early June, male lyrebirds vocalise from their territory and clear display courts (Fig. 1.6), known as 'mounds', where their complex courtship display and mating takes place through winter months (Kenyon 1972). Male territories are generally placed in topographical areas of acoustic prominence, often on saddles or ridges (Maisey et al. 2018). Each day during the winter breeding season, males vocalise, often from elevated logs or from tree limbs, to attract inspecting females. Up to 50% of daylight hours are spent vocalising, representing ~45% of basal metabolic rate (Lill 1986).

Figure 1. 5 The bulky domed nest of a superb lyrebird. Note the shed tail feather from a male lyrebird woven into the lining.

When females are detected, the male flies to a nearby mound (Fig. 1.6), of which there may be in excess of a dozen in each territory (Kenyon 1972), to produce one of the most complex courtship displays of song and dance in the animal kingdom (Dalziell et al. 2013). Males produce a suite of mimicry referred to as 'recital mimicry' while in tail display (Dalziell et al. 2013); but when the female enters the mound the male produces a predictable sequence of lyrebird-specific song types, which are contextualised by the female's behaviour.

Figure 1. 6 A typical male display ‘mound’ surrounded by dense ground fern.

After laying, a six-week incubation follows. The nestling is confined to the nest for a further 6-7 weeks (Smith 1988). During this period, female lyrebirds defend the nest against intruders with piercing alarm whistles and visual threat displays (Fig. 1.7). Females are highly territorial and conspecific nest destruction by colour-marked neighbouring females has been recorded on motion-sensing cameras in Sherbrooke Forest (Austin et al. 2019). After fledging, the chick remains with its parent until the next breeding attempt, typically in the following year but occasionally two seasons thereafter (Sherbrooke Lyrebird Survey Group, unpublished data).

Figure 1. 7 Female superb lyrebird in threat display near its nest site.

1.9.4 Foraging

The diet of the superb lyrebird consists of macro-invertebrates foraged from the leaf-litter and topsoil (Lill 1996). Lyrebirds use their powerful legs and large claws to rake through the litter layer and soil, generally foraging upslope while soil and litter are displaced in a downslope direction (Ashton and Bassett 1997) (see supplementary material S1: video of litter and soil displacement by a superb lyrebird). In situations where the litter layer is open, foraging sites are chaotically

distributed across the forest floor (Ashton and Bassett 1997). Foraging disturbances cause small 'micro-terraces' creating structural complexity in the litter layer. Ashton and Bassett (1997) suggested that lyrebird foraging activity may follow seasonal topographical cycles, with foraging excursions to drier, sup-optimal habitat in the wetter months of winter and spring, while contracting foraging activity to moist gullies over summer months.

Prey items are varied. Lill (1986) analysed the contents of 43 nestling meals, indicating that amphipods (order: Amphipoda) and earthworms (order: Opisthopora) were the most common prey items, composing 25% and 19.2% of prey, respectively. Beetles (order: Coleoptera) comprised 16.3% of prey items, with centipedes (order: Chilopoda) at 12.5% followed by fly larvae and pupae (order: Diptera) at 10.6%, with lesser occurrences of spiders (order: Araneida - 8.7%), millipedes (order: Diplopoda - 2.9%) and slaters (order: Isopoda – 1.9%). Invertebrates represented by at least 1% of prey items included earwigs (order: Dermaptera), lacewings (order: Neuroptera) and the ootheca (egg cluster) of cockroaches (order: Blattodea). Robinson and Frith (1981) described a similar diet in the Australian Capital Territory, but with the addition of scorpions (order: Scorpiones); while Smith (1988) recorded scorpions and land yabbies (genus: *Engaeus*) in the adult lyrebird's diet at Sherbrooke Forest. In the sandstone country of the Sydney basin, Webb and Whiting (2006) found that lyrebirds readily attacked plasticine models of two species of juvenile snake, but accounts of lyrebirds attacking live snakes are not substantiated (Lill 2006).

1.10. THE SUPERB LYREBIRD AS AN ECOSYSTEM ENGINEER

When superb lyrebirds forage they dramatically alter the forest floor with their scratchings. This disturbance regime is likely to affect ecological processes and habitat structure for other organisms through alteration to litter, nutrients, fire behaviour and vegetation structure. The aim of the research documented in this thesis was to investigate the potential role of the superb lyrebird as an ecosystem engineer.

1.10.1 Nutrient cycling

Forest productivity relies on nutrient availability and cycling, especially in the nitrogen-rich forests of the Victorian Central Highlands (Adams and Attiwill 1986). Nitrogen (N) and phosphorus (P) are essential for plant growth but are limiting nutrients in most Australian forest systems (Raison 1980). The amount of N and P in mineralised form (and therefore available for plant uptake) is moderated by edaphic factors such as moisture, temperature and pH, including the activity of microbial communities.

Superb lyrebirds are likely to directly increase the rate of nutrient cycling in forest soils via their perturbation of the litter and soil layer. Under the effects of foraging, mineral soil is brought into close contact with litter, physically fragmenting litter and increasing aeration and infiltration. These actions are likely to interact with soil bacterial and fungal communities.

Furthermore, if superb lyrebirds alter the forest habitat in ways that influence macro-invertebrates, a secondary pathway leading to nutrient cycling may include structural changes caused by detritivores. Detritivore guilds perform the essential ecosystem service of litter breakdown, playing an important antecedent role to nutrient cycling by bacteria and fungi (Aerts 1997).

1.10.2 Litter and soil habitats

As lyrebirds forage over an area, micro-habitats are created in the form of discrete litter piles that are interposed with soil, litter-free pits (Tassell 2014) and micro-terraces (Ashton and Bassett 1997), arranged within a matrix of continuous leaf litter (Fig. 1.8). A suite of micro-organisms and macro-invertebrates may potentially take advantage of such spatial heterogeneity (Hansen 2000), from bacteria and fungi to detritivore predators such as chilopods and arachnids (Bultman and Uetz 1982, Langellotto and Denno 2006). Lyrebirds may interact with invertebrate assemblages, either by selecting specific spatial contexts for foraging, or by preying on invertebrates more likely to occur in open areas that are accessible to lyrebirds. Surprisingly, the role of habitat alteration by lyrebirds on litter invertebrates within the native range of the species is entirely unknown, and evidence of such associations in the literature is largely speculative (Adamson et al. 1983).

While it is difficult to disentangle the effects of predation (on invertebrates) from those of habitat modification, it is possible that lyrebirds promote the abundance of macro-invertebrate species by increasing habitat complexity and microbial biomass (food source for many macro-invertebrates), thereby ‘farming’ their prey. This interaction would fit Case 4 described by Jones et al. (1994), extending this to include a positive feedback on the engineer (Fig. 1.9). In this scenario, lyrebirds modulate the litter layer (represented by the transition from State 1 to State 2 in Case 4; Fig. 1.9), thereby altering resource flows (i.e. habitat quality) to invertebrates. These invertebrates would, in turn, provide a food resource for the superb lyrebird in a positive feedback loop.

Figure 1. 8 Image showing ‘terracette’ formed by a foraging superb lyrebird at the axis of a large tree root.

Farming interactions have been documented in ants, termites and some beetles (Mueller and Gerardo 2002), with scant evidence that some mammals may ‘farm’ their food plants over extended periods of time (Oldfield and Evans 2016); however, examples of non-human vertebrate ‘farming’ mutualisms are rare. Testing a ‘farming’ hypothesis in lyrebirds forms the basis for part of this study (see below).

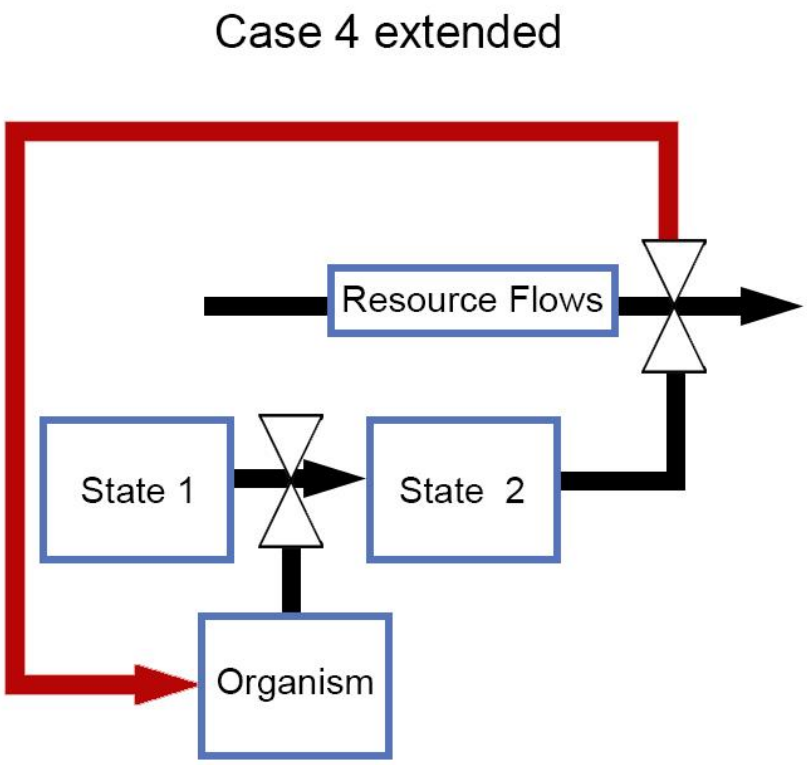


Figure 1. 9 Conceptual model of the superb lyrebird's role as an allogenic engineer as described by Case 4 (Jones et al. 1994), extended to include a hypothesised positive feedback loop (denoted by the red arrow) that may emerge from a 'farming' mutualism.

1.10.3 Vegetation composition and structure

The interaction between lyrebird foraging and vegetation structure is likely to be complex. Foraging lyrebirds may promote the germination of seeds by clearing leaf litter and disturbing the topsoil (Fig. 1.10), while decreasing the survivorship of seedlings by uprooting and smothering them with litter. The net result on plant recruitment may be related to the structure of pre-existing understorey plants such as ground ferns, and the traits of such species. Song et al. (2012) tested for relationships between ground ferns, seedlings and the presence of the litter-foraging brush turkey *Alectura lathami* and Albert's lyrebird in eastern Australia's subtropical rainforest. Where vegetative ground cover was high, ground ferns impeded light transmission and exerted a negative effect on seedling survival. Conversely, where ground ferns were sparse, they decreased litter-smothering of seedlings, increasing their survival. Importantly, ferns also impeded the access of the two litter-foraging birds, resulting in an overall net increase in seedling survival. When litter-foraging birds were excluded, the positive effect of ground ferns on seedlings was non-significant, suggesting that foraging disturbance at low levels among sparse ground ferns promoted high germination rates and a net increase in seedling survivorship. Such interactions have not been investigated in eucalypt forests inhabited by the superb lyrebird.

Figure 1. 10 Large lignotubers of the musk daisy *Olearia argophylla* excavated by lyrebirds in Sherbrooke Forest. Note the extensive mineral soil visible where the leaf litter has been buried. A pair of binoculars is included for scale.

Despite behavioural and physiological traits of the superb lyrebird suggesting this species may be an important ecosystem engineer, the engineering effects of lyrebirds on other species are yet to be determined. Further, the ecological function performed by lyrebirds may vary between forest types. For example, in temperate rainforests where most plant species germinate on elevated logs and treeferns (Ashton 2000), litter smothering may be less influential than in forest types that rely on wildfire to drive massive episodic regeneration, such as in a wet eucalypt forest. The relationships between the superb lyrebird and its environment are complex (Fig. 1.11) and careful consideration of these is required to understand the ecological role this species plays in forest landscapes.

1.11 THESIS – AIMS AND OBJECTIVES

This thesis outlines the first comprehensive study of the superb lyrebird *Menura novaehollandiae* as an ecosystem engineer. The study was conducted in the southern fall of Victoria's Central Highlands, in three forest types. A two-year manipulative study, in which observational and mensurative data were recorded within replicated experimental units, was undertaken to rigorously assess the functional role of the superb lyrebird. Data were systematically collected to test the engineering effect of this species on key abiotic features of their habitat and to determine whether such effects influenced other organisms in the environment (invertebrates, plants, litter and soil fungi).

1.11.1 Overview of thesis chapters and key questions

Chapter 1 (this chapter) introduces the role of ecosystem engineers, outlining key concepts and knowledge in a global context. It provides an overview of the classification of, and mechanisms underlying, ecosystem engineering and the ecological processes associated with engineered habitats. Current research directions in the field are recognised, in particular the need for broad-scale manipulative experiments to test the theoretical framework of the ecosystem engineering concept. This chapter also presents a general introduction to the study species, proposing key processes concerning nutrient cycling and litter and soil habitats that may constitute engineering by foraging lyrebirds.

Chapter 2 characterises the physical changes to ecosystems arising from foraging by the superb lyrebird. It sets out the design of a manipulative experiment to test hypotheses relating to engineering by the superb lyrebird. This experiment is the foundation on which subsequent chapters are based. Key experimental contrasts between engineering and trophic impacts on the ecosystem are detailed. The results presented relate to the physical abiotic changes caused by foraging lyrebirds and the landscape pattern of foraging activity. Key questions include:

How much litter and soil does the superb lyrebird displace?

How does the foraging activity of the superb lyrebird affect the physical characteristics of litter and soil (i.e. litter depth, soil compaction, moisture, soil nutrients)?

Does the superb lyrebird show seasonal patterns when foraging in three different forest types?

Chapter 3 details the interactions between lyrebird foraging and invertebrates. In addition to testing for engineering impacts on litter and soil-dwelling invertebrates, this chapter tests the hypothesis that lyrebirds 'farm' their invertebrate prey. The key questions posed are:

Does foraging by the superb lyrebird:

- *affect species richness of invertebrates?*
- *influence the abundance of invertebrates?*
- *influence the community composition of invertebrates?*
- *affect the biomass of invertebrate prey species?*

Chapter 4 investigates the engineering impacts of lyrebirds on vegetation. This chapter details the findings from the manipulative experiment relating to seedlings, plant species composition and vegetation structure, and contrasts engineering impacts with herbivory from mammal species. The key questions posed in the chapter include the following:

Does foraging by the superb lyrebird:

- *interact with germination and seedling density?*
- *influence floristic richness?*
- *influence plant community composition?*
- *impact ground covers (herbs and ferns)?*
- *affect low vegetation structure?*

Chapter 5 addresses the impacts of foraging by lyrebirds on litter and soil fungal communities. It presents the application of next-generation DNA sequencing techniques in a microbial ecology framework to understand ecological processes that affect the diverse fungal community of litter and soil. The specific questions posed include:

Does superb lyrebird foraging affect:

- *fungal richness and diversity?*
- *fungal community structure?*

Do litter and soil fungal communities differ between forest types?

Chapter 6 brings together the main conclusions of each data chapter to provide a comprehensive appraisal of the superb lyrebird as an ecosystem engineer. This synthesis expounds the contribution of this study to the ecosystem engineering literature and interprets the outcomes in both a theoretical and management context.

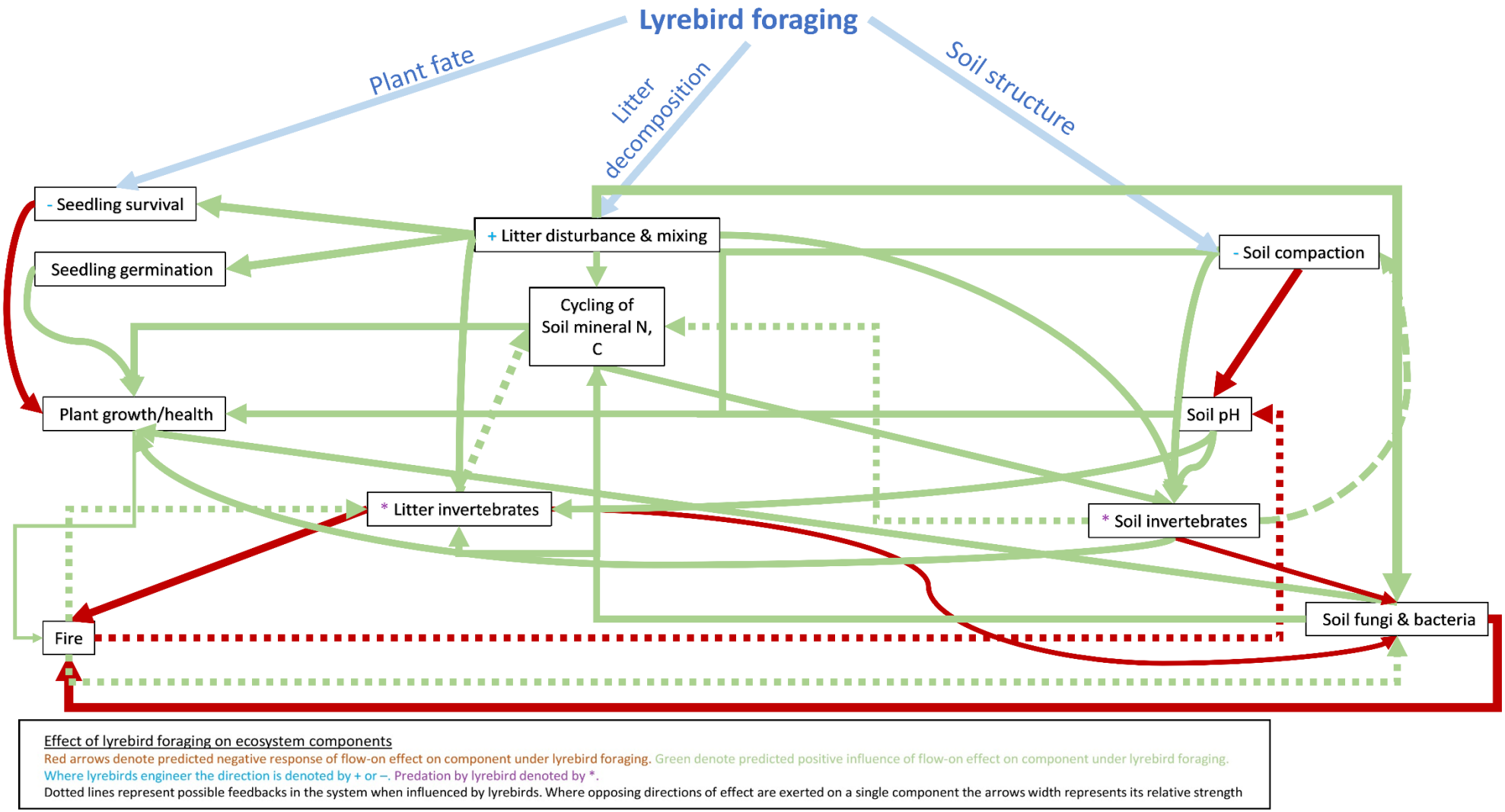


Figure 1. 11 Conceptual diagram outlining the hypothesised flow-on effects and feedbacks for the superb lyrebird when functioning as an ecosystem engineer

Chapter Two

Foraging by an avian ecosystem engineer extensively modifies litter and soil layer in forest ecosystems

Plate 3. Mature male superb lyrebird in display on an elevated branch.

This chapter has been accepted for publication in *Ecological Applications* (accepted June 2020).

ABSTRACT

Ecosystem engineers physically modify their environment, thereby altering habitats for other organisms. Increasingly, 'engineers' are recognised as an important focus for conservation and ecological restoration because their actions affect a range of ecosystem processes and thereby influence how ecosystems function. The superb lyrebird *Menura novaehollandiae* is proposed as an ecosystem engineer in forests of south-eastern Australia due to the volume of soil and litter it turns over when foraging. We measured the seasonal and spatial patterns of foraging by lyrebirds and the amount of soil displaced in forests in the Central Highlands, Victoria. We tested the effects of foraging on litter, soil nutrients and soil physical properties by using an experimental approach with three treatments: lyrebird exclusion, lyrebird exclusion with simulated foraging, and non-exclusion reference plots. Treatments were replicated in three forest types in each of three forest blocks. Lyrebirds foraged extensively in all forest types in all seasons. On average, lyrebirds displaced 155.7 t/ha of litter and soil in a 12-month period. Greater displacement occurred where vegetation complexity (<50 cm height) was low. After two years of lyrebird exclusion, soil compaction (top 7.5 cm) increased by 37% in exclusion plots compared with baseline measures, whilst in unfenced plots it decreased by 22%. Litter depth was almost three times greater in fenced than unfenced plots. Soil moisture, pH and soil nutrients showed no difference between treatments. The enormous extent of litter and soil turned over by the superb lyrebird is unparalleled by any other vertebrate soil engineer in terrestrial ecosystems globally. The profound influence of such foraging activity on forest ecosystems is magnified by its year-round pattern and widespread distribution. The disturbance regime that lyrebirds impose has implications for diverse ecosystem processes including decomposition and nutrient cycling, the composition of litter- and soil-dwelling invertebrate communities, the shaping of ground-layer vegetation patterns, and fire behaviour and post-fire ecosystem recovery. Maintaining lyrebird populations as a key facilitator of ecosystem function is now timely and critical as unprecedented wildfires in eastern Australia in summer 2019/2020 have severely burned ~10 million ha of forest, including ~30% of the geographic range of the superb lyrebird.

2.1 INTRODUCTION

Ecosystem engineers modify the physical environment in ways that create, maintain or destroy habitat used by other organisms (Jones et al. 1994, Wright and Jones 2006, Hastings et al. 2007). Increasingly, engineers also are recognised for their role in maintaining ecosystem functions, such as hydrological regulation and nutrient cycling (Moore 2006, Kristensen 2008, Cui et al. 2019). Owing to these important interactions, ecosystem engineers are becoming a focus for much conservation and ecosystem restoration (Polak and Saltz 2011, Gibbs et al. 2014), with mounting examples of success (Decleer et al. 2013, Seddon et al. 2014, McCullough Hennessy et al. 2016, Law et al. 2017). To fulfil conservation expectations of engineers, a critical first step is to understand the impacts of the engineer, including its pattern of activity and extent of physical habitat alteration (Byers et al. 2006, Sandom et al. 2013).

In ecosystems worldwide, engineers that cause bioturbation feature in the literature for their profound impact on the structure and character of the topsoil (Coggan et al. 2018, Mallen-Cooper et al. 2019). In arid and semi-arid ecosystems, for example, many fossorial mammals create new microhabitats through excavation of foraging pits and the construction of burrows for shelter (Eldridge et al. 2010, James et al. 2011, Fleming et al. 2014). Most engineers fulfil facilitative roles (e.g., increase the diversity of micro-habitats available to other organisms) within their natural habitats and their activities enhance soil moisture, increase decomposition and nutrient cycling, and promote the availability of nutrients, thus affecting plant growth (Valentine et al. 2018) and microbial activity (Dauber and Wolters 2000, Eldridge et al. 2015, Decker et al. 2019a).

A wide range of faunal species are involved in bioturbation of soils. Charles Darwin's publications on earthworms are perhaps the earliest descriptions of the activities of an ecosystem engineer (Feller et al. 2003, Meysman et al. 2006), and describe one of the most influential animal engineers acting upon soils. Many vertebrates are also prolific in moving soil: Arctic ground squirrels *Citellus undulatus* displaced up to 19.7 t ha^{-1} $year^{-1}$ on southern exposures in the Arctic (Price 1971), while foraging by the northern pocket gopher *Thomomys talpoides* may displace 11-14.5 t ha^{-1} $year^{-1}$ in prairie habitats of North America (Butler 1995). In a global meta-analysis of soil-disturbing vertebrates, Mallen-Cooper et al. (2019) found that phylogeny did not predict the mode or scale of engineering effects, therefore surmising that "the same functionality could readily evolve in different taxa". Surprisingly, there has been limited research on the role of avian engineers worldwide (Coggan et al. 2018), yet many ground-foraging bird species are likely to interact with soil characteristics in important ways.

The superb lyrebird *Menura novaehollandiae* has been proposed as an ecosystem engineer due to the volume of litter and soil displaced by the birds when foraging (Nugent et al. 2014, Tassell 2014). This species is a large ground-dwelling passerine (800-1000 g), widespread in temperate forests on

the eastern seaboard of Australia. It is renowned for its mimetic ability, in which advertising males incorporate extensive mimetic signals with complex courtship displays during the winter breeding season (Putland et al. 2006, Dalziell et al. 2013). Foraging lyrebirds rake the forest floor in search of invertebrate prey, and in doing so shift large quantities of litter and soil (Ashton and Bassett 1997). This disturbance has the potential to influence other biota (e.g., macro-invertebrates, plants, microbes), through fine-scale effects on litter and soil properties (e.g., depth, compaction, moisture). When foraging, lyrebirds are influenced by a range of ecological drivers including vegetation characteristics (Maisey et al. 2018), availability of food resources (Lill 1996) and perceived risk of predation; such that the extent and pattern of their engineering impacts are likely to differ spatially between vegetation communities and locations, and temporally between seasons.

We examined the impact of foraging by the superb lyrebird on the forest-floor litter and soil in eucalypt forests of the central highlands of Victoria, south-eastern Australia. To understand the potential importance of the engineering actions of this species, this study had two main aims: 1) to quantify the spatial pattern of foraging by lyrebirds and the extent of their soil displacement in three forest types over a seasonal cycle; and 2) to use a manipulative experiment to test the impact of lyrebird foraging on soil compaction, litter depth, soil moisture, and the composition of soil nutrients.

2.2 MATERIALS AND METHODS

2.2.1 Study area

This study was conducted in the southern fall of the Central Highlands of Victoria, Australia (Fig. 2.1). The topography is characterised by moderate to steep slopes and high plateaus; valleys are comprised of alluvial flats. In this region, lyrebirds commonly occur in three distinct forest types; damp forest, wet forest and cool temperate rainforest (Loyn 1985, van der Ree and Loyn 2002).

Three forest blocks were selected: 1) Sherbrooke Forest, part of the Dandenong Ranges National Park; 2) Yarra Ranges National Park, between Healesville and Warburton; and 3) Britannia Creek catchment between Warburton and Powelltown within the Yarra State Forest. Each location is geographically isolated from others by the Yarra Valley (i.e. >10 km between forest blocks, mostly semi-rural land). Experimental manipulations were undertaken at each location (Fig. 2.1).

Sherbrooke Forest ranges from 400-600 m above sea level (ASL) and receives ~1200 mm of rainfall per annum. It is predominantly wet forest, with cool temperate rainforest restricted to linear streamside areas (Parks Victoria 2006). Sections of the park with a westerly aspect support damp

forest. Most of Sherbrooke Forest has regrown from intense historic logging that ceased in 1927 (Friends of Sherbrooke Forest 2000).

The Britannia Creek catchment has an elevation 400-800 m ASL and mean annual rainfall >1400 mm. This area has experienced intense logging over the past century, but is not subject to active forestry, and thus retains mature stands of the three forest types (van der Ree and Loyn 2002). This forest block is subject to seasonal firewood collection, intense use by recreational vehicles, recreational hunting, and management to reduce bushfire risk.

Yarra Ranges National Park has a large range in elevation (400-1300 m ASL) and similar mean annual rainfall and logging history to that at Britannia Creek (Fig. 2.1). While the Yarra Ranges National Park was historically a timber production forest, since 1995 it has been managed primarily for nature conservation.

Cool temperate rainforest (CTR) is dominated by southern sassafras *Atherosperma moschatum* and myrtle beech *Nothofagus cunninghamii* (the latter absent from Sherbrooke Forest), with a fern-rich understorey. Typically, low vegetation may be sparse due to the dense shade provided by the dominant rainforest tree species.

Wet forest is widespread in each forest block, much of which is regrowth mountain ash *Eucalyptus regnans* that regenerated following severe bushfires in 1939. This forest type typically has a tall canopy of eucalypts, with a middle storey comprised of blackwood and silver wattle *Acacia melanoxylon* and *A. dealbata* over a diverse mix of small trees. The ground layer is often scattered with terrestrial groundferns. Soft treeferns *Dicksonia antarctica* and rough treeferns *Cyathea australis* are widespread in this forest type.

Damp forest is a drier forest type, dominated by messmate *E. obliqua* and mountain grey gum *E. cypellocarpa*. The middle storey is similar in composition to wet forest, but sometimes is absent, with more bracken *Pteridium esculentum*, forest wiregrass *Tetrarrhena juncea* and a diverse herb layer.

The superb lyrebird is ubiquitous in all three forest blocks (Higgins et al. 2001). Lyrebirds forage in each forest type (Ashton and Bassett 1997, Maisey et al. 2018), but avoid forest that has recently experienced bushfire (Nugent et al. 2014). They prefer to forage in areas with open ground cover (Ashton and Bassett 1997, Maisey et al. 2018) and thus are likely to avoid young regrowth forest. Consequently, each study location was chosen because it contained mature stands of each forest type and had not undergone logging or experienced severe wildfire for >30 years.

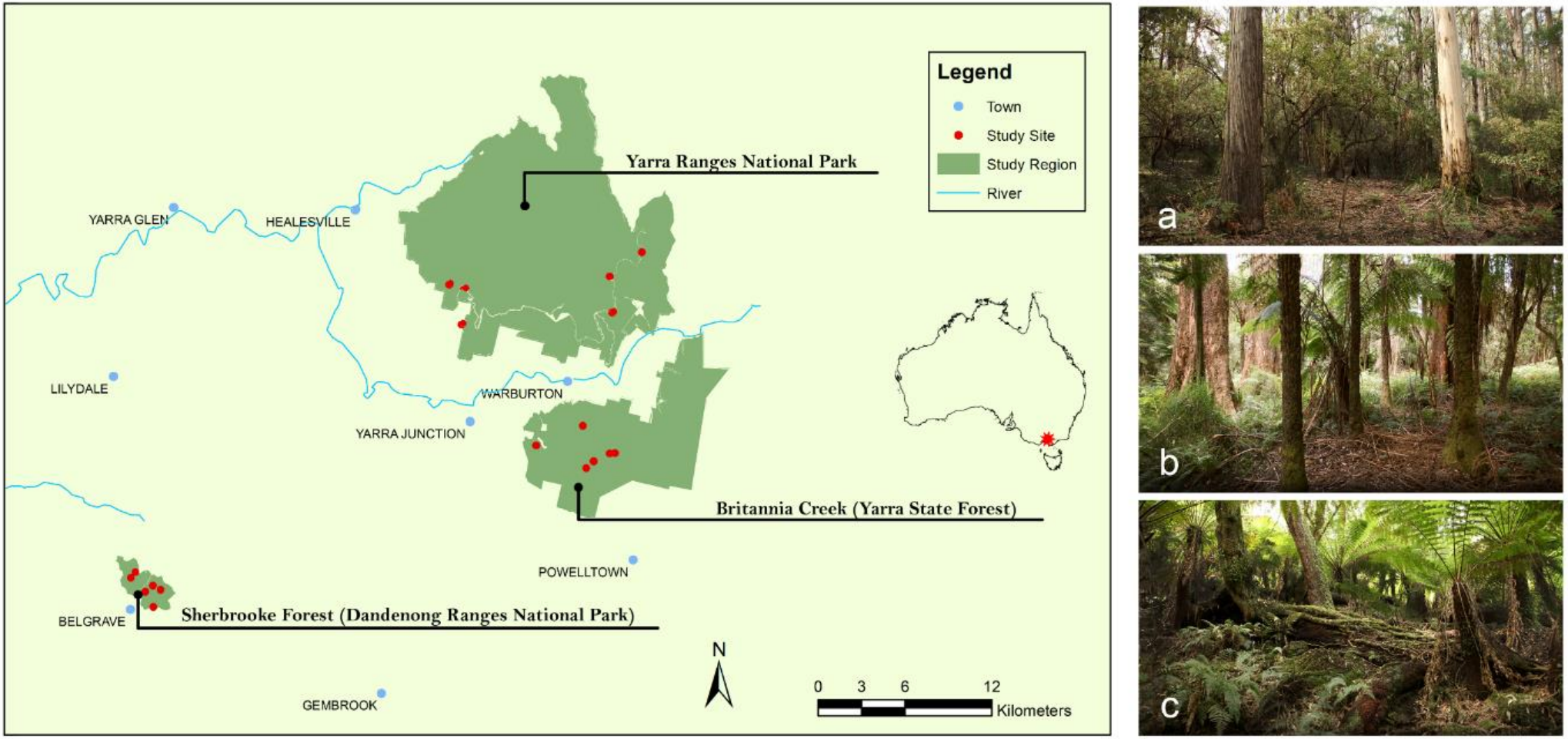


Figure 2. 1 The study region showing three forest blocks and the location of study sites within each. The panel at right provides exemplar images of a) damp forest, b) wet forest and c) cool temperate rainforest.

2.2.2 Study design

In each forest block, potential sites in each of cool temperate rainforest, wet forest and damp forest, were compiled using computer-generated coordinates. Only sites between 40 and 300 m from access tracks were assessed for suitability. Sites were repositioned if they fell within 400 m of one another, as the territory of a single lyrebird may encompass this distance (Smith 1988). Forest type and fire history were assessed from publicly available mapping undertaken by the Victorian government land management agency, the Department of Environment, Land, Water and Planning, and field visits made to ground-truth the vegetation. In total, 18 sites were selected; two sites in each forest type, in each forest block.

At each site, three experimental plots (each 3 x 3 m) were established in October 2015. Plots were positioned along the contour of the slope, with each plot placed at a random distance between 5 and 40 m from the first established plot (Fig. 2.2). Vegetation was surveyed in the field before plot establishment to ensure low vegetation (<50 cm) would not inhibit foraging lyrebirds. A ranging pole was used to ensure no more than five out of nine point measures (arranged in a cross centred on each plot) intersected with vegetation, as lyrebirds avoid foraging in vegetation beyond this density (Maisey et al. 2018). If the vegetation structure was not sufficiently open at the first randomly selected distance, the contour was followed until the vegetation was sufficiently open and each plot conformed. One of the three plots was randomly assigned to remain unfenced, allowing lyrebirds to access the plot (unfenced treatment). The two remaining plots were fenced to exclude access by lyrebirds; one remained undisturbed (fenced treatment), and the other was subject to simulated lyrebird foraging (simulated treatment; see below) on a monthly basis between October 2015 and September 2017.

At fenced and simulated plots, fences were constructed of wire netting (5 cm mesh) to a height of 120 cm, with steel stakes at each corner. Netting was pinned at ground level and flagging tape strung across the top of the fence to deter lyrebirds from flying into the plot (Fig. 2.2). At unfenced plots, four steel stakes were used to mark the corners. Between November 2015 and August - October 2016, a single motion-sensing camera (Reconyx hyperfire, model HC600) was set at the unfenced plot at each site to confirm the presence of lyrebirds. Cameras were programmed to capture two images per trigger event, with a 60 s rest period. Lyrebirds were confirmed to be present at every site.

Fences were monitored on a monthly basis. At a small proportion of monthly checks (at 6 plots, representing <3% of all fenced plot observations), fences were thought to have been breached by lyrebirds, particularly during the first six months. Lyrebird scratching in a fenced plot was so seldom observed that we assume any effects to be negligible.

2.2.3 Foraging simulation

On each monthly visit to a site, the area disturbed by lyrebirds in the unfenced plot was visually assessed and recorded as a percent cover estimate. In the simulated plot at that site, foraging was then simulated using a three-pronged hand rake (the approximate width of a lyrebird foot, ~10 cm), to replicate the foraging cover and configuration in the unfenced plot. This treatment was included to control for the nutritive inputs (in faeces) and offtake (predation of invertebrates) by lyrebirds, thereby isolating their engineering effects.

2.2.4 Effect of fencing on litter and soil

To determine the effect of fencing on litter and soil attributes, a true procedural control would involve sampling fenced plots in these forest types *without* lyrebirds. Such forests do not exist; however, by comparing the simulated plot with the fenced plot, we can separate the effect of lyrebirds (of interest) from the effect of fencing (not of interest), as the effect of fencing is present for both treatments.

We expected that, over time, leaf litter would accumulate against the upslope edge of fences due to abiotic (i.e. wind and gravity) displacement. Likewise, litter may fall away downslope. To determine the degree and distance to which this 'halo' effect of the fence may occur, litter depth was measured at 10 cm increments beginning 10 cm from the fence or unfenced plot edge, running perpendicular to the contour, for 100 cm into each plot (Fig. 2.2). This procedure was repeated 1 m from each corner of the plot, and the two measurements for each distance increment were averaged. This procedure was repeated for both up-slope and down-slope positions within the plot.

2.2.5 Litter and soil displaced by lyrebirds

To compute a forest-level measure of litter and soil displacement by lyrebirds, a randomly oriented 5 m transect line was established at the original coordinate for each experimental site (n=18). Five free-draining soil collection buckets, 14 cm diameter and 25 cm depth, were placed 1 m apart, dug into the soil to sit flush with the surface, and secured with steel pins. Two additional buckets were randomly positioned within fenced plots (without simulated foraging) (Fig. 2.2).

Collection buckets were monitored monthly for 12 months from October 2015. Litter and soil were collected at six-monthly intervals. If a bucket was close to filling within this period, contents were collected, dried (as below), and stored until calculation of the six-monthly plot totals. The contents were oven dried at 70°C for 72 hours, then weighed. To correct for litter-fall and soil displaced by non-lyrebird agents (e.g., wind, burrowing crayfish, small mammals), the per-area value of the oven-dried weight (ODW) of litter and soil (combined) collected in the fenced plot was subtracted

from that collected on the transect at each site. The mass of litter and soil displaced was expressed as tonnes of material per hectare, per year.

2.2.6 Structural complexity of vegetation

The structural complexity of vegetation below 0.5 m height influences where lyrebirds forage (Maisey et al. 2018). Vegetation structure was measured at each site along four 25 m transects, oriented in the cardinal directions (Fig. 2.2). The number of vegetation contacts (alive or dead: <50 cm height) on a ranging pole at every metre along each transect was summed across transects to provide an overall measure of structural complexity.

2.2.7 Physical characteristics of the soil

Physical characteristics of the soil were measured at three-monthly intervals for 24 months (n = 9 measurements) starting with a baseline measurement in early October (austral spring) 2015 (at the time of fence establishment). For each soil property (below), measures were recorded at five points arranged in a cross, within a 1 m^2 area at the centre of each plot (Fig. 2.2). Compaction of litter and soil was measured with a mechanical penetrometer (pounds per square inch) in three consecutive depth increments (each 7.5 cm). Volumetric soil moisture was recorded in the top 12 cm of soil with a digital moisture meter (% volumetric moisture content). Soil pH was measured with a hand-held flat-surface electrode pH meter ('Fieldscout' instruments were used for compaction, moisture and pH, Spectrum Technologies, Aurora, Illinois, USA). Litter depth was measured with a mechanical combination square, with a reading taken from mineral earth to the litter surface and including elevated litter pressed to the ground.

2.2.8 Soil nutrients

A 200 g sample of mineral soil was collected from each plot at the baseline (October 2015) and twelve-monthly sampling periods for two years (n = 3 samples), from a randomly selected position within 1 m of the centre of each plot. The top 5 cm of litter and topsoil was removed to allow access to mineral soil. A steel cylinder (10 cm diameter, 10 cm deep), was used to collect the sample, before sifting through a 5 mm sieve to remove remaining leaf litter. Samples were refrigerated and sent to the CSBP Soil and Plant Analysis Laboratory (Bibra Lakes, Western Australia). Samples were sent within one week of collection, except for the baseline sample. For this sample, after an initial attempt at analysis, samples were sent to the CSBP laboratory six months after collection. The standard soil testing package was selected to examine nutrients potentially important for plant growth: ammonium nitrogen (mg/kg), nitrate nitrogen (mg/kg), Colwell phosphorus (mg/kg), Colwell potassium (mg/kg), sulphur (mg/kg) and organic carbon (%).

2.2.9 Statistical analysis

All analyses were performed in R version 3.5.0 (R Core Team 2012) in the RStudio environment (RStudio 2012).

Effect of fencing on litter

Analysis of variance (ANOVA), with Tukey HSD post-hoc tests, was used to compare litter depth in each distance increment upslope and downslope from the fence edge for each plot. Tukey HSD tests were performed and visualised using the 'multcompView' package (Graves et al. 2012)

Litter and soil displacement and seasonal foraging pattern

We used a linear mixed-effects model (LMM) to model the relationship between the mass of litter and soil displaced by lyrebirds and vegetation structural complexity (<50 cm). The slope at each site (degrees) was included in the model because it potentially influences litter and soil displaced downhill by foraging lyrebirds. Forest type was also included as lyrebirds may differ in their use of forest types. Forest block was fitted as a random term. Vegetation structural complexity (number of contacts) was transformed ($\log_{10}$) to meet the assumption of normality.

To compare foraging activity between forest types, and to test for seasonal variation, an LMM was used. Monthly foraging estimates (% cover foraged in each plot) were converted to proportions and a logit transformation applied following Warton and Hui (2011). The logit-transformed proportion was specified as the response variable, with season and forest type specified as predictors including their interaction. Site, nested within forest block, was included as a random term. We hypothesised that lyrebirds may favour the drier forest type (damp forest) during winter months when invertebrate prey are more likely to be accessible near the surface, but contract their foraging activity to wetter forest types (rainforest and wet forest) in summer months. Consequently, we tested for an interaction in foraging activity between season and forest type.

Physical characteristics of the soil

If lyrebird foraging activity affects soil characteristics, we would expect the difference between treatment plots to change over time. Consequently, we used an LMM to examine the interaction between treatment and time for each soil characteristic. This approach allows for the simultaneous comparison between treatments and their interactions through time, using a single test. Variables included in models were specified individually, depending on the hypothesis posed for each response variable (Table 2.1). Site was nested within forest block and specified as a random factor in all models. Correlograms and residual plots were examined for each model to ensure model assumptions were met. When required, variables were log-transformed to meet assumptions of normality.

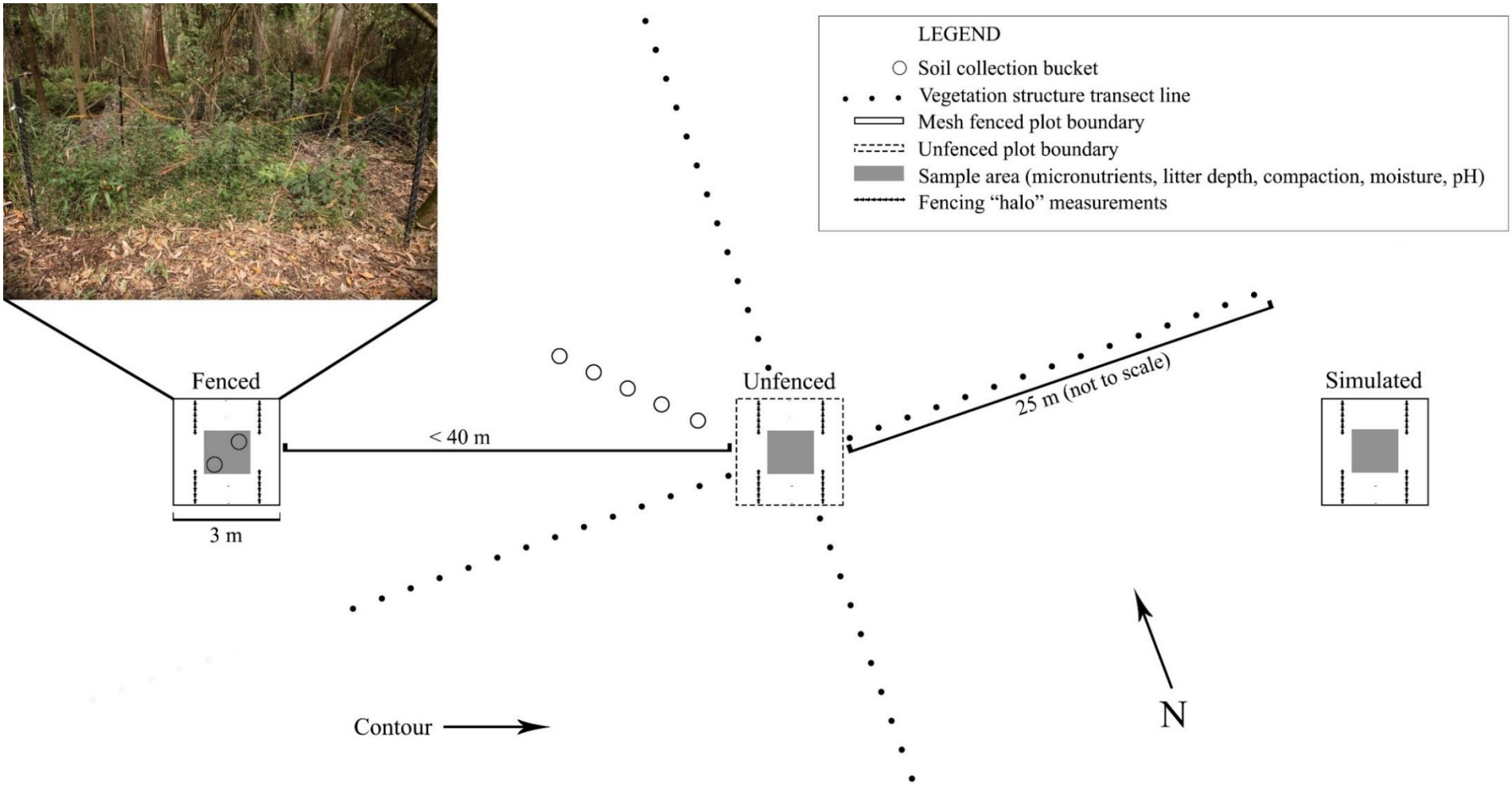


Figure 2. 2 Diagram representing a typical site and plot layout. Inset depicts a fenced lyrebird exclosure in Sherbrooke Forest showing orange flagging tape to discourage lyrebirds from flying into the plot.

Table 2. 1 Response and predictor variables included in linear mixed-effects models to examine the effect of treatments on litter and soil characteristics through time. Site was nested within forest block and specified as a random factor in all models.

Characteristic	**Predictors included in model**	**Hypothesis**
Soil compaction	Treatment * Time	Soil in fenced plots will become more compacted in the absence of soil turnover caused by foraging lyrebirds, while simulated and unfenced plots will maintain a lower level of soil compaction under the influence of real or simulated lyrebird foraging.
	Season	Season will have a strong influence on soil compaction, with drier periods of the year (summer, autumn) having greater compaction.
Soil moisture	Treatment * Time	Soil moisture will change through time, with fenced plots becoming more resistant to infiltration due reduced foraging disturbance compared with simulated and unfenced plots.
	Season	Season will influence soil moisture, with drier periods of the year (summer, autumn) having reduced soil moisture.
	Forest type	Forest type will represent a gradient in soil moisture from cool temperate rainforest with high moisture levels to wet forest and then damp forest.
Soil pH	Treatment * Time	Soil pH will change through time, with fenced plots becoming less acidic compared with simulated and unfenced plots due to absence of lyrebird foraging affecting decomposition rate.
	Forest type	Soil pH will differ between forest types owing to different rates of decomposition in each.
Litter depth	Treatment * Time	Litter depth will change through time. Fenced plots will accumulate litter due to a lack of foraging disturbance compared with unfenced and simulated plots in which the mixing and burying of litter will continue.
	Forest type	Forest type will influence litter depth due to the leaf physiognomy of rainforest canopy species (smaller leaf area) resulting in shallow litter layers compared with sclerophyll-dominated wet forest and damp forest.

For all analyses, LMMs were fitted using restricted maximum-likelihood estimation (REML) in the 'lme4' package (Bates et al. 2014). Mean estimates ± standard errors (SE) are reported, with p-values generated using the Satterthwaite's method of approximation in the 'lmerTest' package (Kuznetsova et al. 2017), and conditional and marginal R^2 computed with the 'MuMIn' package (Barton 2011). All graphic visualisations were generated with the 'ggplot2' package (Wickham 2016).

Soil nutrients

A multivariate approach was taken to analyse soil nutrients. We used non-metric multidimensional scaling (NMDS), undertaken using the R package 'vegan' (Oksanen et al. 2007), to examine patterns in ordination space for sites associated with each treatment, at each sampling time. NMDS was based on a Bray-Curtis dissimilarity matrix, calculated using the functions *vegdist* and *metaMDS*. To test for significant differences between treatments, and the interaction between treatment and time, we used the *adonis* function to apply Permutational Multivariate Analysis of Variance (PERMANOVA) with 9,999 permutations. Forest type was included as a fixed factor, and site as a random factor using the argument 'strata'. We further tested whether soil properties in fenced treatments became more homogenised than simulated and unfenced treatments through time by using the *betadisper* function as a test for multivariate homogeneity of group variances between treatments.

2.3 RESULTS

2.3.1 Effect of fencing on litter

Variation in litter depth from the edge of fenced plots (after two years of treatment) suggested that the fence influenced litter for up to 20 cm into the plots on the downslope edge (litter falling away from the fence; Appendix 2.2). Beyond 20 cm, there was no difference in litter depth with increasing distance increments (Tukey's P >0.05). This effect was closely mirrored in upslope measures, with no difference in litter depth beyond 10 cm from the fence (Tukey's P >0.05) (Appendix 2.2).

Plots with simulated foraging showed less marked effects than for fenced plots; while for unfenced plots, as expected, there was no 'fence effect' on litter depth (Appendix 2.2). These results confirm that a fence effect (interacting with litter) should not affect measures of soil physical characteristics or soil nutrients in plots as all samples were taken at least 1 m from the fence.

2.3.2 Litter and soil displacement by lyrebirds

Overall, lyrebirds displaced a mean of 155.7 tonnes per ha (SD = 132.4 t/ha) in a one-year period (October 2016 – September 2017), with the variation between sites ranging from 6.6 to 478.4 t/ha. The mass of litter and soil displaced by lyrebirds did not differ between forest types (Table 2.2a), however, the amount of litter and soil displaced was strongly related to the structural complexity of vegetation <50 cm height. Less litter and soil was displaced with increasing complexity of the low-stratum vegetation (Fig. 2.3). Slope did not significantly influence the amount of litter and soil displaced (Table 2.2a). The model accounted for 44% of variation in the data.

2.3.3 Foraging activity

Foraging activity (measured as % cover and converted to proportion of disturbed soil in unfenced plots) varied with season (Fig. 2.4, Table 2.2b). Foraging activity in winter was less than in autumn and spring, although no season differed from summer (Fig. 2.4). There was little overall difference in foraging activity between forest types, but an important interaction occurred between season and forest type. In cool temperate rainforest, foraging activity decreased from autumn to winter, while in wet forest it increased (Fig. 2.4). Thus, lyrebirds shifted foraging activity away from cool temperate rainforest in favour of wet forest during winter, the wettest season. Overall, season and forest type accounted for only a limited amount of variation in foraging activity (Table 2.2b).

Table 2. 2 Model outputs for linear mixed-effects models of a) litter and soil displaced by lyrebirds and b) the relationship between lyrebird foraging, forest type and season. Autumn was the reference category for season, and cool temperate rainforest was the reference category for forest type. Coefficients for which the 95% confidence interval does not include zero are shown in bold. '^' denotes where non-reference categories within a level differed from one another and '*' denotes interactions between fixed effects.

Response	Fixed effect	Estimate	SE	*t* value	$R^2_{(marginal)}$	$R^2_{(conditional)}$
a) Soil displaced (t ha-1 ODW)	(Intercept)	0.12	0.33	4.05	0.44	0.44
	Vegetation (log10)	**-0.71**	**0.20**	**-3.46**		
	Slope	-0.22	0.20	-1.10		
	Forest type - Wet forest	0.00	0.48	<0.01		
	Forest type - Damp forest	-0.35	0.46	-0.75		
b) Proportion of plot foraged (logit-transformed)	(Intercept)	-1.66	0.18	-9.05	0.03	0.15
	^Season – Winter	**-0.43**	**0.20**	**-2.17**		
	^Season – Spring	-0.28	0.18	-1.49		
	Season – Summer	**-0.45**	**0.19**	**-2.35**		
	Forest type – Wet forest	-0.33	0.26	-1.29		
	Forest type - Damp forest	0.03	0.26	0.12		
	Season (Winter) * Forest type (Wet forest)	**0.58**	**0.28**	**2.07**		
	Season (Spring) * Forest type (Wet forest)	0.49	0.26	1.87		
	Season (Summer) * Forest type (Wet forest)	0.37	0.27	1.36		
	Season (Winter) * Forest type (Damp forest)	0.15	0.28	0.54		
	Season (Spring) * Forest type (Damp forest)	-0.05	0.26	-0.21		
	Season (Summer) * Forest type (Damp forest)	-0.04	0.27	-0.14		

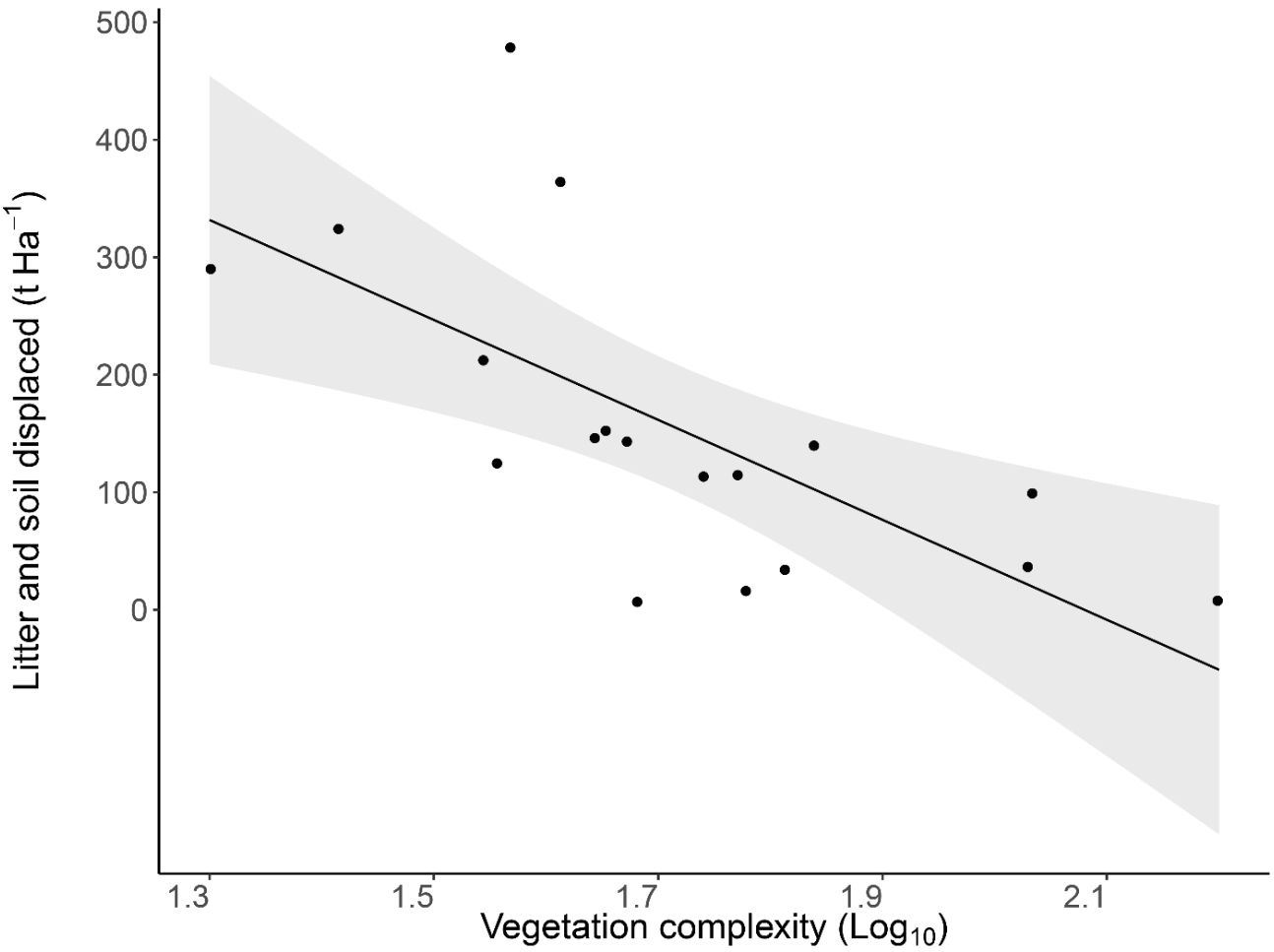


Figure 2. 3 The modelled relationship (solid line ± 95 % C.I. shaded) between litter and soil (t/ha (oven dry weight) displaced by lyrebirds in a one-year period and the complexity of surrounding vegetation (contacts <50 cm height). Actual values for each site (n=18) are plotted (black circles).

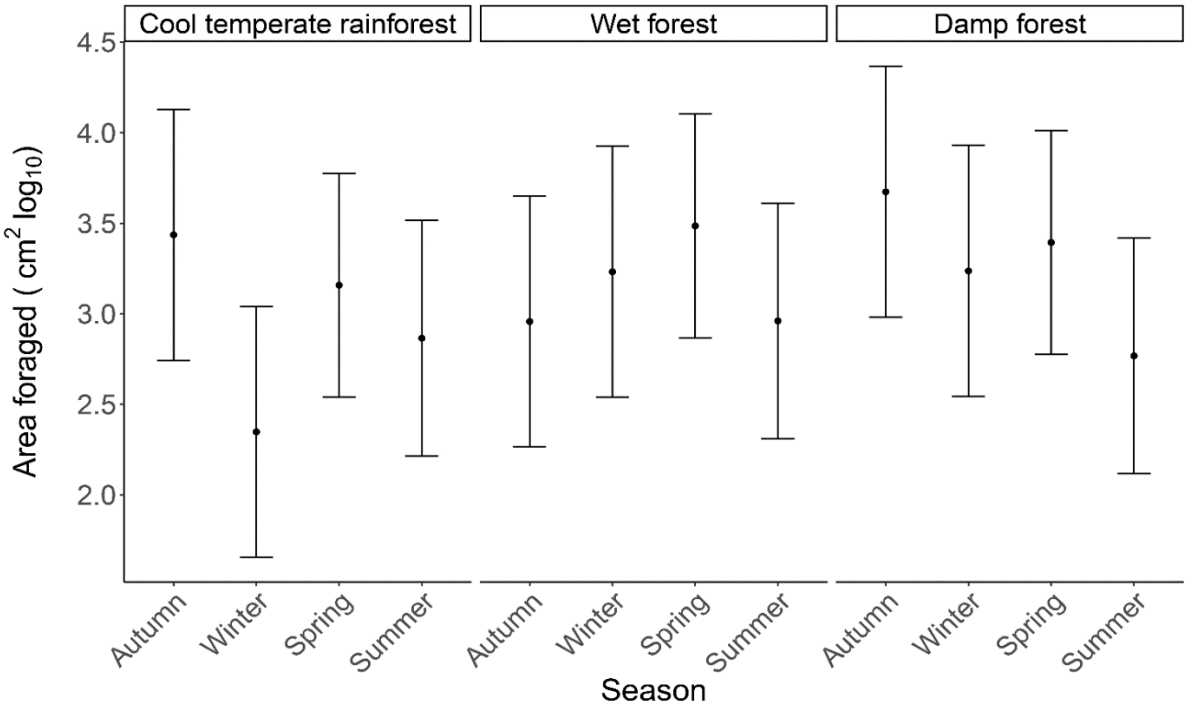


Figure 2. 4 Modelled estimates of foraging activity (± 95 % C.I.s) by lyrebirds in unfenced plots per month for each season over the two-year study period (October 2015 – September 2017). Panels represent each forest type.

2.3.4 Physical characteristics of the soil

A linear mixed-effects model of soil compaction (0-7.5 cm depth) showed a significant interaction between treatment and time: the unfenced and simulated plots showed different trajectories through time to the fenced treatment (Fig. 2.5a, Table 2.3a). During the 24-month manipulative experiment, soil compaction in the top 7.5 cm of the soil surface in fenced plots increased on average by 37% from baseline (pre-fence construction) measures (Fig. 2.5a). In comparison, in unfenced and simulated plots, soil compaction decreased from baseline measures by 22% and 13%, respectively (Fig. 2.5a). Soil compaction deeper in the soil profile (7.5-15 cm) showed a significant, although less pronounced, interaction between treatment and time (Fig. 2.5b, Table 2.3b). Finally, soil compaction at the deepest level (15-22.5 cm) showed no evidence of an interaction between treatment and time (Table 2.3c). These results indicate that foraging disturbance by lyrebirds, and simulated foraging, both reduced soil compaction relative to the fenced plots where foraging was excluded, but that this effect primarily occurs in the upper layers of the soil profile.

Litter depth also changed markedly between treatments over the 24-months, with a strong interaction between treatment and time (Fig. 2.6, Table 2.3d). Baseline measures showed no difference in litter depth between treatments ($F_{(2,51)} = 0.802$, $P = 0.454$). After two years, mean litter depth in fenced plots had increased (from 3.02 to 3.40 cm, on average); whereas in unfenced and

simulated plots it decreased (from 2.5 to 1.1 cm and 2.9 to 1.3 cm, respectively) (Fig. 2.6). Thus, after two years, litter depth in fenced plots was almost three times deeper, on average, than for plots with either actual or simulated lyrebird foraging.

Soil moisture varied strongly with season and between forest types, being higher in winter and spring and lower in summer (cf autumn), and higher in cool temperate rainforest. There was no interaction between treatment and time (Table 2.3e). Similarly, soil pH showed no evidence of an interaction between treatment and time, the only variation being between forest types (lower pH in cool temperate rainforest) (Table 2.3f).

2.3.5 Soil nutrients

NMDS ordination revealed no clear pattern for soil nutrients in relation to treatment for either the baseline, 12-month or 24-month sampling times (Fig. 2.7), suggesting lyrebird activity did not affect the mineral composition of soil over the two years of the study. The PERMANOVA analysis (*adonis* model) revealed a significant effect of time ($P<0.001$) and forest type ($P<0.001$), but the interaction between treatment and time was not significant ($P=0.7$). The strong effect of time is likely associated with storage of soil samples from the baseline sampling in the first year.

Analysis of multivariate group variances (distance to centroid) for soil nutrients in plots at each sampling time showed no evidence for a difference between treatments (*betadisper* tests, baseline: $F_{(2,51)} = 0.12$, $P = 0.89$; 12-month: $F_{(2,51)} = 0.18$, $P=0.84$; 24-month: $F_{(2,51)} = 0.34$, $P = 0.72$; Fig. 2.8). Fencing of plots did not result in more (or less) homogenisation of soil nutrients.

Table 2. 3 Results from linear mixed-effects models of the effect of treatment and time on soil characteristics in study plots. Coefficients for which the 95% confidence interval does not include zero are shown in bold. '*' denotes interactions between fixed effects. Fenced was the reference category for treatment, autumn was the reference category for season, and damp forest was the reference category for forest type.

Characteristic	**Fixed effect**	**Estimate**	**SE**	***t* value**	$R^2_{(marginal)}$	$R^2_{(conditional)}$
Soil compaction	(Intercept)	1.87	0.11	16.46	0.14	0.76
(0 - 7.5 cm) (log_{10})	**Time**	**0.02**	**0.01**	**4.71**		
	Treatment - Simulated	0.06	0.06	1.04		
	Treatment - Unfenced	0.11	0.06	1.92		
	Season - Winter	**-0.28**	**0.02**	**-12.28**		
	Season - Spring	**-0.21**	**0.02**	**-10.64**		
	Season - Summer	**-0.07**	**0.02**	**-3.10**		
	Treatment$_{(Simulated)}$ * Time	**-0.03**	**0.01**	**-4.44**		
	Treatment$_{(Unfenced)}$ * Time	**-0.03**	**0.01**	**-4.75**		
Soil compaction	(Intercept)	151.40	17.77	8.52	0.17	0.65
(7.5 - 15 cm)	Time	0.80	1.28	0.63		
	Treatment - Simulated	16.11	10.66	1.51		
	Treatment - Unfenced	**25.49**	**10.66**	**2.39**		
	Season - Winter	**-63.62**	**5.82**	**-10.93**		
	Season - Spring	**-43.24**	**5.08**	**-8.52**		
	Season - Summer	0.15	5.54	0.03		
	Treatment$_{(Simulated)}$ * Time	**-3.53**	**1.78**	**-1.98**		
	Treatment$_{(Unfenced)}$ * Time	-3.37	1.78	-1.89		
Soil compaction	(Intercept)	2.22	0.06	37.21	0.17	0.54
(15 - 22.5 cm) (log_{10})	Time	<0.01	0.01	0.27		
	Treatment - Simulated	0.03	0.04	0.68		
	Treatment - Unfenced	0.06	0.04	1.30		
	Season - Winter	**-0.24**	**0.02**	**-10.15**		
	Season - Spring	**-0.11**	**0.02**	**-5.40**		
	Season - Summer	0.03	0.02	1.27		
	Treatment$_{(Simulated)}$ * Time	<0.01	0.01	0.03		
	Treatment$_{(Unfenced)}$ * Time	<0.01	0.01	0.14		

Table 2.3 continued

Characteristic	Fixed effect	Estimate	SE	t value	$R^2_{(marginal)}$	$R^2_{(conditional)}$
Litter depth (log_{10})	(Intercept)	0.51	0.05	10.23	0.56	0.79
	Time	<0.01	<0.01	0.82		
	Treatment - Simulated	-0.05	0.04	-1.14		
	Treatment - Unfenced	**-0.16**	**0.04**	**-3.66**		
	Forest type - Rainforest	**-0.12**	**0.04**	**-2.85**		
	Forest type - Wet forest	0.06	0.04	1.46		
	Treatment$_{(Simulated)}$ * Time	**-0.02**	**<0.01**	**-9.70**		
	Treatment$_{(Unfenced)}$ * Time	**-0.02**	**<0.01**	**-9.71**		
Soil moisture (log_{10})	(Intercept)	1.10	0.04	25.60	0.58	0.81
	Time	**<0.01**	**<0.01**	**2.05**		
	Treatment - Simulated	0.03	0.03	0.92		
	Treatment-– Unfenced	0.01	0.03	0.42		
	Forest type - Rainforest	**0.17**	**0.05**	**3.83**		
	Forest type - Wet forest	0.05	0.05	1.11		
	Season - Winter	**0.22**	**0.01**	**17.17**		
	Season - Spring	**0.22**	**0.01**	**19.12**		
	Season - Summer	**-0.12**	**0.01**	**-9.53**		
	Treatment$_{(Simulated)}$ * Time	<0.01	<0.01	-1.24		
	Treatment$_{(Unfenced)}$ * Time	<0.01	<0.01	-0.59		
Soil pH	(Intercept)	5.31	0.19	27.65	0.32	0.71
	Time	<0.01	<0.01	-0.82		
	Treatment - Simulated	-0.13	0.10	-1.33		
	Treatment - Unfenced	0.10	0.10	1.01		
	Forest type - Rainforest	**-0.81**	**0.20**	**-4.09**		
	Forest type - Wet forest	-0.29	0.20	-1.48		
	Treatment$_{(Simulated)}$ * Time	0.00	0.01	0.76		
	Treatment$_{(Unfenced)}$ * Time	0.00	0.01	0.33		

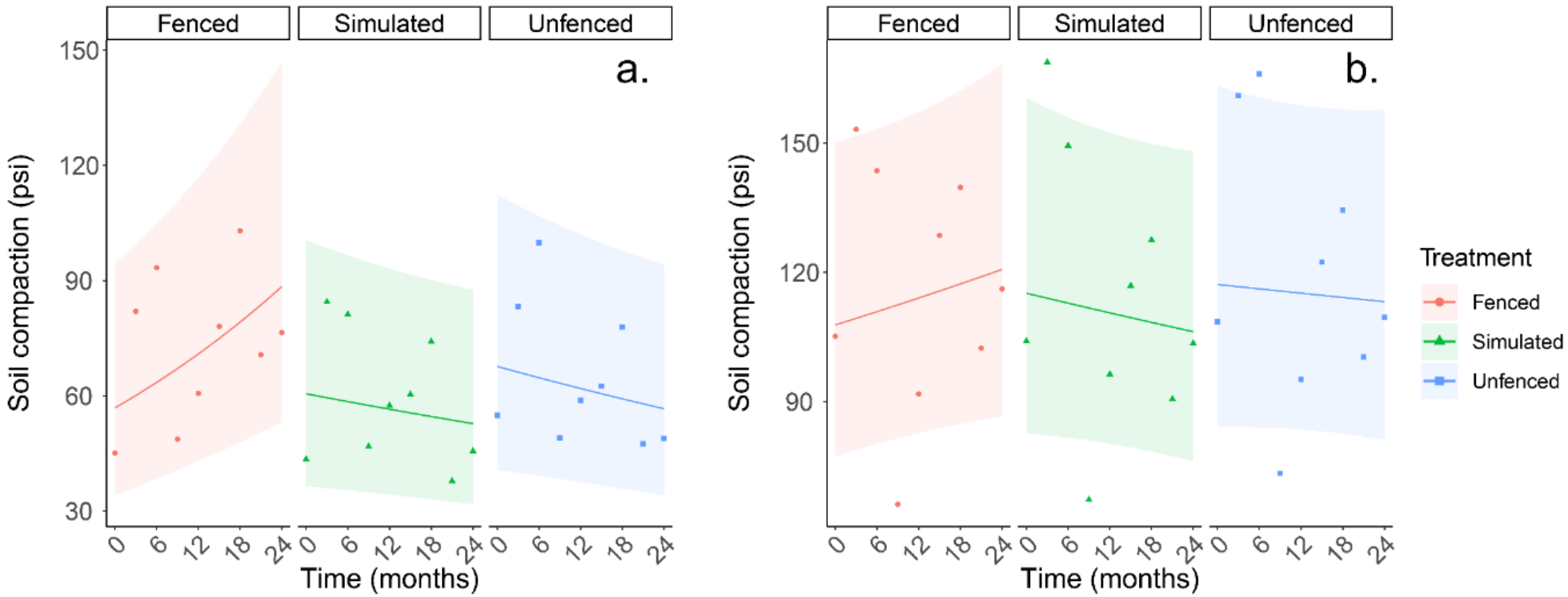


Figure 2. 5 Changes in soil compaction in the top a) 7.5 cm and b) 15 cm of soil, measured at three-monthly intervals over two years. The prediction plots were generated from linear mixed models (solid lines; 95% C.I.s shaded), with data points for mean soil compaction overlayed (symbols). Red circles represent the fenced treatment, green triangles represent the simulated and blue squares represent the unfenced treatment. Each treatment is presented in a separate panel for clarity.

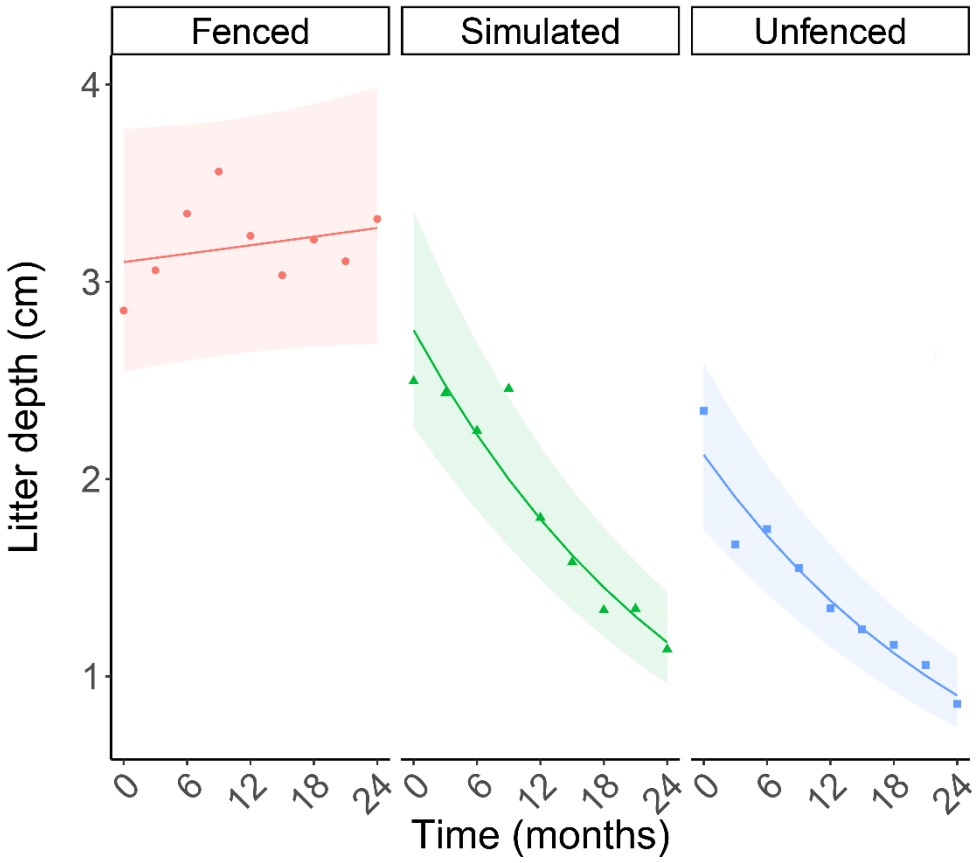


Figure 2. 6 Changes in litter depth (cm), measured at three-monthly intervals over a two-year period. Prediction plots were generated from a linear mixed model (solid lines; 95% C.I.) with values for mean litter depth overlayed (symbols). Red circles represent the fenced treatment, green triangles represent the simulated and blue squares represent the unfenced treatment.

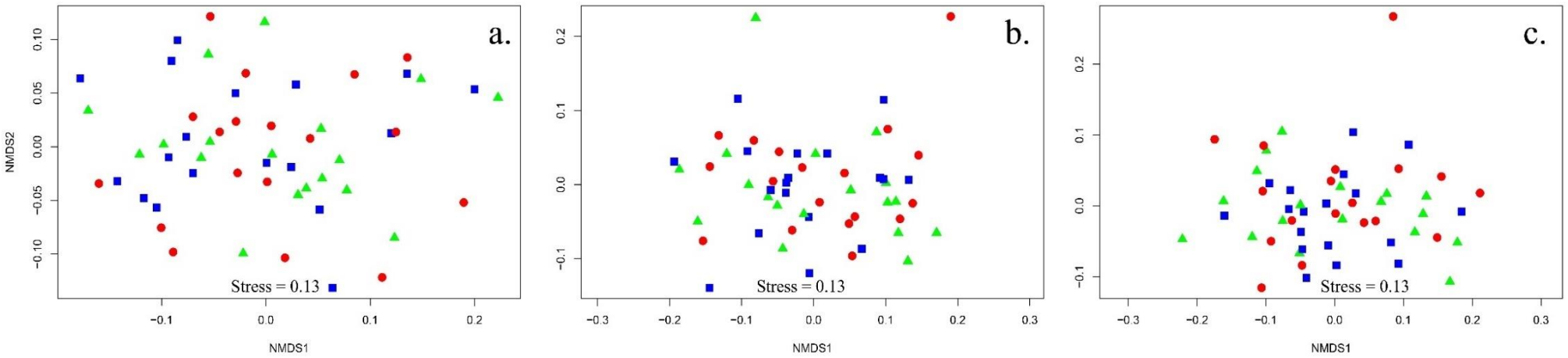


Figure 2. 7 NMDS ordinations of soil nutrients at plots for (a) baseline, (b) 12-month, and (c) 24-month sampling times. Red triangles represent fenced plots, green circles represent simulated plots and blue squares represent unfenced plots. Ordinations were computed based on soil nutrient measures (ammonium nitrogen, nitrate nitrogen, Colwell phosphorus, Colwell potassium, sulphur and organic carbon).

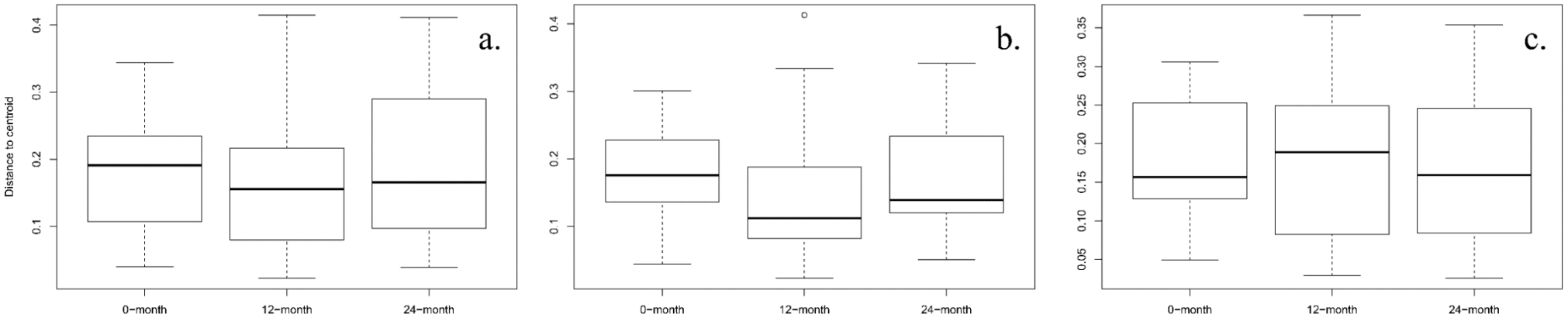


Figure 2. 8 Distance to centroids from NMDS ordinations of soil nutrients for (a) fenced, (b) simulated and (c) unfenced treatments for each sampling period.

2.4 DISCUSSION

Foraging by lyrebirds profoundly alters the characteristics of litter and topsoil in forest ecosystems of Victoria's central highlands. On average, lyrebirds displaced 155.7 t/ha of litter and soil across the forest landscape, during a single year. The amount of soil displaced was greatest in areas with sparse vegetation structure in the low stratum. Foraging activity was spatially and temporally widespread in all three forest types, with seasonal variation between rainforest and wet forest. Lyrebird foraging, by raking the litter and soil, mixes and buries leaf litter over extensive areas of the forest floor. This dynamic process reduces litter depth and soil compaction at the surface, and likely has far-reaching effects on forest ecosystem function.

2.4.1 Scale and pattern of engineering

The scale of engineering by lyrebirds in Victoria's Central Highlands can be attributed to at least two main factors. First, lyrebird density is high in forests of this region (Emison et al. 1987, Higgins et al. 2001). The forest types surveyed occur in high rainfall areas (~1200 mm p.a.) with fertile soils and a complex overstorey, thus creating a deep, moist litter layer, which harbours a high abundance of invertebrates year-round (Loyn 1985). This represents optimal habitat (i.e. food, cover) for the superb lyrebird (Maisey et al. 2018). Second, forest soils in this region are sensitive to soil disturbance, with deep, well-developed macroporous structure (Ashton 1975, Nyman et al. 2011), and are easily manipulated by foraging lyrebirds.

The extraordinary amount of litter and soil displaced annually by lyrebirds is, to our knowledge, unparalleled by any other vertebrate soil engineer in terrestrial ecosystems (Butler 1995, Haussmann 2017). Our landscape-scale measure (mean 155.7 t/ha over 12 months, range 6.6 – 478 t/ha) across three forest types in each of three locations is comparable to that reported by Ashton and Bassett (1997) (200 t/ha) for a more localised estimate. This mass of soil displaced is much greater than annual estimates for small mammals, such as 8.7 t/ha for the woylie *Bettongia penicillata* (Garkaklis et al. 2004) and 11.2 t/ha for the northern pocket gopher *Thomomys talpoides* (Ellison 1946, Butler 1995), typical of digging mammals considered to be important engineers. Casting rates for earthworms have been shown to displace much larger quantities of material compared with vertebrates, with studies typically recording between 10-50 t ha^{-1} y^{-1} but in some tropical regions exceeding 100 t ha^{-1} y^{-1} (Wilkinson et al. 2009). Our results show lyrebirds may indeed displace more litter and soil than any other species worldwide.

Lyrebirds actively foraged in all forest types, throughout the year. There was evidence of some shift in foraging from rainforest to wet forest in winter, likely related to resource availability. In summer, invertebrates (particularly earthworms) may undergo vertical migration, such that wet and damp forest types are less productive foraging areas (Ashton and Bassett 1997). Lyrebirds may take

advantage of abundant food resources in wet forest during winter, with the consequence of saving resources in moist rainforest gullies for the drier seasons. At a local scale, extent of foraging was moderated by vegetation structure in the ground layer (<50 cm height): where vegetation was dense, less soil was displaced. This relationship likely represents the need for lyrebirds to balance foraging effort with reward (Whittingham and Evans 2004). The energetic cost to access prey in dense vegetation, such as among colonies of ground fern, is likely to be high (Devereux et al. 2004). Further, there may be an increased risk of predation to ground-foraging lyrebirds if dense vegetation inhibits detection and escape from predators (Metcalfe 1984).

2.4.2 Impacts on litter and soil

Lyrebird foraging activity had a marked impact on the physical characteristics of the soil and litter layer. By raking litter and soil, and mixing and burying leaf litter, lyrebirds decreased soil compaction in the top 7.5 cm of soil, while also decreasing litter depth. Areas where foraging has occurred will have greater aeration and infiltration properties, and potentially be more conducive to the production of microorganisms and, in turn, macro-invertebrates (Eldridge et al. 2015). Further, by burying material as they forage, lyrebirds increase the surface area of litter in contact with mineral soil. This, in turn, will increase the availability of nutrients to micro-organisms and increase nutrient cycling rates, likely having wider implications on the soil micro-habitat for microbial communities and invertebrates.

Soil nutrients showed little change over the two-year period. These soil properties are likely to be slow to change in response to the experimental treatments. Soil samples were collected from below the top 5 cm of litter and soil, a section of the soil horizon that may be too deep to be affected by lyrebird disturbance at this timescale. It is likely though, that over a longer time-period, soil nutrients will be altered by lyrebird foraging simply by the downhill movement and accumulation of litter and soil on lower slopes. This may result in a nutrient gradient along a slope, whereby ridges are comparatively depleted of topsoil, while lower slopes accumulate nutrient-rich material.

2.4.3 Implications for ecosystem function

The scale and extent of foraging activity by lyrebirds has implications for diverse aspects of ecosystem function in these forests. This includes, for example, the spatial structure and composition of invertebrate communities, the spatial pattern and cover of ground-layer vegetation, and disturbance processes such as fire.

The extensive physical modification of litter and soil suggests that lyrebird foraging will have marked impacts on processes that shape ground-layer invertebrate communities. Many invertebrate assemblages are sensitive to changes in soil structure and litter quality (Bultman and Uetz 1982,

Blair et al. 1994, Hansen 2000). Lyrebird foraging increases the local diversity of microhabitats available to the invertebrate fauna by creating a complex mosaic of recently raked patches of exposed soil adjoining finely mixed litter and mineral soil ejecta, embedded in a matrix of an undisturbed litter layer. Together with changes arising from the mixing of litter and soil (greater aeration, surface contact between litter and mineral soil, altered decomposition rates), the composition and abundance of invertebrate communities are likely to be altered across large spatial scales.

Extensive raking of litter and soil likely affects the survival and density of seedlings, the cover of ground-layer vegetation, and potentially the process of vegetation succession from wet forest to cool temperate rainforest. Ashton and Bassett (1997) posited that lyrebirds may increase the density of tree ferns by creating, through their foraging, germination sites on litter-free ledges of soil. This may facilitate colonisation of rainforest plant species over time because many such species readily germinate upon the trunks of soft tree ferns and, by growing high above the litter layer, seedlings survive physical destruction. Ultimately, with intense lyrebird disturbance and the development of a dense and shady mid-storey, ground cover species in rainforest are likely to become sparse and the habitat highly suited for exploitation by lyrebirds.

Fire is a major natural disturbance process in these forests (McCarthy et al. 1999). Foraging by lyrebirds has the potential to influence the fire regime by its effect on the amount and spatial pattern of forest-floor fuels (Nugent et al. 2014); and in turn, fire influences the suitability of forest habitats for lyrebirds. Wet forest and cool temperate rainforest communities are fire sensitive. Wildfire is infrequent (many decades or centuries between fires) and often is stand-replacing in wet forest (Lindenmayer et al. 1999). Lyrebird foraging, and the associated burial and decomposition of litter, represents a directional and sustained ‘ramp’ disturbance (Lake 2000) toward a less fire-prone state. In contrast, the rare fire events create a major ‘pulse’ disturbance that transforms the ecosystem and resets the successional process. In summer 2019/2020, multiple wildfires of an unprecedented scale burned some 12 million ha of forests in eastern Australia, including ~34% of the geographic distribution of the superb lyrebird in the state of Victoria and over 50% in New South Wales (Birdlife Australia, pers. comm.). This has profound implications for lyrebird-facilitated ecosystem function in these forests. Lyrebirds can persist in unburned patches, particularly in damp gullies (Nugent et al. 2014, Robinson et al. 2014), but their future distribution across this vast area will be affected by the availability of such unburnt refuges, their rate of reproduction and recolonisation, and the density of regenerating vegetation (lyrebirds avoid dense regrowth).

2.5 CONCLUSION

The superb lyrebird, as an avian ecosystem engineer, causes physical changes to litter and soils on a scale unparalleled in the zoo-geomorphology literature. The magnitude of soil disturbance by lyrebirds is greater than for any other digging vertebrate in terrestrial ecosystems. Engineering by this species is distinctive in both its spatial and temporal pattern: its extensive raking and displacement of litter and soil occurs during all seasons of the year, and on a landscape scale throughout the dominant forest types in Victoria's central highlands. Lyrebirds are a primary geomorphological driver of forest ecosystems in this region, with wildfire the only comparable natural disturbance process shaping ecosystem structure at this scale. While rare fire events have a profound influence on forest ecosystems, foraging by lyrebirds is a dynamic, ongoing process that influences the litter and soil of the forest floor on a daily basis. Given their ecosystem role, conservation of this species should be a key priority in the management of wet forests of south-eastern Australia for biodiversity. Further, consideration of this species should be incorporated into long-term planning relating to fire dynamics, fuel management, and post-wildfire recovery of forest ecosystems.

Chapter Three

Farming by engineering: interactions between the superb lyrebird *Menura novaehollandiae* and litter and soil invertebrates

Plate 4. A mature male superb lyrebird transforms his appearance in a full tail display.

ABSTRACT

Ecosystem engineers increasingly are recognised for their role in shaping ecological communities in terrestrial and aquatic ecosystems worldwide. In some circumstances, the effects of ecosystem

engineers on other organisms may generate a positive feedback loop that benefits the engineer. This study was designed to examine the impacts of an ecosystem engineer, the ground-dwelling superb lyrebird *Menura novaehollandiae*, on the invertebrate populations upon which it feeds in tall wet eucalypt forests in south-eastern Australia. To distinguish potential engineering effects arising from foraging by lyrebirds from their trophic effects as a predator on invertebrates, a two-year experiment was established with three treatments: 1) fenced exclosures, representing a lyrebird-free environment; 2) fenced exclosures with simulated foraging, to represent the engineering effects in the absence of predation; and 3) unfenced plots, accessible to foraging lyrebirds and hence both engineering and predation effects. Invertebrates were systematically sampled in replicate plots of each treatment at sites in each of three forest types (damp forest, wet forest, cool temperate rainforest), across each of three geographic forest blocks. Variation between treatments in the composition and overall abundance of invertebrate communities was largely related to predation effects by lyrebirds. In contrast, taxonomic richness and the biomass of invertebrate communities were strongly influenced by engineering effects. The biomass of invertebrates (including favoured prey taxa of lyrebirds) increased over time in the treatments with simulated lyrebird foraging compared with the fenced treatments (no disturbance). Further, in unfenced treatments accessible to lyrebirds, overall richness and biomass were predicted to be maintained at a similar or higher level than in the lyrebird-free state, despite being subject to significant offtake due to predation. Thus, through their disturbance to soil and litter while foraging, lyrebirds increase the biomass and taxonomic richness of their prey base, consistent with the concept of resource ‘farming’ by this species. The superb lyrebird may represent a special case of extended phenotype engineering, whereby their foraging structures (the extended phenotype) increases the productivity of their environment, creating a positive feedback loop. This process is operating on a scale unprecedented in non-human vertebrates, with far-reaching implications for ecosystem function in these forest ecosystems.

3.1 INTRODUCTION

Animal species that function as 'ecosystem engineers' increasingly are recognised worldwide for their important contribution to ecosystem function (Wright and Jones 2006, Romero et al. 2014, Coggan et al. 2018). By causing physical change to the environment, engineers moderate the quality and quantity of resources available to other species. Engineering activities often elicit a profound response in species sensitive to such change, primarily through mechanisms flowing from increased habitat heterogeneity (e.g., creation of niche opportunities), that in turn support greater community diversity (MacArthur and MacArthur 1961, Wiens 1974, Tews et al. 2004, Fahrig et al. 2011). In addition to modifying habitat for other species, physical alteration of habitat by an animal engineer may also provide a benefit or maintain feedbacks for itself, potentially functioning as an extended phenotype (Jones et al. 1994). A model example of an extended phenotype is dam-building by American beaver *Castor canadensis* (Jones et al. 1997). A beaver dam results in the flooding of large areas of riparian forest, facilitating the collection of woody material in an energetically efficient manner that increases the beaver's fitness. Furthermore, the dam floods the beaver's trail network through the forest, providing protection from predation, thereby directly increasing survivorship. Other animal species may also be catalysts for processes that feedback to increase their fitness.

Where engineering feedbacks occur, especially through foraging activities, cultivation mutualisms may evolve in which a species effectively 'farms' its food resource. Where 'farming' mutualisms occur, the relationship between two species may become extraordinarily tight. For example, the reef-dwelling damselfish *Stegastes nigricans* farms a single species of filamentous algae in the genus *Polysiphonia*, the likes of which rarely occur outside damselfish territories (Hata and Kato 2006). Similarly, the crested porcupine *Hystrix indica* in the Negev Desert creates foraging patches in soil that concentrate runoff and nutrient, increasing the overall landscape productivity of the below-ground plant-storage organs on which the animals feed (Gutterman 1987). In many such mutualisms, the trophic impacts of the engineer (e.g., removal of tubers by porcupine) may obscure the effects of engineering (e.g., increasing growth of tuberous plants), because these processes occur simultaneously and may work in opposing directions.

Cultivation mutualisms resulting in farming effects have been described in only a handful of non-human animals. This may be due to the complexity in decoupling engineering effects from trophic interactions (Sanders and van Veen 2011). Manipulative experiments provide a solution to address this complexity (Coggan et al. 2018), yet an experimental approach is not straightforward: it may involve logistic difficulties in manipulating populations of animal engineers in the field, and the problem of undertaking long-term and time-consuming field experiments (Coggan et al. 2018). Nonetheless, where manipulative experiments can be undertaken, strong inference is gained. For example, by using an exclusion experiment to manipulate the density of two species of ant

(*Myrmica rubra* and *Lasius niger*), Sanders and van Veen (2011) separated engineering effects of soil modification from predation effects, allowing valuable insight into the mechanisms of ecosystem engineering by ants, previously only considered within the context of food web theory.

Many animal engineers disturb the environment through bioturbation activities, and thereby create, modify or maintain habitats (Fleming et al. 2014). Much attention has been directed toward arid zone digging mammals, where nutrient coupling effects are pronounced (Eldridge and James 2009, Eldridge 2011). Soil disturbance may increase nutrient cycling, ameliorate harsh environments (Pike and Mitchell 2013), alter soil hydrology (Eldridge and Mensinga 2007) and moderate the amount and configuration of habitat available to other organisms (Sinclair and Chown 2005).

To date, very few avian species have been studied for their ecosystem engineering role (Coggan et al. 2018), despite phylogeny showing little relation to the evolutionary likelihood of engineers developing in any particular taxonomic group (Mallen-Cooper et al. 2019). Although avian engineers have been largely overlooked (but see El-Hacen et al. (2019)), the ubiquity and abundance of birds in ecosystems worldwide suggests that at least some species must maintain important roles as ecosystem engineers.

The superb lyrebird *Menura novaehollandiae* is a large, ground-dwelling passerine that occurs in moist forests on the eastern seaboard of Australia. It is renowned for its remarkable courtship displays, in which males mimic the calls of an array of forest co-habitants (Dalziell et al. 2013). Less known is the species' ability to displace enormous volumes of litter and soil while foraging on the forest floor (Ashton and Bassett 1997, Maisey et al. 2020). For this reason, the lyrebird has been proposed as an ecosystem engineer (Nugent et al. 2014, Maisey et al. 2018). This assumption remains largely untested and the ecosystem effects of lyrebird foraging on biotic communities are not documented.

The effects of lyrebird foraging on litter and soil presents the alluring possibility that they may effectively 'farm' their prey through their engineering activities. Lyrebirds feed on a broad range of invertebrates that live in the litter and soil on the forest floor (Lill 1996), and thus impose top-down effects of predation on invertebrate communities. Their foraging activity, however, is likely to also induce bottom-up, ecosystem engineering effects on such communities. When lyrebirds forage, they rake over the leaf litter and dig into the soil, creating a fine-scale mosaic of exposed soil and foraging ejecta within a matrix of leaf litter. Ejecta is comprised of a rich mix of leaf litter and soil, an important component of the formation of mull humus in wet forests (Ashton 1975). With prolonged lyrebird activity and turnover, litter and soil is likely to be less compacted and more aerated, while having increased infiltration, potentially creating conditions conducive to the invertebrates that comprise its prey (Wardle 2006, Cole et al. 2010).

A major challenge in understanding the influence of animal ecosystem engineers on other species is the difficulty associated with disentangling engineering effects from trophic effects (such as predation), as all species are embedded in food webs. In the current study, a manipulative experimental approach was used to explicitly separate engineering effects of lyrebirds from trophic effects of predation on invertebrates (Fig. 3.1). Three experimental treatments were employed: fenced plots with no foraging (lyrebirds excluded); fenced plots in which lyrebird foraging was simulated, and unfenced plots where lyrebirds had access for foraging. Engineering effects were identified by comparing the richness and abundance of invertebrates in fenced plots (no foraging) with fenced plots with simulated foraging. The only difference between these treatments is physical habitat modification, and as such provides a test for the engineering hypothesis (Fig. 3.1a). Similarly, comparison of fenced plots experiencing simulated foraging and unfenced open plots accessible to lyrebirds, allows a test of the effects of predation by lyrebirds, as both treatments include physical habitat modification, but only open plots are subject to predation (Fig. 3.1b).

3.2 METHODS

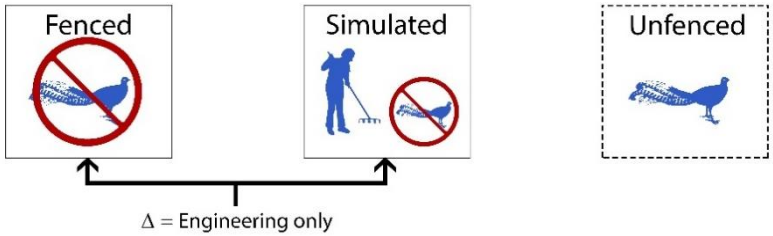
3.2.1 Study area

This study was conducted in the southern fall of the Central Highlands of Victoria, Australia (Fig. 3.2), where lyrebirds commonly occur in three main forest types; damp forest, wet forest and cool temperate rainforest (Loyn 1985).

Three locations were selected (Fig. 3.2): 1) Sherbrooke Forest, part of the Dandenong Ranges National Park; 2) Yarra Ranges National Park between Healesville and Warburton; and 3) Britannia Creek catchment between Warburton and Powelltown within the Yarra State Forest. Each location is geographically isolated from one another by sections of the Yarra Valley (>20 km between forest blocks, semi-rural land use not suitable for lyrebirds), and thus were considered as three separate forest blocks. Experimental manipulations were undertaken in each of the three locations.

a. The ecosystem engineering hypothesis

Supported if a significant interaction between treatment and time is detected for the fenced treatment compared with the simulated treatment.



b. The predation hypothesis

Supported if a significant interaction is detected between treatment and time for the unfenced treatment compared with the simulated treatment.

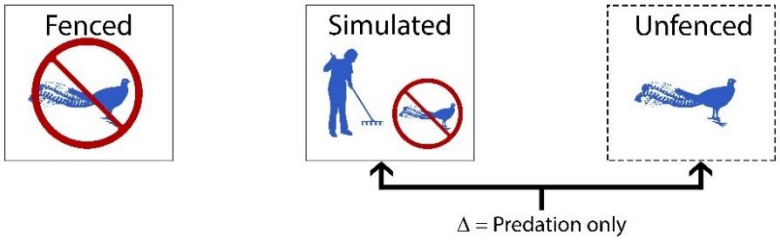


Figure 3. 1 Schematic diagram representing three treatments and the hypotheses of interest in a manipulative experiment on the effects of foraging by the superb lyrebird on invertebrate communities. Fenced plots have no habitat modification by lyrebirds, nor do they have any predation by lyrebirds. Simulated plots have monthly, hand-raked foraging simulation, in the absence of predation by lyrebirds. Unfenced plots remain accessible to lyrebirds. The 'Δ' defines which hypothesis is tested by the comparisons between treatments. Solid lines denote fenced boundary, dashed lines denote unfenced plot boundary. Note: both hypotheses are tested simultaneously with each test performed.

Sherbrooke Forest has an elevational range of 400-600 m above sea level (ASL) and receives approximately 1200 mm of rainfall per annum. It is predominantly comprised of wet forest, dominated by an overstorey of mountain ash *Eucalyptus regnans*. Some small sections of the park are comprised of damp forest, dominated by messmate *Eucalyptus obliqua* and mountain grey gum *Eucalyptus cypellocarpa*. Gullies are comprised of cool temperate rainforest, with southern sassafras *Atherosperma moschatum* the dominant species. Historically the park has experienced intense logging and as such the rainforest gullies are linear in form, and the wet forest canopy is even-aged in most of the study area.

The Britannia Creek catchment in the Yarra State Forest is a large forest block south-east of Healesville and north of Powelltown (Fig. 3.2). With an elevation 400-800 m ASL and average annual rainfall exceeding 1400 mm, this area has also experienced intense logging over the past century but retains mature stands of each of the three forest types. The cool temperate rainforest (CTR) is dominated by myrtle beech *Nothofagus cunninghamii* and southern sassafras. This forest block is subject to domestic firewood collection, intense use by recreational vehicles (trail motorcycles and 4x4 vehicular use), recreational hunting and management to reduce bushfire risk.

Yarra Ranges National Park has a greater range in elevation (400-1300 m ASL), rainfall >1100 mm per annum and comparable forest structure to Yarra State Forest; the two forest blocks are geographically separated by the Warburton valley (Fig. 3.2). The Yarra Ranges National Park has historically experienced a high degree of logging, but the area is now managed primarily for nature conservation.

The superb lyrebird is ubiquitous in all three forest blocks (van der Ree and Loyn 2002). Lyrebirds may seasonally shift their foraging activity between forest types (Ashton and Bassett 1997, Maisey et al. 2018, Maisey et al. 2020), but avoid forest that has recently burned in a bushfire (Nugent et al. 2014). They prefer to forage in areas with open ground cover (Ashton and Bassett 1997, Maisey et al. 2018) and avoid young regrowth forest with dense cover. Each study location contained mature stands of the three forest types and had not undergone recent change (within ~30 years) to forest structure due to logging or wildfire.

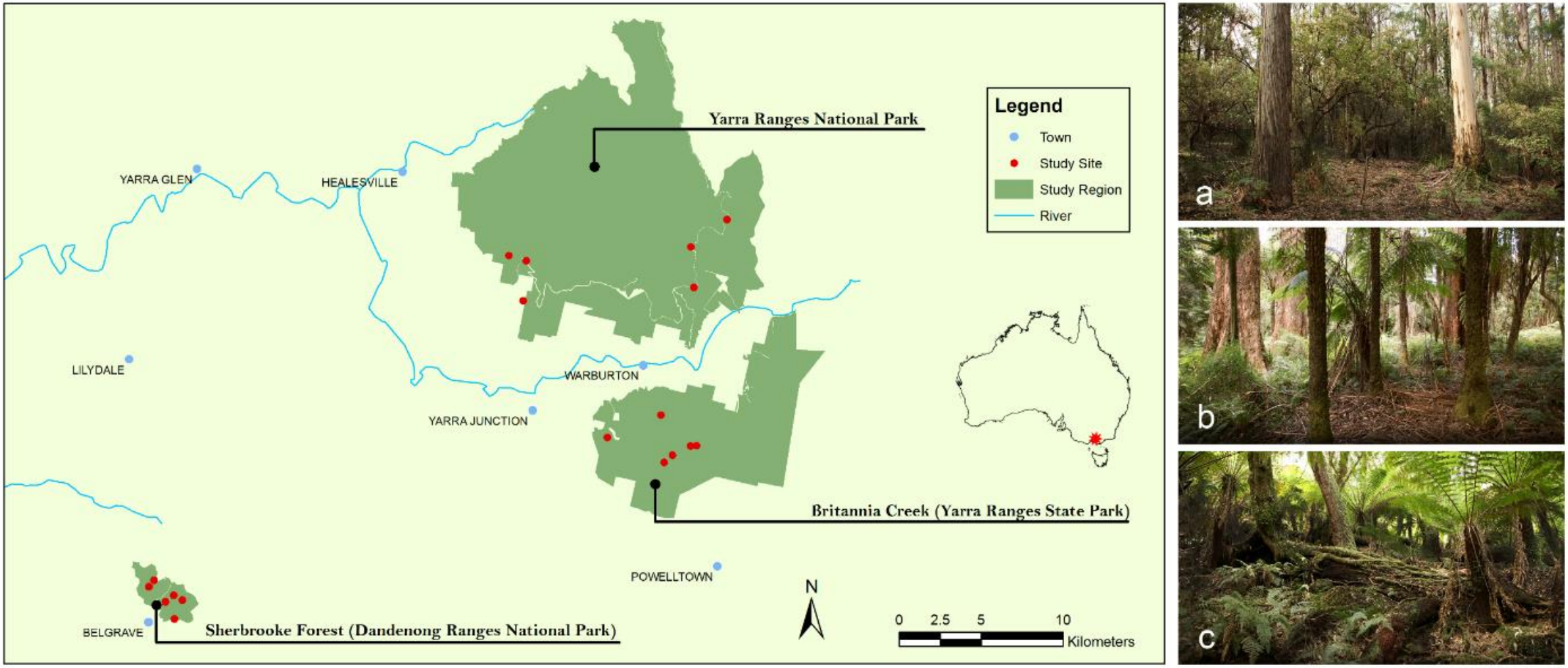


Figure 3. 2 Map of the study region in Victoria's central highlands, Australia, showing the location of experimental sites. Included are exemplar images of a) damp forest, b) wet forest and c) cool temperate rainforest.

3.2.2 Experimental treatments

In each forest block, two replicate sites in each of damp forest (Fig. 3.2a), wet forest (Fig. 3.2b) and cool temperate rainforest (Fig. 3.2c) were randomly selected using computer-generated random coordinates. Selection criteria were identified in the planning stage and assessed on location (Appendix 2.3). Forest type and fire history were assessed from Victorian Government biodiversity interactive maps (DELWP 2019). Field visits were undertaken to ground-truth the vegetation characteristics at each site.

At each site, three experimental plots (each 3 x 3 m) were established, positioned along the contour, with a random distance between 5 and 40 m between each plot. If vegetation structure was not sufficiently open (see criterion 5, Appendix 2.3) at the first randomly selected distance, the contour was followed until each plot conformed. One of the three was randomly assigned as a reference plot to remain unfenced and allow access to foraging lyrebirds (unfenced treatment). The two remaining plots were fenced, one left undisturbed (fenced treatment) and the other subject to simulated lyrebird foraging (simulated treatment – see below) on monthly visits. Fences were 120 cm high, constructed of wire netting (5 cm mesh size) with a steel fencing stake at the corner of each plot. Netting was pinned at ground level, and flagging tape was strung over the top of the fences to deter lyrebirds from flying into the plots. Steel stakes were also used to mark the corners of unfenced plots.

The distance into plots to which wire mesh fences influenced litter depth (i.e. accumulation or depletion of litter along the slope adjacent to a fence) was quantified. Litter depth was measured in all plots after the two-year period at 10 cm increments away from the plot edge. No significant difference was detected in litter at distances greater than 20 cm from a fence (Appendix 2.3).

3.2.3 Foraging simulation

At each monthly visit from October 2015 to September 2017, the area disturbed by lyrebirds in the unfenced plot was visually assessed and recorded as a percent cover estimate. In the simulated plot, foraging was simulated using a three-pronged hand rake (10 cm span, approximately the width of a spread lyrebird foot), replicating the foraging depth (approximately 5-10 cm deep), cover and configuration recorded in the unfenced plot at each site. Thus, the difference between the fenced and simulated treatments represents the effect of ecosystem engineering, as plots differ in physical disturbance regime but neither treatment allows predation of invertebrates by lyrebirds (Fig. 3.1). Conversely, the difference between the simulated treatment and unfenced treatment represents the effect of predation by lyrebirds on invertebrate communities (i.e. both have the same physical disturbance regime).

During several observation periods, a small number of plots were breached by lyrebirds (6 plots, representing <3% of plot observations), particularly in the first six months when fences were new to the environment. When lyrebird scratching was evident in a fenced plot it was recorded, although this was so seldom observed that any effects are assumed to be negligible.

3.2.4 Sampling procedure

Invertebrate sampling was undertaken concurrently with fence construction at the beginning of the study, October 2015 (austral spring) (baseline), then at one year (Oct 2016) and two years (Oct 2017) after fence construction. On each occasion, three randomly located sub-samples of litter and soil were collected from a 1 x 1 m area at the centre of each plot. Litter depth (to mineral earth) was measured with a combination square at the centre and at each corner of the invertebrate sampling area, for inclusion as an explanatory variable in models.

Each sub-sample of litter and soil was collected by driving a 15 x 15 cm steel frame, 5 cm deep, to sit flush with the surface of the litter horizon, then excavating the contents of the frame with a clean hand trowel. This resulted in a fixed volume of 3375 cm^3 of soil and litter collected from each plot.

Litter and soil samples were held in a cool room (~4°C) for no longer than 1 week before invertebrates were extracted using Tullgren funnels. Each sample was split between two funnels. Tullgren cylinders measured 50 cm in height with a diameter of 20 cm. Incandescent 25 W light bulbs were used for six days, and each sample mixed and re-established in its funnel on the third day to ensure an effective heat and moisture gradient was achieved. Invertebrates migrate away from the heat source to avoid desiccation, falling into ethanol (75% mix in water) in a collection vial at the base of the funnel.

3.2.5 Sorting invertebrates

Invertebrates were sorted, counted and identified by morphospecies to the lowest practical taxonomic level using a light microscope, with expert taxonomic assistance (see acknowledgements). Counts were made of small (<2 mm length), medium (2-5 mm) and large (>5 mm) individuals within each taxon.

3.2.6 Biomass estimation

The biomass oven dry weight (ODW) of each taxonomic group was estimated for each sample by applying a taxon-specific length-weight relationship sourced from the literature (see Appendix 2.4). For taxa sorted into the ‘large’ size class (>5 mm), the mean length was calculated from 20 individuals randomly selected from samples spanning the three sampling seasons. If there were <20 individuals, all were measured. The mean length was used in length-weight functions. This

procedure was applied because mean length of taxa >5 mm is highly taxon-specific. For the small size-class (<2 mm) mean length was assumed to be 1.5 mm and for the medium size-class (2 – 5 mm) it was assumed to be 3.5 mm. Where possible, length-weight relationships were taken from Gowing and Recher (1984) as this study was undertaken in south-eastern Australia. Nonetheless, comparison of relationships for taxonomic groups worldwide indicate little inter-continental difference (Gowing and Recher 1984).

For insect groups for which higher resolution functions could not be obtained (Appendix 2.4), the 'all insects' power function provided by Gowing and Recher (1984) was used. When this was the case for non-insect groups, a function for a taxonomic group that shared a similar body plan was applied. As such, the function used for Chilopoda was extended to Symphyla and Onycophora; the Dermaptera function extended to Diplura and Protura; the Diplopoda function extended to Pauropoda; and the Oligochaeta function extended to Nematoda. The power function was applied for all groups where it was provided. For juvenile Coleoptera, only a linear function was available, while for Dermaptera and juvenile (larvae) Diptera an exponential function was the only one available. For taxon-specific analyses where both adult and larval forms were present, biomass estimates were summed.

3.2.7 Statistical analysis

A priori contrasts were planned to compare: 1) fenced treatments with simulated treatments, to test for an interaction effect due to engineering effects only; 2) simulated treatments and unfenced treatments, to test for an interaction effect due to predation effects only; and 3) fenced and unfenced treatments, to test for an interaction effect due to the combined effects of engineering plus predation (Fig. 3.1, Table 3.1). If ecosystem engineering by lyrebirds influences invertebrate communities, there will be a significant interaction between fenced and simulated treatments through time (i.e. both treatments are predator free but differ in engineered habitat) (Fig. 3.1). If predation by lyrebirds influences these attributes, there will be an interaction between simulated and unfenced treatments (both have engineered habitats but differ in predation) (Fig. 3.1). The impacts of engineering and predation on invertebrate populations are likely to be in opposing directions, as engineering is typically facilitative (e.g., causes greater abundance, more species), whilst predation is expected to lower such measures. The simulated treatment was set as the reference category when constructing models, to evaluate the engineering and predation hypotheses for each measure of the invertebrate community from each model output (Table 3.1).

The engineering and predation hypotheses for invertebrate composition, taxonomic richness, total abundance and biomass were tested. Taxonomic richness was the number of taxa identified to the lowest level possible for each taxonomic group. The composition measure included all invertebrate size-classes, providing a single count (number of individuals) for each taxonomic group.

To test for compositional change in the invertebrate community between treatments and through time, non-parametric permutational analysis of variance (PERMANOVA) was used. This was applied by using the *adonis* function in the 'vegan' package, using 9999 permutations (Oksanen et al. 2007). Included in the model was forest type, forest block and a treatment × time interaction. Time was modelled as a continuous count (in years 0-2). Site was specified as a blocking factor using the 'strata' command. PERMANOVA is sensitive to heterogeneity of multivariate dispersion among groups (Anderson 2006); therefore, dispersion was tested using 'beta-disper' (vegan package).

Linear mixed models (LMMs) with a normal error distribution were used to assess the degree and direction of change between treatments (treatment × time interaction) for taxonomic richness and biomass of invertebrates (both variables conformed to a normal distribution). For invertebrate abundance generalised linear mixed models (GLMMs) were used. When fitting GLMMs, a Poisson distribution (log link) was assumed. Where overdispersion was detected, an observation-level random effect was added to the model. For all models (LMMs and GLMMs), a nested hierarchy was specified for the random effects to account for repeat measures through time at a plot level, in addition to two levels of spatial clustering (i.e. site and forest block). Specifically, plot was nested within site, which was in turn nested within forest block. In addition to the treatment × time interaction, forest type was included in all models, as this was expected to capture much of the fine-scale variation associated with the differences in vegetation community between sites. Litter depth (cm) was also included as a predictor variable, as a high degree of variability was expected between plots owing to fine-scale vegetation structure. Litter depth was transformed ($\log_{10}$) to improve linearity. Time was modelled as a continuous variable as above. Model fit was assessed using marginal (i.e. fixed terms only) and conditional (i.e. full model) values of R^2 for the global model (Nakagawa and Schielzeth 2013).

Models were constructed in the package 'lme4' (Bates et al. 2014). Prediction plots were generated with the 'effects' package (Fox 2003) and visualised with 'ggplot2' (Wickham 2016). All statistical analyses were implemented in the R programming language (R Core Team 2012) using the R Studio interface (RStudio 2012).

Table 3. 1 Hypotheses and predictions of the likely effects of experimental manipulations on different measures of the invertebrate communty.

Measure	Predictions
Community composition	Lyrebirds may cause shifts in the composition of invertebrate communities by changing the nature of litter and soil (engineering) in a way that advantages some taxa over others. If so, a significant interaction between simulated and fenced treatments through time is predicted. Conversely, lyrebirds may affect community composition through predation by disproportionately selecting certain taxa. If so, a significant interaction between the simulated and unfenced treatments is predicted, suggesting taxa are differentially sensitive to predation.
Abundance	Lyrebirds may affect abundance by engineering litter and soil habitat in ways that increase resource availability to invertebrates. A significant interaction between simulated and fenced treatments, with increasing macroinvertebrate abundance in simulated treatments through time is predicted. Conversely, predation may exert a strong force on abundance from direct removal of invertebrates. If so, a significant interaction between simulated and unfenced treatments through time is predicted, with simulated plots showing increasing abundance through time when compared with unfenced.
Richness	Lyrebirds may influence macroinvertebrate richness through litter and soil disturbance by creating a more habitat niches available to invertebrates. If so, a significant interaction between simulated and fenced treatments through time is predicted, with an increase in richness in simulated plots. Lyrebirds may also alter richness by way of predation. If so, an interaction between the simulated and unfenced treatments is predicted, with decreasing richness in unfenced plots through time.
Taxon-level biomass	Lyrebirds may disproportionally alter biomass of invertebrate taxa through engineering and/or predation depending on habitat preference, size and locomotion. Specifically, it is predicted that soil-dwelling taxa (i.e. class Oligochaeta) will be less likely to be impacted by engineering than taxa with habitat preferences for litter habitats (all other taxa). If engineering by lyrebirds affects a taxon, an interaction between simulated and fenced treatments is predicted. Alternatively, lyrebirds may alter biomass of invertebrate taxa through predation. It is hypothesised that larger taxa (e.g., classes Chilopoda, Diplopoda and Amphipoda) are more likely to be impacted than smaller taxa (e.g., classes Coleoptera, Isopoda and Diptera), and more active organisms will be more detectable (and preyed upon) because they move vigorously with disturbance to litter and soil (e.g., classes Amphipoda and Araneae). If so, an interaction between simulated and unfenced treatments is predicted.
Biomass	Lyrebirds may alter biomass of invertebrate communities through engineering, in a 'farming' interaction. If so, it is predicted that biomass will increase in the simulated treatment through time, compared with fenced treatments. Further, it is predicted that this effect will be greater when considering only favoured dietary items. Conversely, if biomass is impacted through lyrebird predation effects, an interaction between simulated and unfenced treatments is predicted, with increasing biomass through time in simulated plots compared with unfenced.

3.3. RESULTS

From three sampling periods in spring (October) of 2015, 2016 and 2017, a total of 197,880 invertebrates (including larvae and pupae) was counted and identified by morphospecies to the lowest practical taxonomic level. This represented 99 taxonomic units, spanning six phyla, of which 49 were identified to family level, 41 to order or sub-order, seven to class or sub-class and two to phylum or sub-phylum (Appendix 2.4).

Of all invertebrates identified and counted, the most dominant groups were mites (sub-class: Acari, 51% of sample) and springtails (sub-class: Collembola, 30% of sample). Further, 86% of all invertebrates counted were classified as small (< 2 mm in length), 10% were medium (2-5 mm) and only 4% were large (> 5 mm in length).

Detritivores were the most abundant functional feeding group, comprising 78% of invertebrates. These were overwhelmingly dominated by oribatid mites (sub-order Oribatida) and collembolans (order Entomobryomorpha; families Sminthuridae and Onychiuridae), although amphipods, isopods and oligochaetes were also present in almost every sample (orders Amphipoda, Isopoda; sub-class Oligochaeta). Predatory taxa comprised 9% of total invertebrates, with predatory mites (sub-order Mesostigmata), spiders (order Araneae) and centipedes (order Lithobiomorpha) most represented. Fungivores made up 31% of invertebrates and overlapped with detritivore collembolans, although Pauropods (class Pauropoda) were well represented. Fungivorous Coleopteran beetles (families Leiodidae and Ptiliidae), thrips (order Thysanoptera) and Dipteran flies (families Mycetophilidae and Sciaridae) were uncommon in samples. Herbivorous invertebrates were in low abundance overall, comprising only 2% of the entire sample. The most abundant herbivorous taxa identified were weevils (order Curculionidae) and herbivorous mites (sub-order Prostigmata). True bugs (order Hemiptera), gastropods (order Gastropoda), butterflies and moths (order Lepidoptera) were also present in most samples.

3.3.1 Community composition of invertebrates

Three sets of pairwise comparisons were made with PERMANOVA to test for compositional differences between treatments (Table 3.2). There was a significant interaction between treatment and time for the paired comparisons of unfenced and simulated treatments (PERMANOVA; $F_{1,100}$=2.17, P=0.04; Table 3.2) and for fenced and unfenced treatments (F = 2.91, P=0.02), but not for the comparison of the fenced and simulated treatments (PERMANOVA; $F_{1,100}$=0.40, P=0.84; Table 3.2). Thus, there was no evidence of compositional change due to the engineering effects of lyrebird foraging, but strong evidence that predation affects invertebrate community composition through direct or indirect trophic pathways. In all comparisons there were significant differences in the composition of the invertebrate community between forest types, forest blocks and the three

years of sampling (time) (Table 3.2). The variance in the invertebrate community did not differ between treatments (Beta-disper, $F_{2,51}$=0.27, P=0.76).

3.3.2 Taxonomic richness of invertebrates

The linear mixed model for taxonomic richness revealed a significant interaction between simulated and fenced treatments through time (Table 3.3), supporting the engineering hypothesis. When controlling for the effects of forest type and litter depth, taxonomic richness in simulated plots was predicted to increase by ~14% during the two years, while in fenced plots it was predicted to decrease by ~2%. The predicted change in taxonomic richness through time for unfenced treatments was positive (though the 95% confidence intervals overlapped with zero), compared with the fenced treatment which showed a negative trend through time (Fig. 3.3). Model fit was moderate (marginal R^2 = 0.19).

3.3.3 Overall abundance of invertebrates

There was no significant interaction between the simulated and fenced treatments, suggesting that engineering had little impact on overall invertebrate abundance (Table 3.4). Nonetheless, an interaction was identified between simulated and unfenced treatments, supporting the predation hypothesis for invertebrate abundance. Abundance was predicted to increase by ~46% in simulated plots, compared with a predicted increase of ~3% in unfenced plots. A significant interaction between simulated and fenced treatments through time indicates a higher rate of increase in abundance occurred during the two-year study in simulated plots than fenced (Fig. 3.4), although the 95% CI for the interaction overlapped zero (Table 3.4). Abundance differed between years, but not between forest types, nor with litter depth (Table 3.4). Model fit was moderate (marginal R^2 = 0.16).

Table 3. 2 PERMANOVA results for pairwise comparisons of the composition of invertebrate communities between treatments. The conceptual hypothesis tested by comparison of each pair of treatments is also included for clarity of interpretation.

Factor	**PERMANOVA comparison**											
	Fenced and Simulated (difference = Engineering)				**Simulated and Unfenced (difference = Predation)**				**Fenced and Unfenced (difference = Predation + Engineering)**			
	F	**df**	***R^2***	***p***	**F**	**df**	***R^2***	***p***	**F**	**df**	***R^2***	***p***
Forest type	**3.61**	**2**	**0.06**	**<0.01**	**3.52**	**2**	**0.06**	**<0.01**	**3.66**	**2**	**0.06**	**<0.01**
Block	**4.94**	**2**	**0.08**	**<0.01**	**5.62**	**2**	**0.09**	**<0.01**	**4.24**	**2**	**0.07**	**<0.01**
Time	**10.87**	**1**	**0.08**	**<0.01**	**4.63**	**1**	**0.04**	**<0.01**	**4.84**	**1**	**0.04**	**<0.01**
Treatment	0.36	1	<0.01	0.88	0.81	1	0.01	0.41	0.84	1	<0.01	0.40
Time × Treatment	0.40	1	<0.01	0.84	**2.17**	**1**	**0.02**	**0.04**	**2.91**	**1**	**0.02**	**0.02**

Table 3. 3 Model outputs from a linear mixed effects model for experimental manipulation of foraging activity by the superb lyrebird on the taxonomic richness of invertebrate communities of the soil and litter layer. Parameter coefficients, standard errors (SE) and *t*-values are given for the fixed effects for treatments and the treatment × time interaction, and R^2 values of the fixed terms (marginal) and fixed and random terms (conditional). Coefficients for which the 95% confidence interval does not include zero are shown in bold. Reference level of factors: Treatment (Simulated), Forest type (Damp Forest). Litter depth was $\log_{10}$ transformed to improve linearity.

Response	**Predictor variable**	**Coefficient**	**SE**	***t***	$\mathbf{R^2}_{\text{(marginal)}}$	$\mathbf{R^2}_{\text{(conditional)}}$
Taxonomic richness	Intercept	33.13	1.65	20.12	0.19	0.22
	Time	**2.43**	**0.90**	**2.71**		
	Treatment – Fenced	0.26	1.49	0.17		
	Treatment – Unfenced	-0.24	1.49	-0.16		
	Litter	**6.25**	**2.24**	**2.79**		
	Forest type - Rainforest	**-2.72**	**1.03**	**-2.63**		
	Forest type - Wet Forest	0.23	0.98	0.24		
	Treatment (Fenced) × Time	**-2.69**	**1.23**	**-2.18**		
	Treatment (Unfenced) × Time	-1.32	1.15	-1.14		

Table 3. 4 Model outputs from a generalised linear mixed model for experimental manipulation of foraging activity by the superb lyrebird on invertebrate abundance. Parameter coefficients, standard errors (SE) and *z*-values for the fixed effects are given. Coefficients for which the 95% confidence interval does not include zero are shown in bold. Included are R^2 values of the fixed terms (marginal) and fixed plus random terms (conditional). Reference level of factors: Treatment (Simulated), Forest Type (Damp Forest). Abundance was $\log_n$ transformed and litter depth $\log_{10}$ transformed to improve linearity.

Response	**Predictor variable**	**Coefficient**	**SE**	***z***	$\mathbf{R^2}_{\text{(marginal)}}$	$\mathbf{R^2}_{\text{(conditional)}}$
Total invertebrate abundance	Intercept	6.73	0.17	39.82	0.16	1.0
	Time	**0.23**	**0.07**	**3.13**		
	Treatment – Fenced	-0.01	0.12	-0.08		
	Treatment – Unfenced	0.18	0.12	1.53		
	Litter	0.24	0.20	1.19		
	Forest type - Rainforest	-0.18	0.15	-1.17		
	Forest type - Wet Forest	0.14	0.15	0.92		
	Treatment (Fenced) × Time	-0.06	0.10	-0.57		
	Treatment (Unfenced) × Time	**-0.21**	**0.09**	**-2.27**		

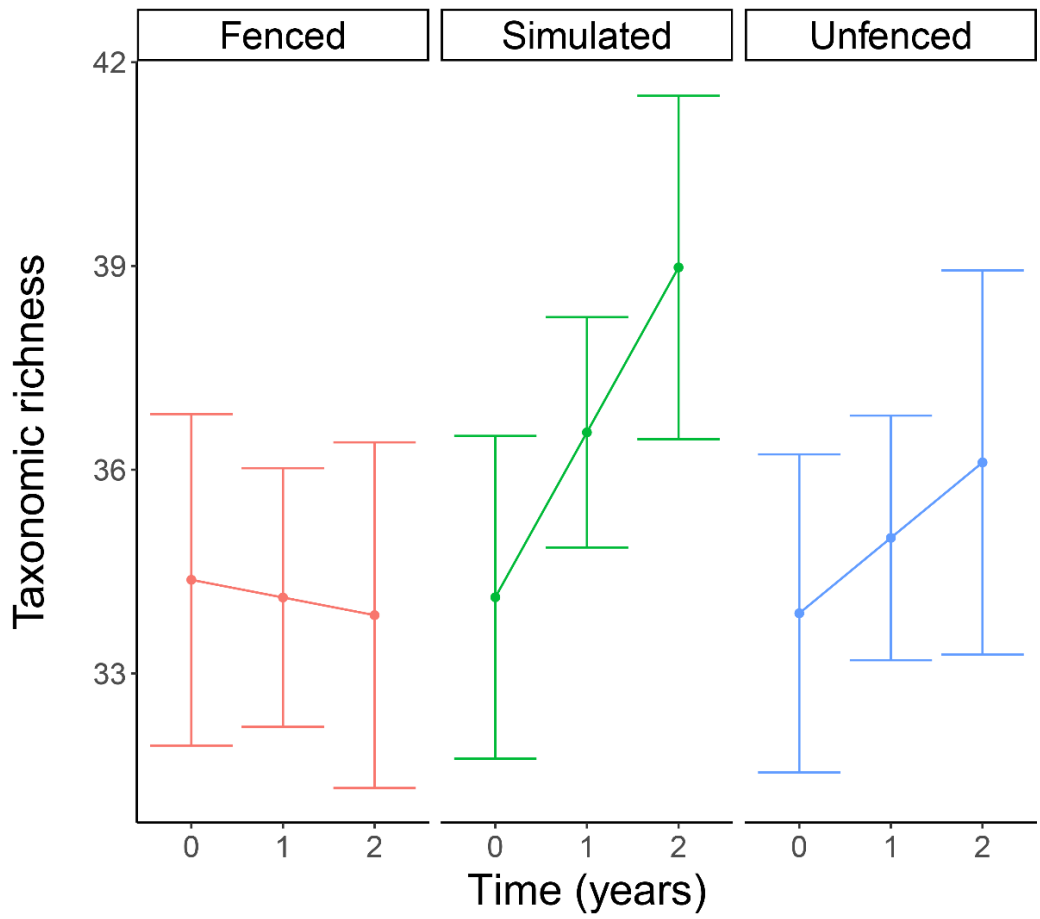


Figure 3. 3 Model prediction plot (±95% CI) of invertebrate taxonomic richness (number of taxonomic units) detected per plot during each of three years for three experimental treatments. Richness is modelled as a linear function of time and panels represent each experimental treatment. Other parameters in the model were held at constant values.

3.3.4 Biomass of different classes of invertebrates

There was high variability in biomass among and within invertebrate classes, making it difficult to detect engineering or predation effects for any one taxon. Class Amphipoda was the only group for which a statistically significant interaction was observed between simulated and fenced treatments, supporting an engineering hypothesis (Table 3.5, Fig. 3.5a). Similarly, class Amphipoda was the only taxon to show a predation effect (Fig. 3.5a). A trend for an engineering effect was, however, evident for all groups, signified by a negative coefficient for the (non-significant) interaction between fenced and simulated treatments through time (Table 3.5; Fig. 3.5a-h). That is, generally there was a trend for higher predicted biomass through time in simulated plots than in fenced plots, supporting the engineering hypothesis for these taxa. Model fit varied greatly between taxonomic groups, from being very low for millipedes (marginal R^2 = 0.03), to moderate for spiders (marginal R^2 = 0.21).

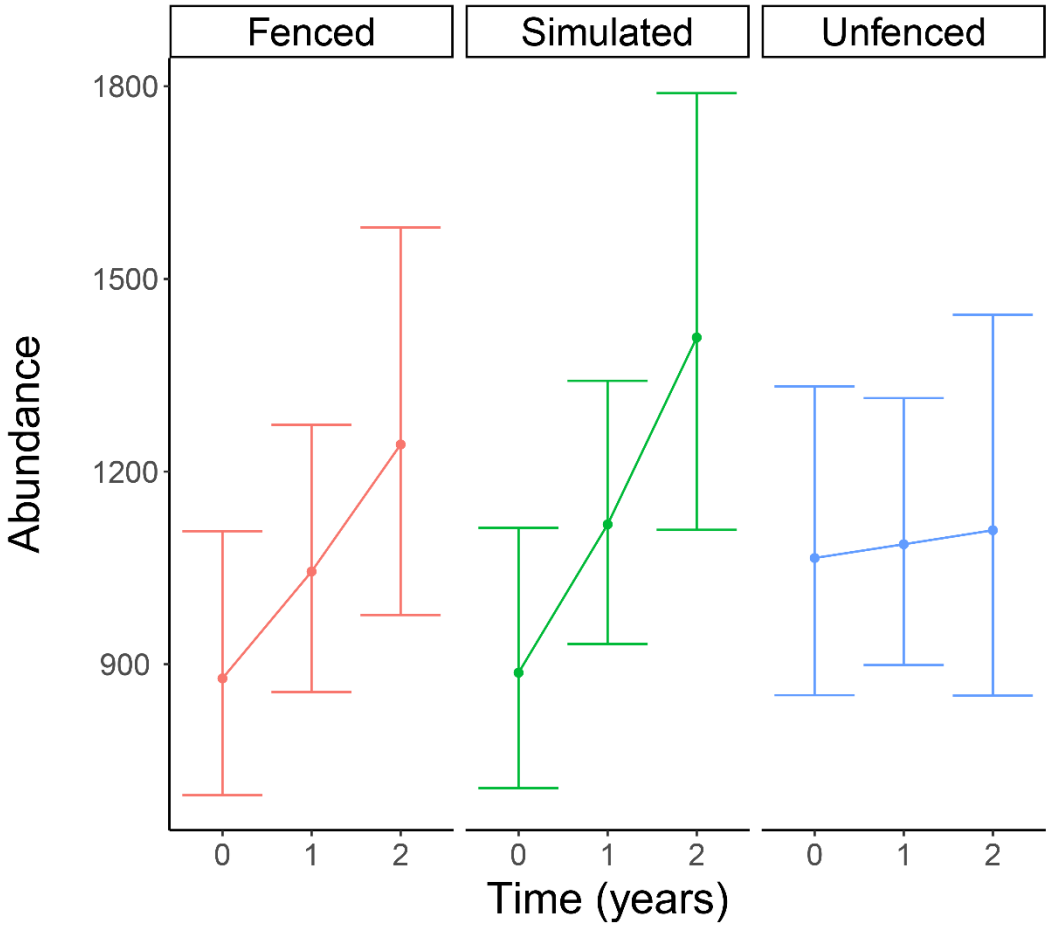


Figure 3. 4 Model prediction plot (±95% C.I.s) of overall invertebrate abundance during each of three years for the three experimental treatments. Abundance is modelled as a linear function of time and panels represent each experimental treatment. Other parameters in the model were held at constant values.

3.3.5 Biomass of combined taxa

For both measures of biomass (i.e. all invertebrates combined, and favoured prey items only), there was a significant interaction between simulated and fenced treatments through time (95% CI of coefficient did not overlap zero; Table 3.6), supporting the engineering hypothesis. That is, there was a greater increase in biomass through time in the simulated plots than in the fenced plots (Fig. 3.6). The biomass of all taxa combined was predicted to increase by ~40% in simulated plots during the two-year study compared with a predicted increase of ~3% in fenced plots (Fig. 3.6a).

There also was a significant interaction between simulated and unfenced treatments through time for total biomass, but not biomass of favoured prey items, suggesting the predation hypothesis was also supported (Table 3.6). Model prediction plots indicated little change in total biomass during the study period for both fenced and unfenced treatments (Fig. 3.6a), although for favoured food items the interaction term had a negative coefficient for fenced treatments, indicating a decreasing trend (Fig. 3.6b). Litter depth was an important explanatory variable in both biomass models (Table

3.6), having a positive effect on biomass. Model fit was moderate for total biomass and relatively low for biomass of favoured food items (marginal R^2 = 0.15 and 0.09 respectively).

3.4 DISCUSSION

This study used an experimental approach to decouple the potential impacts of ecosystem engineering and predation by the superb lyrebird on litter and soil macroinvertebrate communities in three forest types in south-eastern Australia. It found evidence that lyrebirds, through their foraging activities, function as ecosystem engineers in these highly productive forests, maintaining a greater species richness and biomass of macro-invertebrates (including favoured prey taxa) in the litter and soil-dwelling fauna. These results not only provide strong evidence of ecosystem engineering, but also that through these engineering activities lyrebirds are effectively 'farming' their prey.

3.4.1 Composition and overall abundance on invertebrates

Community composition and the overall abundance of macroinvertebrates were strongly influenced by trophic effects (i.e. predation) by lyrebirds in this two-year study. While lyrebirds are considered to be indiscriminate predators (Lill 1996), it is likely that they disproportionately prey upon larger invertebrates based on their detectability (i.e. size and/or movement when disturbed). Large prey items, such as species in the orders Chilopoda or Diplopoda, may have higher detectability due to increased body size. Additionally, these larger prey items are expected to be relatively sparse in the litter environment and thus sensitive to even low levels of predation. Taxa that are highly mobile when disturbed, such as species in the orders Collembola and Amphipoda, are also likely encountered with high detectability due to their vigorous locomotory response to disturbance of litter. Conversely, smaller, less mobile taxa, such as those in the order Acari, may be less affected by predation. These differential effects on taxa, combined with the patchy distribution of invertebrates in lyrebird habitat (Lill 1996), provide an explanation for a shift in the composition and decrease in abundance due to predation by foraging lyrebirds, while having little impact on composition through engineering.

Relatively few larger (>2 mm) invertebrates were detected, likely attributable to two aspects of the study design: First, stratification of plots ensured that they did not occur where there was dense vegetation at ground level, because lyrebirds avoid such areas when foraging (Maisey et al. 2018). Dense vegetation may provide cover for larger invertebrates, whereas in areas of open litter they would be more exposed to predation. Second, litter and soil samples (and therefore invertebrates) were collected during the day (to correspond with lyrebird foraging activity), when most larger (nocturnal) invertebrates would likely be sheltering in more complex habitats (Callan et al. 2011).

There was much variation in overall abundance, including between years, which may be attributable to environmental conditions such as rainfall. On average, invertebrate abundance increased during the two years of experimental manipulation. The overall abundance was lowest in 2015 (baseline) with a mean (± SE) of 1024±72 macro-invertebrates (including larvae and pupae) per plot. The year 2015 was also the driest of the three study years, with an annual total rainfall of 652 mm (weather station located at Warburton, Victoria). The highest rainfall year during the study period was 2016 (rainfall = 1074 mm), coinciding with the highest level of mean invertebrate abundance, at 1361±92.7 individuals per plot. With slightly lower precipitation in 2017 (rainfall = 1011 mm) overall mean abundance showed a modest decrease to 1280±83.8 organisms per plot.

3.4.2 Taxonomic richness

Analysis of taxonomic richness revealed a significant interaction through time between simulated and fenced treatments, indicating a strong engineering effect. In fenced plots, the number of taxa decreased, while in simulated plots it increased. This result is consistent with the initial hypothesis (Table 3.1) that in the lyrebird-free state with less disturbance and turnover, litter and soil would undergo a loss of fine-scale microhabitats and therefore taxonomic richness. In the treatments subject to physical disturbance of litter and soil, by real or simulated lyrebirds, a patchy pattern of microhabitats was available.

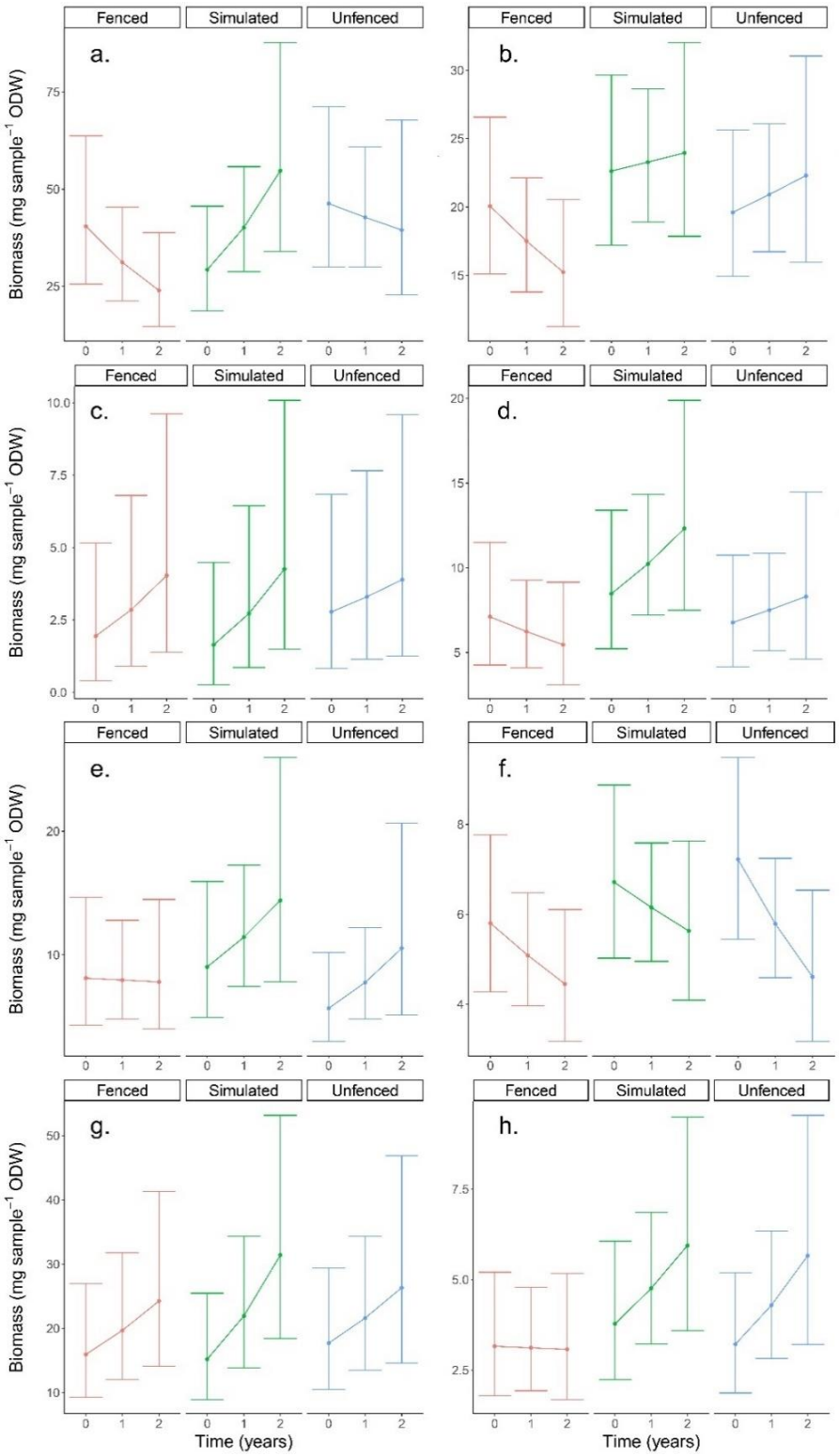


Figure 3. 5 Model prediction plots (± 95% C.I.s) for linear mixed models of biomass for a) Amphipoda, b) Coleoptera, c) Oligochaeta, d) Araneae, e) Diplopoda, f) Diptera, g) Chilopoda and h) Isopoda. These taxonomic groups are important prey items for lyrebirds, representing taxa found in >50% of meals fed to nestling lyrebirds by brooding females (Lill 1986).

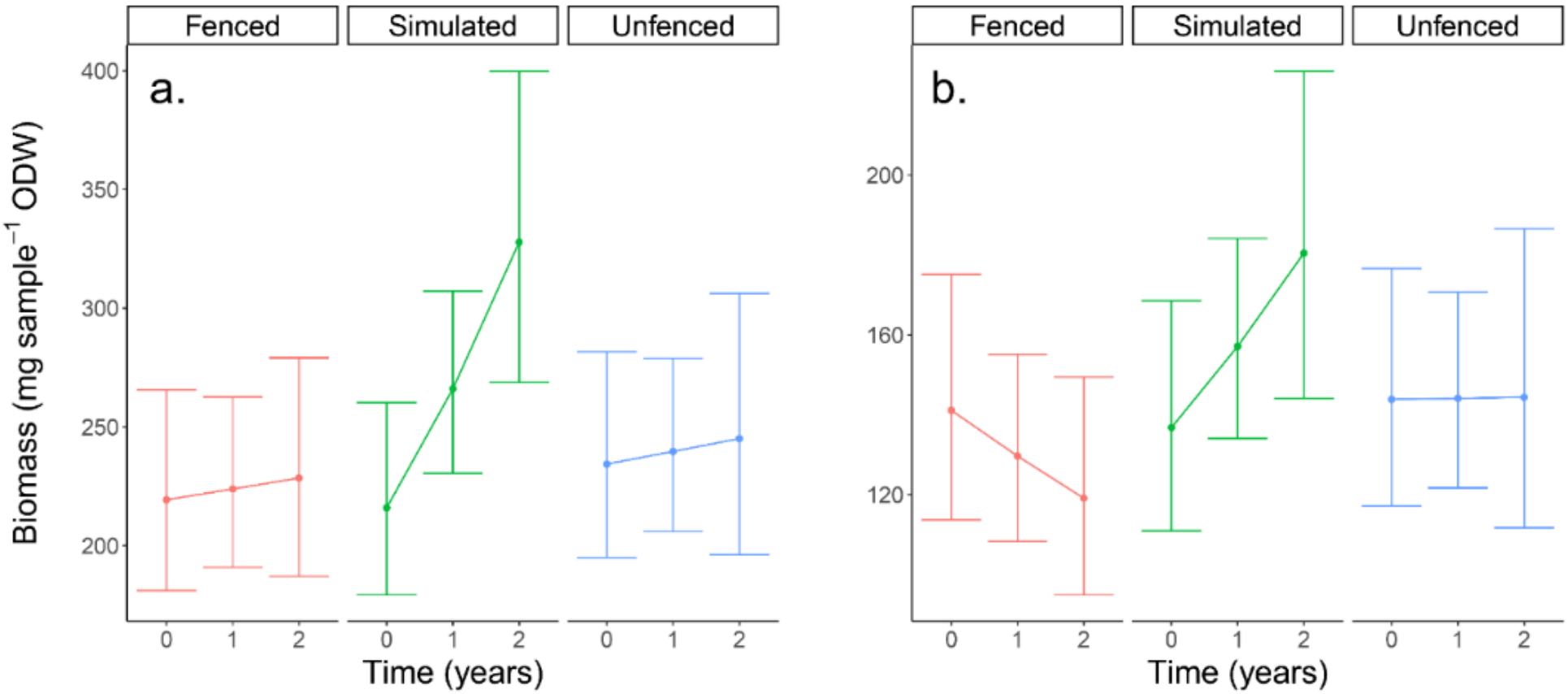


Figure 3. 6 Model prediction plot (± 95% CI) for a) total invertebrate biomass and b) biomass of favoured lyrebird prey items during each of three years for three experimental treatments. Biomass is modelled as a linear function of time and panels represent each experimental treatment.

Table 3. 5 Parameter coefficients, standard errors (SE) and *t*-values for the fixed effects in linear mixed models examining the relationship between treatment × time for biomass (oven dry weight) of invertebrate taxa known to be prominent in the lyrebird diet. R^2 values of the fixed terms (marginal) and fixed plus random terms (conditional) are included. Coefficients for which the 95% confidence interval does not include zero are shown in bold. Reference level of factors: Treatment (Simulated), Forest type (Damp Forest). Response variables were measured in mg sample^{-1} and $\log_n$ transformed to improve linearity. Litter depth was $\log_{10}$ transformed.

Response	**Predictor variable**	**Coefficient**	**SE**	***t***	**R^2 (marginal)**	**R^2 (conditional)**
Amphipods (Amphipoda)	Intercept	3.13	0.33	9.43	0.17	0.40
	Time	**0.31**	**0.16**	**2.00**		
	Treatment – Fenced	0.33	0.28	1.16		
	Treatment – Unfenced	0.46	0.28	1.61		
	Litter	**1.55**	**0.45**	**3.45**		
	Forest type - Rainforest	-0.31	0.28	-1.12		
	Forest type - Wet Forest	-0.24	0.27	-0.89		
	Treatment (Fenced) × Time	**-0.57**	**0.21**	**-2.65**		
	Treatment (Unfenced) × Time	**-0.40**	**0.19**	**-2.05**		
Earthworms (Oligochaeta)	Intercept	0.84	0.48	1.76	0.08	0.65
	Time	**0.34**	**0.13**	**2.63**		
	Treatment – Fenced	0.11	0.21	0.51		
	Treatment – Unfenced	0.36	0.21	1.69		
	Litter	0.38	0.35	1.08		
	Forest type - Rainforest	-0.27	0.46	-0.59		
	Forest type - Wet Forest	0.32	0.45	0.70		
	Treatment (Fenced) × Time	-0.08	0.18	-0.43		
	Treatment (Unfenced) × Time	-0.22	0.17	-1.31		
Beetles (Coleoptera)	Intercept	2.98	0.20	14.70	0.05	0.34
	Time	0.03	0.09	0.33		
	Treatment – Fenced	-0.11	0.17	-0.66		
	Treatment – Unfenced	-0.13	0.17	-0.79		
	Litter	0.32	0.27	1.19		
	Forest type - Rainforest	0.08	0.18	0.43		
	Forest type - Wet Forest	0.18	0.18	1.00		
	Treatment (Fenced) × Time	-0.16	0.13	-1.27		
	Treatment (Unfenced) × Time	0.03	0.12	0.26		
Spiders (Araneae)	Intercept	1.36	0.31	4.34	0.21	0.36
	Time	0.17	0.15	1.12		
	Treatment – Fenced	-0.15	0.26	-0.59		
	Treatment – Unfenced	-0.20	0.26	-0.75		
	Litter	**1.61**	**0.42**	**3.85**		
	Forest type - Rainforest	**0.62**	**0.25**	**2.46**		
	Forest type - Wet Forest	**0.64**	**0.24**	**2.65**		
	Treatment (Fenced) × Time	-0.29	0.21	-1.36		
	Treatment (Unfenced) × Time	-0.08	0.19	-0.43		

Table 3.5 continued

Response	Predictor variable	Coefficient	SE	*t*	$R^2_{(marginal)}$	$R^2_{(conditional)}$
Centipedes (Chilopoda)	Intercept	2.46	0.40	6.12	0.09	0.67
	Time	**0.36**	**0.13**	**2.76**		
	Treatment – Fenced	0.06	0.25	0.25		
	Treatment – Unfenced	0.16	0.24	0.66		
	Litter	-0.01	0.39	-0.03		
	Forest type - Rainforest	0.63	0.47	1.35		
	Forest type - Wet Forest	0.29	0.46	0.63		
	Treatment (Fenced) × Time	-0.16	0.17	-0.90		
	Treatment (Unfenced) × Time	-0.16	0.16	-1.05		
Millipedes (Diplopoda)	Intercept	2.12	0.41	5.18	0.03	0.25
	Time	0.22	0.19	1.11		
	Treatment – Fenced	-0.09	0.32	-0.30		
	Treatment – Unfenced	-0.41	0.32	-1.28		
	Litter	0.33	0.51	0.64		
	Forest type - Rainforest	0.18	0.39	0.46		
	Forest type - Wet Forest	0.10	0.38	0.27		
	Treatment (Fenced) × Time	-0.23	0.27	-0.87		
	Treatment (Unfenced) × Time	0.06	0.25	0.24		
Flies (Diptera)	Intercept	1.88	0.19	9.73	0.10	0.32
	Time	-0.08	0.09	-0.84		
	Treatment – Fenced	-0.13	0.15	-0.85		
	Treatment – Unfenced	0.06	0.15	0.43		
	Litter	0.16	0.24	0.68		
	Forest type - Rainforest	0.07	0.19	0.36		
	Forest type - Wet Forest	0.27	0.18	1.48		
	Treatment (Fenced) × Time	-0.04	0.12	-0.28		
	Treatment (Unfenced) × Time	-0.12	0.11	-1.01		
Slaters (Isopoda)	Intercept	0.91	0.29	3.18	0.13	0.36
	Time	0.19	0.13	1.47		
	Treatment – Fenced	-0.13	0.22	-0.61		
	Treatment – Unfenced	-0.12	0.22	-0.56		
	Litter	**1.00**	**0.35**	**2.84**		
	Forest type - Rainforest	**0.56**	**0.24**	**2.28**		
	Forest type - Wet Forest	**0.53**	**0.24**	**2.22**		
	Treatment (Fenced) × Time	-0.20	0.18	-1.14		
	Treatment (Unfenced) × Time	0.04	0.16	0.23		

Table 3. 6 Parameter coefficients, standard errors (SE) and *t*-values for the fixed effects in a linear mixed model examining the relationship between treatment × time for invertebrate biomass, and R^2 values of the fixed terms (marginal) and fixed plus random terms (conditional). Coefficients for which the 95% confidence interval does not include zero are shown in bold. Reference level of factors: Treatment (Simulated), Forest type (Damp Forest). Response variables were measured in mg sample^{-1} and $\log_{10}$ transformed to improve linearity.

Response	**Predictor variable**	**Coefficient**	**SE**	***t***	**R^2 (marginal)**	**R^2 (conditional)**
Total biomass	Intercept	5.20	0.14	36.45	0.15	0.40
	Time	**0.21**	**0.06**	**3.27**		
	Treatment – Fenced	0.02	0.11	0.20		
	Treatment – Unfenced	0.09	0.11	0.79		
	Litter	**0.46**	**0.18**	**2.60**		
	Forest type- Rainforest	-0.03	0.13	-0.25		
	Forest type – Wet Forest	0.16	0.13	1.25		
	Treatment (Fenced) × Time	**-0.19**	**0.09**	**-2.16**		
	Treatment (Unfenced) × Time	**-0.19**	**0.08**	**-2.37**		
Biomass of favoured prey items	Intercept	4.66	0.16	29.10	0.09	0.39
	Time	**0.14**	**0.07**	**1.96**		
	Treatment – Fenced	0.05	0.14	0.36		
	Treatment – Unfenced	0.07	0.14	0.48		
	Litter	**0.52**	**0.22**	**2.43**		
	Forest type- Rainforest	0.16	0.14	1.16		
	Forest type – Wet Forest	0.15	0.13	1.14		
	Treatment (Fenced) × Time	**-0.23**	**0.10**	**-2.28**		
	Treatment (Unfenced) × Time	-0.15	0.09	-1.64		

This included areas of freshly exposed mineral soil in recently foraged patches and complex ejecta mounds of mixed and buried litter and mineral soil, amid a matrix of intact leaf litter cover. The alternation between these microhabitats due to foraging activity was spatially and temporally dynamic. Conversely, in fenced plots a largely uniform litter layer was quickly established in the absence of real or simulated foraging, representing a less diverse microhabitat. These findings suggest the positive influence of lyrebird foraging on taxonomic richness of invertebrates is the result of fine-scale niche construction by lyrebird activities (Odling-Smee et al. 2003). Further, lyrebirds present a unique case of dynamic niche maintenance, sustained over time and to a broad spatial extent in these wet forest ecosystems.

While a strong engineering effect on richness was identified in this experiment, the unfenced treatment did not differ significantly from other treatments, suggesting predation effects may dampen the effect of engineering. This highlights the importance of using manipulative experiments to disentangle the intricacies of trophic and engineering effects, allowing a more nuanced appreciation of the role of ecosystem engineers.

3.4.3 Taxon-level biomass

Class Amphipoda was the only taxonomic group for which biomass strongly responded to the experimental treatments. Interestingly, Lill (1986) quantified the dietary items fed to nestling lyrebirds, finding that amphipods were present in ~98% of meals, and comprised 32% of prey animals identified, by far the most numerous of all dietary items recorded. Because litter and soil-dwelling macro-invertebrates vary in their response to habitat heterogeneity (Vanbergen et al. 2007), a high degree of variability between taxa was expected. Classes Oligochaeta, Chilopoda and Diptera showed little response to experimental treatments, while classes Aranae, Coleoptera and Isopoda showed much stronger trends. This may reflect the niche breadth of each group and the relative overlap with the foraging space of lyrebirds. Despite this variation, the (non-significant) trend for all of these taxonomic groups was for a greater increase in biomass through time in the simulated treatment than the fenced treatment, consistent with a beneficial effect from ecosystem engineering.

3.4.4 Biomass of combined taxa

At the conclusion of the two-year experiment, the predicted biomass of invertebrates in simulated treatments was greater than that found in fenced and unfenced treatments. Further, unfenced treatments were predicted to contain slightly greater biomass than fenced treatments, suggesting that despite removing invertebrates as prey there is an indirect effect of lyrebird foraging that acts to increase invertebrate biomass. The simulated treatments clearly showed that this indirect effect is due to the manipulation and turnover of litter and soil during foraging activities. Neither the

simulated nor fenced treatments were subject to predation by lyrebirds, but the simulation of foraging activities in the litter and soil resulted in a marked increase in biomass compared with plots where such disturbance was absent. This beneficial effect of engineering was strongly evident when only favoured lyrebird prey taxa were included, yet was also evident for all invertebrate taxa.

These results provide strong evidence that lyrebirds effectively 'farm' their prey through the physical modification of soil and litter habitats that occurs when foraging. The proximal cause can be attributed to changes to litter and soil structure that are well-documented to interact with invertebrates. First, lyrebird-modified soil was less compact, therefore providing greater aeration, water infiltration and pore space, all of which improve microhabitat quality for invertebrate communities (Hassink et al. 1993, Clapperton et al. 2002, Larsen et al. 2004). Second, litter was mixed and buried in soil, increasing the total surface area of leaf organic material in contact with mineral earth and therefore conducive to breakdown by detritivore and microbial communities (Coulis et al. 2016). Third, the fine-scale pattern of these processes across the forest floor provides gradients in litter depth, soil compaction and mixing that increase habitat heterogeneity (Anderson 1978, Niemelä et al. 1996, Hansen 2000). This highly dynamic disturbance regime in the litter and soil ecosystem likely maintains greater microbial productivity concomitant with increasing the trophic resource base available to invertebrates.

3.4.5 Feedbacks on the ecosystem engineer

The experimental design of this study made it possible to disentangle engineering from trophic impacts of lyrebirds on invertebrate communities. This experimental approach represents a powerful tool to test the ecosystem engineer hypothesis. These findings suggest that over time, ecosystem engineering by lyrebirds may increase invertebrate biomass beyond the level that would be supported in the absence of their habitat alteration. Further, the offtake associated with predation, while significant, was less than the gain in invertebrate biomass when foraging was simulated in the absence of predation. This positive feedback is of clear benefit to the lyrebird population, and apparently functions to increase the carrying capacity of the forest environment through a 'farming' effect on invertebrate prey.

This intriguing effect may be a form of extended phenotype engineering (Jones et al. 1994, 1997), whereby the physical modification caused by the animal engineer delivers a positive feedback to its population through increased availability of food resources. Such relationships have rarely been described for non-human animals. Notable examples exist for some invertebrate taxa, such as fungal 'farming' by attine ants, termites (Aanen et al. 2002) and curculionid beetles (Farrell et al. 2001). Such mutualisms typically are remarkably tight, having evolved over long evolutionary lines (Farrell et al. 2001). Only one other bird species has been described as benefiting from a similar interaction in a unique dual-species mutualism. The greater flamingo *Phoenicopterus roseus* and

fiddler crab *Uca tangeri* share an intriguing relationship that synergistically increases food resources (algal biofilms). This mutually beneficial engineering interaction involves the structural modification of mud flats by the feeding action of the flamingo and the burrowing and re-working of sediments by fiddler crabs. Their interactive effects are moderated by tidal forces to produce a complex drainage pattern promoting accrual of biofilm in West-African mudflats (El-Hacen et al. 2019). The spatial extent of engineering by these species is restricted to mudflats.

Most extended phenotypes, like the fungal farms of termites, are spatially restricted (e.g., the effect is localised within galleries of termite mounds). In the case of the superb lyrebird, ecosystem engineering occurs as a widespread, dynamic landscape process in wet forests. Moreover, the magnitude of these engineering effects on forests may vary temporally, mediated by forest succession. Following wildfire, lyrebird populations are reduced, as many individuals are either directly killed by fire or move away from burned areas due to the depletion of invertebrate food resources (Nugent et al. 2014). With few individuals remaining *in situ* after fire (Arthur et al. 2012, Doty et al. 2015), engineering effects of lyrebirds are likely to be negligible; however, as forest vegetation and lyrebird populations recover, a threshold may be reached where soil disturbance by lyrebirds is sufficient to restore their engineering role. As such, foraging is likely to function as an extended phenotype only when forest conditions (i.e. vegetation structure) meet optimal habitat requirements for lyrebirds.

In conclusion, this study confirms the superb lyrebird as an important ecosystem engineer and highlights the ways in which its foraging activity moderates and maintains the invertebrate biota of litter and soil ecosystems in wet forests of south-eastern Australia. Lyrebird foraging imposes top-down predation pressure on macro-invertebrate communities, in parallel with bottom-up ecosystem engineering effects that increase the taxonomic richness and biomass of these communities. Thus, the superb lyrebird is carrying out foraging activities in a manner that effectively ‘farms’ its prey to ensure they are available for future foraging. Manipulative field experiments represent a rigorous approach for distinguishing the trophic and non-trophic roles of animal ecosystem engineers, a critical step towards greater understanding and appreciation of the function of these important species.

Chapter Four

An avian ecosystem engineer facilitates seedling germination in wet forests

Plate 5. Colour-banded female superb lyrebird with curved tail caused by the domed nest during incubation.

ABSTRACT

Animal ecosystem engineers exert strong influence over vegetation communities in ecosystems worldwide. Understanding the interactions between animal engineers and vegetation in the presence of large herbivores is challenging, especially as most vegetation communities are simultaneously affected by both processes of engineering and herbivory. The superb lyrebird *Menura novaehollandiae* is proposed to act as an ecosystem engineer in south-eastern Australia, recognised for its extensive changes to the litter and soil on the forest floor. The impact of this species on vegetation is likely to have important implications for ecosystem function, yet remains poorly understood. This study aims to uncover the ecosystem engineering impacts of foraging by lyrebirds on the composition and structure of groundcover vegetation in wet forests. The study involved a two-year manipulative exclusion experiment, within the southern fall of Victoria's Central Highlands, to separate the impacts of engineering (by lyrebirds) from those of herbivory (by large mammals). Using a linear mixed modelling and multivariate approach, the engineering and herbivory effects on germination rates, seedling density, vegetation cover and structure, and community composition were investigated. Engineering effects of lyrebirds strongly facilitated the germination of seeds in the litter layer. At the conclusion of the two-year experiment there was a greater than two-fold difference in germinant counts between 'engineered' and 'non-engineered' plots. Engineering did not alter the density of seedlings, however herbivory had strong detrimental effects. Herbivory also reduced floristic richness and structural complexity (<0.5 m), including the cover of herbs and ground ferns. Ecosystem engineering by lyrebirds was a strongly facilitative process for the germination of the soil-stored seed bank, but had no impact on richness, composition, or vegetation structure. Engineering by lyrebirds should be considered as a key facilitative process for seedling germination. The two-fold increase in the number of seeds stimulated to germinate is likely to lead to important evolutionary advantages for plants, allowing greater phenotypic expression that would not occur in the absence of engineering by lyrebirds.

4.1 INTRODUCTION

Ecosystem engineers are widespread and play important roles in most ecosystems (Wright and Jones 2006). In terrestrial ecosystems worldwide, digging vertebrates, particularly mammals, have received much attention for their impacts on soils, especially in arid environments (Romero et al. 2014, Coggan et al. 2018). Soil manipulation by animals when foraging or constructing burrows may alter plant communities through both direct and indirect pathways (Fleming et al. 2014). Digging animals directly destroy individual plants (Song et al. 2012), while facilitating the spread of seeds through caching (Murphy et al. 2005) or epizoochory, where vertebrate animals carry seeds that have evolved hooks, spines or adhesive mucus (Wilby et al 2002). Soil turnover by small mammals alters the chemical and structural properties of soils, increases water infiltration (Garkaklis et al. 1998), run-off and erosion (Eldridge and Myers 2001), and moderates the availability of soil nutrients such as labile carbon, nitrogen and sulphur (Eldridge and Mensinga 2007). Conditions within foraging pits can provide a micro-climate conducive to plant germination (Martin 2003), while the burying and mixing of litter and soil by small mammals facilitates greater assimilation by macro and micro invertebrates, leading to higher rates of nutrient cycling (Valentine et al. 2013). This in turn improves soil condition and thus plant growth (Fleming et al. 2014, Valentine et al. 2018).

The role of avian ecosystem engineers has, to date, been largely overlooked (Sekercioglu 2006, Coggan et al. 2018), although there is growing evidence to suggest that many birds moderate the quality of habitats in ways that affect vegetation (Sekercioglu et al. 2016). On a local scale within breeding colonies, sea birds such as the wedge-tailed shearwater *Puffinus pacificus* alter vegetation through both their physical soil disturbance when excavating nesting burrows and the deposition of guano (Bancroft et al. 2005). Vegetation within colony boundaries shows profound differences in plant structure, composition and productivity compared with the surrounding landscape (Bancroft et al. 2005). In tidal environments, the feeding activity of the greater flamingo *Phoenicopterus roseus* and fiddler crab *Uca tangeri* interact to create intricate and heterogenous patterns of tidal inundation, thereby concentrating the accumulation of nutrients and thus biofilm food resources for both species (El-Hacen et al. 2019).

In terrestrial ecosystems, interaction with leaf litter by ground-foraging birds can moderate vegetation structure, increase fine-scale habitat heterogeneity, and affect ecological processes. In Australia, the mound-nesting malleefowl *Leipoa ocellata* alters litter when mound-building, amassing large quantities of material, thereby stripping the ground of litter connectivity and affecting the spread of fire. The likelihood and intensity of fire is reduced around active malleefowl mounds, which act to increase vegetation heterogeneity in the landscape (Smith et al. 2017). Similarly, males of the greater bowerbird *Chlamydera nuchalis* interrupt fine fuel connectivity when collecting material to build their courtship bower, effectively creating localised firebreaks in

these areas (Mikami et al. 2010). For fire-sensitive plants, unburnt areas may act as important refugia during fires, and as a seed source when recolonising after fire events.

While ground-foraging birds physically destroy small plants, their activities may also promote germination. The net effect on plant recruitment and survival may be related to the presence and traits of existing understorey plants. Song et al. (2012) investigated the relationship between the ground fern *Lastreopsis decomposita*, survivorship of rainforest plant seedlings and the combined activities of the litter-foraging brush turkey *Alectura lathami* and Albert's lyrebird *Menura alberti* in eastern Australia's subtropical rainforest. Ground ferns impeded light transmission where their cover was high, exerting a negative influence on germinant survival. Conversely, where fern cover was low, and in the presence of the ground-foraging birds, light interception and abiotic litter-smothering decreased, while ferns provided some protection to the seedlings from lyrebirds and brush turkeys. When the litter-foraging birds were excluded, the positive effect of ground ferns on seedlings was non-significant.

The superb lyrebird *Menura novaehollandiae* is recognised as an ecosystem engineer owing to its ability to move vast amounts of litter and soil (Ashton and Bassett 1997, Maisey et al. 2020). As lyrebirds work through an area of forest, micro-habitats and niche opportunities for ground-layer plants may be created in the form of discrete litter piles that are interposed with soil, litter-free pits (Tassell 2014) and micro-terraces (Ashton and Bassett 1997), chaotically arranged within a matrix of leaf litter covering the soil. A suite of organisms may potentially take advantage of such spatial heterogeneity (Hansen 2000), from bacteria and fungi to micro- and macro invertebrates, to detritivore predators such as arachnids (Bultman and Uetz 1982, Langellotto and Denno 2006), thereby affecting soils and hence vegetation through multiple pathways. The accumulation and decomposition of litter is an important mediator of ecosystem function in many mesic habitats (Xiong and Nilsson 1999), and therefore the implications of foraging by lyrebirds for vegetation are likely to be substantial.

Here, a manipulative exclusion experiment was undertaken to evaluate the impact of foraging by the superb lyrebird in three vegetation types in wet forests of south-eastern Australia. It was hypothesised that lyrebirds would change floristic communities through their foraging, while herbivory by large mammals would also be influential on vegetation. In order to disentangle the contribution of engineering effects from herbivory on plant communities, three treatments were established: fenced, where lyrebirds and large herbivores (e.g., swamp wallaby *Wallabia bicolor*, bare-nosed wombat *Vombatus ursinus* and sambar *Rusa unicolor*) were excluded; simulated, where herbivores and lyrebirds were excluded but foraging was simulated with a three-pronged hand rake; and unfenced, where both foraging by lyrebirds and herbivory from large herbivores continued to occur. By comparing the simulated treatment with the fenced treatment, the impact of engineering

was isolated from those of herbivory, and by comparing the simulated treatment with unfenced, the effects of herbivory could be isolated (Fig. 4.1).

It was hypothesised that lyrebird foraging and herbivory would both alter plant community composition, while having opposing effects on species richness. It was predicted that floristic richness would be increased by foraging, consistent with the expectation the engineered structures would create niche opportunities for plants (Wilby et al. 2001), while herbivory would decrease richness (Fuller and Gill 2001, Parsons et al. 2007) owing to the removal of plants at the plot scale. Foraging was expected to promote the germination of seeds by clearing leaf litter, disturbing the topsoil and exposing buried seeds to light and mechanical abrasion, while at the same time decreasing the survivorship of many growing seedlings (by uprooting or smothering them with litter). Moreover, herbivory was expected to have little influence over germinants (due to their small size and rapid growth) while decreasing the number of seedlings. Hence, the impact of lyrebirds and herbivory on the abundance of germinants and seedlings was tested. As a result of lyrebird disturbance, the overall structural complexity of low-growing vegetation was expected to be maintained at a constant (low) level, conducive to continued foraging by lyrebirds. Accordingly, the influence of foraging on vegetation structure, specifically the cover of herbs and ground ferns, was tested.

Figure 4. 1 Schematic diagram representing the three treatments at each site. Fenced plots exclude habitat modification by lyrebirds and also herbivory by vertebrates. Simulated plots are also fenced, and were hand-raked each month to simulate lyrebird foraging. Unfenced plots remain accessible both to lyrebirds and vertebrate herbivores. The 'Δ' defines which effect is tested by comparisons between treatments. Note: both hypotheses are tested simultaneously with each test performed. Pictured at right are examples of a) a fenced plot after 24 months, b) a male superb lyrebird, c) a native swamp wallaby and d) two introduced sambar deer stags.

4.2 METHODS

4.2.1 Study area

This study was conducted in the southern fall of the Central Highlands of Victoria, Australia (Fig. 4.2). The topography is characterised by moderate to steep slopes and high plateaus; valleys are comprised of alluvial flats. The geology of the region is of Palaeozoic deposits predominantly consisting of sedimentary and granitic rock, giving rise to brown and red Dermosols on the ridges and yellow or red Chromosols and Kurosols in valleys (DELWP 2014). In this region, lyrebirds commonly occur in three distinct forest types; damp forest, wet forest and cool temperate rainforest (Loyn 1985, van der Ree and Loyn 2002).

Three forest blocks were selected: 1) Sherbrooke Forest, part of the Dandenong Ranges National Park; 2) Yarra Ranges National Park, between Healesville and Warburton; and 3) Britannia Creek catchment between Warburton and Powelltown within the Yarra State Forest (Fig. 4.2). Each location is geographically isolated from others by the Yarra Valley (i.e. >10 km between forest blocks, mostly semi-rural land). Experimental manipulations were undertaken at each location (Fig. 4.2).

Sherbrooke Forest ranges from 400-600 m above sea level (ASL) and receives ~1200 mm of rainfall per annum. It is predominantly wet forest, with cool temperate rainforest restricted to linear streamside areas (Parks Victoria 2006). Sections of the park with a westerly aspect support damp forest. Most of the forest has regrown from intense historic logging.

The Britannia Creek catchment in the Yarra State Forest has an elevation 400-800 m ASL and average annual rainfall >1400 mm. This area has also experienced intense logging over the past century, but retains mature stands of the three forest types (van der Ree and Loyn 2002). This forest block is subject to seasonal firewood collection, intense use by recreational vehicles (trail motorcycles and 4x4 vehicular use), recreational hunting, and management to reduce bushfire risk.

Yarra Ranges National Park has a large range in elevation (400-1300 m ASL) and average annual rainfall of >1100 mm (Bureau of Meteorology 2019). It has a similar logging history to that at Britannia Creek, the two forest blocks being geographically separated by the Warburton valley (Fig. 4.2). While the Yarra Ranges National Park was historically a timber production forest, since 1995 it has been managed primarily for nature conservation.

Cool temperate rainforest (CTR) is dominated by southern sassafras *Atherosperma moschatum* and myrtle beech *Nothofagus cunninghamii* (though the latter is absent in Sherbrooke Forest), with a fern-rich understorey. Typically, the ground layer is more open than the other forest types due to the dense shade provided by the dominant tree species and abundant soft treeferns *Dicksonia*

antarctica. Shade-tolerant herbs such as shade nettle *Australina pusilla* and forest pennywort *Hydrocotyle geraniifolia* are common groundcovers. Colonial ground ferns, such as hard water fern *Blechnum watsii* and mother-shield fern *Polystichum proliferum*, are also common, but usually are in loose colonies, owing to the low-light environment.

Wet forest is widespread in each forest block, much of which is regrowth mountain ash *Eucalyptus regnans* that regenerated following severe bushfires in 1939. This forest type typically has a tall canopy of eucalypts, with a multi-structured middle storey comprised of blackwood *Acacia melanoxylon* and silver wattle *A. dealbata* over a diverse mix of small trees such as musk daisy *Olearia argophylla*, hazel pomaderris *Pomaderris aspera* and blanketleaf *Bedfordia arborescens*. The ground layer is a patchwork of colonial groundferns distributed in a loose matrix of open leaf litter. Soft treeferns and rough treeferns *Cyathea australis* are also widespread in this forest type.

Damp forest is dominated by messmate *Eucalyptus obliqua* and mountain grey gum *E. cypellocarpa*. The middle storey is similar in composition to wet forest, but sometimes is absent, with more Austral bracken *Pteridium esculentum*, sedges such as *Lepidosperma elatius* and *Gahnia sieberiana*, and a diverse herb layer present, mixed with grasses such as weeping-grass *Microlaena stipoides* and forest wire grass *Tetrarrhena juncea*. The dominant ground fern present is gristlefern *Blechnum cartilagineum* which may form dense colonies on moist slopes.

The superb lyrebird is ubiquitous in all three forest blocks (van der Ree and Loyn 2002). They forage in each forest type (Ashton and Bassett 1997, Maisey et al. 2018), but avoid forest that has recently experienced bushfire (Nugent et al. 2014, Maisey et al. 2018). They prefer to forage in areas with open ground cover (Ashton and Bassett 1997, Maisey et al. 2018) and thus are likely to avoid young regrowth forest. Consequently, each study location was chosen because it contained mature stands of the three forest types and had not undergone logging or experienced severe wildfire for >30 years.

4.2.2 Experimental design

In each forest block, potential sites within each forest type (cool temperate rainforest, wet forest and damp forest), were compiled using computer-generated coordinates. Selection criteria (Appendix 2.3) were identified in the planning stage and assessed in the field. Forest type and fire history were assessed from maps (DELWP 2019) and field visits were made to ground-truth the vegetation. In total, 18 sites were selected; two sites in each forest type, in each forest block.

At each site, three experimental plots (each 3 x 3 m) were established in October 2015. Plots were positioned along the contour of the slope, with each plot placed at a random distance between 5 and 40 m from one another. If the vegetation structure was not sufficiently open (Criterion 5, Appendix 2.3) at the first randomly selected distance, the contour was followed until the vegetation was

suitable. One of the three plots was randomly assigned as a reference plot, to remain unfenced and accessible to lyrebirds and herbivores. The two remaining plots were fenced to exclude lyrebirds and herbivores; one remained undisturbed, and the other was subjected to simulated lyrebird foraging (see below) on monthly visits. Fences were constructed of wire netting with 5 cm mesh size, and a height of 120 cm. Steel fencing stakes were used at the corner of each plot. Netting was pinned at ground level, and flagging tape was strung across the top of the fence to deter lyrebirds from flying into the plot (Fig. 4.1).

During November 2015 and August - October 2016, a single motion-sensing camera (Reconyx hyperfire, model HC600) was set at the reference (unfenced) plot at each site to confirm the presence of lyrebirds. Cameras were programmed to capture two images per trigger event, with a 60 s rest period. A 16 GB memory card was used, thus ensuring cards did not fill between monthly servicing. Lyrebirds were confirmed present at every site.

Fences were monitored for damage on a monthly basis. In a small proportion of monthly checks (at 6 plots, representing <3% of all observations), fences were thought to have been breached by lyrebirds, particularly during the first six months when fences were new to the environment. If lyrebird scratching was evident in a fenced plot it was recorded, although this was so seldom observed that effects were assumed to be negligible.

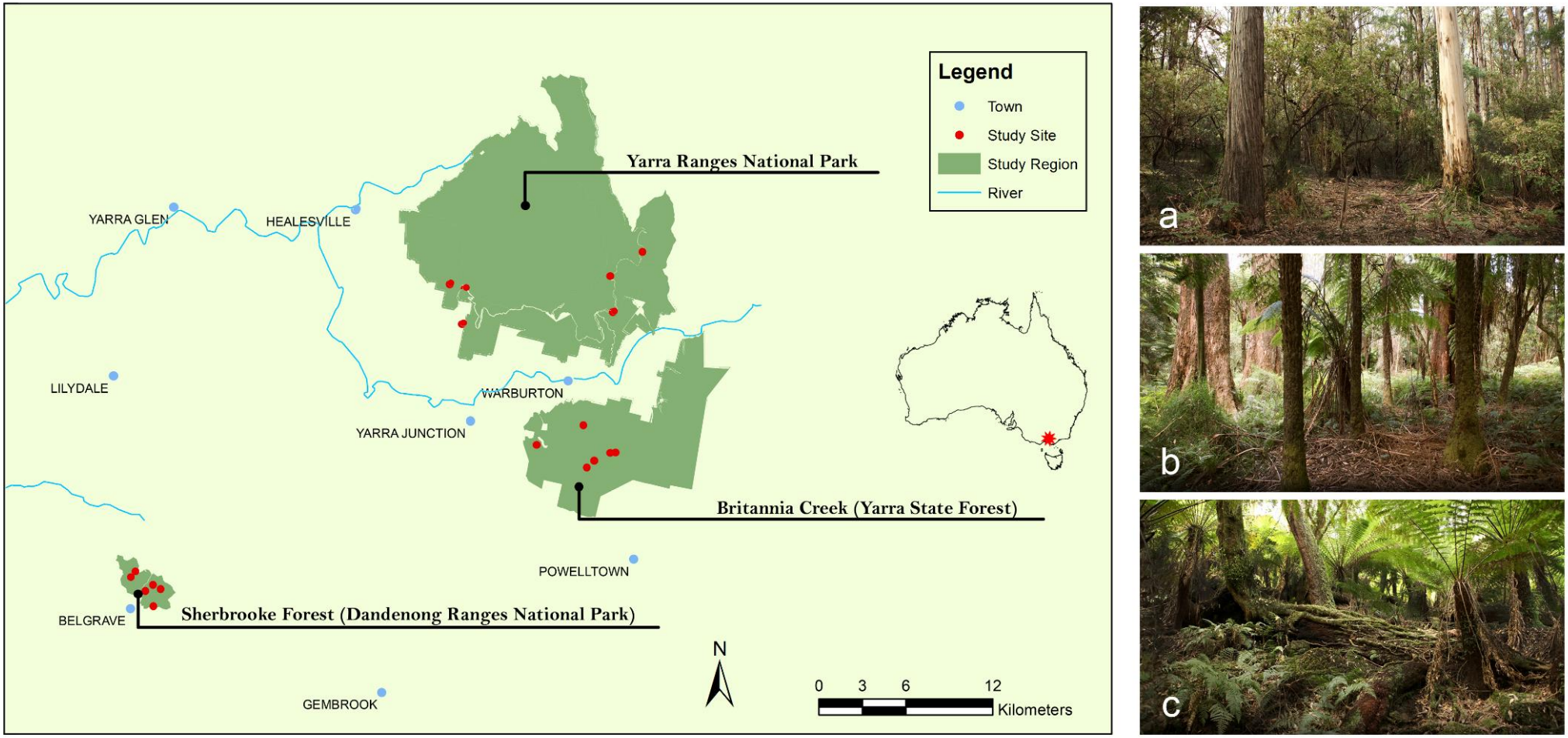


Figure 4. 2 The study region showing three forest blocks and the location of study sites within each. The panel at right provides exemplar images of a) damp forest, b) wet forest and c) cool temperate rainforest.

4.2.3 Foraging simulation

On each monthly visit to a site, the area disturbed by lyrebirds in the unfenced plot was visually assessed and recorded as a percent cover estimate. In the fenced simulated plot at that site, foraging was then simulated using a three-pronged hand rake (the approximate width of a lyrebird foot, ~10 cm), to replicate the foraging cover and configuration recorded in the unfenced plot. This process ensured that simulated foraging matched the level of natural lyrebird foraging observed at each site.

4.2.4 Data collection

All vascular plant species were surveyed in each 3 x 3 m plot during baseline sampling in October 2015, then at 12-month intervals for the two-year experiment (i.e. 3 sample periods in total). The total number of plant species was summed at each visit (floristic richness). Identification of germinating species was not attempted due to the difficulty in distinguishing between similar species.

All germinant dicotyledon plants, hereafter referred to as 'germinants', were counted within a 1 x 1 m subplot, centred on each plot. The subplot was used to avoid the influence of edge effects introduced by the fences interacting with litter (see fence effects on litter, below). Germinant counts were recorded upon plot establishment (baseline, Oct 2015), and then at three-monthly intervals for two years (i.e. 9 sample periods). From the same 1 x 1 m subplot, the number of small dicotyledon plants with only true leaves and a stem diameter <10 mm was recorded, hereafter referred to as 'seedlings'.

Concurrent with three-monthly surveys, vegetation structure was measured with a modified structure-pole technique (Chaffey and Grant 2000). A 2 m long ranging pole was placed vertically to the ground and the presence or absence of vegetation touches, dead or alive, were recorded in 50 cm increments from ground level to 2 m. This procedure was repeated at five points arranged in a cross (at the centre and four corners of the 1 x 1 m subplot) at each plot. Vegetation height increments were chosen to reflect the strata at which vegetation was expected to influence foraging lyrebirds (Maisey et al. 2018), thus each height increment was modelled separately. Cover estimates (% cover) of ground ferns and of herbs (all species combined) were visually assessed for the entire 3 x 3 m plot by a single observer (ACM).

4.2.5 Effect of fencing on litter

It was expected that, over time, leaf litter would accumulate against the upslope edge of fences due to abiotic (i.e. wind and gravity) displacement. Likewise, litter may fall away downslope from a fence. To determine the degree and distance to which this 'halo' effect of the fence may occur, litter depth was measured at 10 cm increments beginning 10 cm from the fence or plot edge, running

perpendicular to the contour, for 100 cm into each plot. This procedure was repeated 1 m from each corner of the plot and the two measurements for each distance increment were averaged. This procedure was repeated for both up-slope and down-slope positions, for all plots. Results confirmed there was no evidence of fence-effects on litter depth extending beyond 20 cm into fenced plots (see Maisey et al. 2020).

4.2.6 Statistical analysis

All statistical analyses were implemented in the R programming language (R Core Team 2012) using the R Studio interface (RStudio 2012).

The 'vegan' package (Oksanen et al. 2007) was used to investigate change in floristic composition through time. PERMANOVA tests were conducted using the *adonis* function, with the Bray-Curtis dissimilarity distance measure and 9,999 permutations. The response was based on the presence or absence of all vascular plant species (including tree species). The interaction between treatment and time (3 sample periods) was examined, and further included forest type as an explanatory variable. The *adonis* function was set to carry out permutations within forest block using the 'strata' argument to account for spatial patterns associated with sampling within different forest blocks. Within-group homogeneity of variance (dispersion) was tested for each time period and treatment by using the *betadisper* function. Beta-dispersion confirmed no difference in group variances (dispersion) between treatments or time periods (*betadisper* $P>0.05$), indicating assumptions for PERMANOVA had been met (Oksanen et al. 2007). An ordination was also conducted using non-metric multi-dimensional scaling for the dataset at 24-months (i.e. end of the experiment): the ordinations were visualised using the *metaMDS* function.

To model the effect of treatment on floristic richness, all epiphytes, treeferns and canopy tree species (*Eucalyptus* and *Acacia*) were excluded from richness measures, as these are large and long-lived species and were assumed to not be affected by the treatments over this two-year study. A linear mixed model (LMM) with a Gaussian distribution was used to assess the degree and direction of change between treatments, through time. Floristic richness was transformed ($\log_{10}$) to improve linearity. The interaction between treatment and time, and vegetation type, were specified as fixed effects and a random term was included that nested plot within site and forest block, to account for repeat measures through time and the spatial clustering of plots.

Counts of germinants and seedlings were each modelled using a generalised linear mixed model (GLMM) assuming a Poisson distribution. In each model the interaction between treatment and time was included, with the simulated treatment as the reference category to allow for explicit comparison between engineering effects (i.e. simulated *c.f.* fenced plots) and herbivory effects from

mammals (i.e. simulated *c.f.* unfenced plots). Forest type and season were included in the model, setting damp forest as the reference. A nested random term was specified as for the LMM above.

Vegetation structure was analysed with logistic regression (GLMM) assuming a binomial distribution, with the response variable being the proportion of vegetation touches from five samples (measured as presence or absence) for each height interval (0-0.5 m, 0.5-1.0 m, 1.0-1.5 m, 1.5-2.0 m) for each plot. Cover estimates (% cover) of ground ferns and of herbs were logit-transformed, as this transformation is suitable for percentage data (Warton and Hui 2011), and modelled with an LMM assuming a Gaussian distribution. Forest type was included as a fixed effect and a nested random factor was included as described above.

All linear models were constructed using the package 'lme4' (Bates et al. 2014); model predictions were generated with the package 'Effects' (Fox 2003) and visualised using the package 'ggplot2' (Wickham 2016).

4.3 RESULTS

4.3.1 Floristic composition

Floristic composition differed between forest types (*adonis* test $P<0.001$) but there was no significant interaction between treatment and time (*adonis* test $P=0.99$; Table 4.1). At the final sampling period (24-months), the NMDS ordination showed no evidence of a clear response (Fig. 4.3a); but there was clustering by forest type (Fig. 4.3b).

Table 4. 1 Summary of the PERMANOVA test (using *adonis*) comparing floristic composition between treatments, over time. Significant effects are shown in bold. '*' denotes the interaction term.

Factor	Df	SumsOfSqs	MeanSqs	F	R^2	*P*
Treatment	2	0.59	0.30	1.12	1.12	0.26
Time	1	0.26	0.26	1.00	1.00	0.38
Forest type	**2**	**12.84**	**6.42**	**24.39**	**24.39**	**<0.01**
Treatment * Time	2	0.13	0.06	0.25	0.25	1.00
Residuals	153	40.27	0.26	1.12		

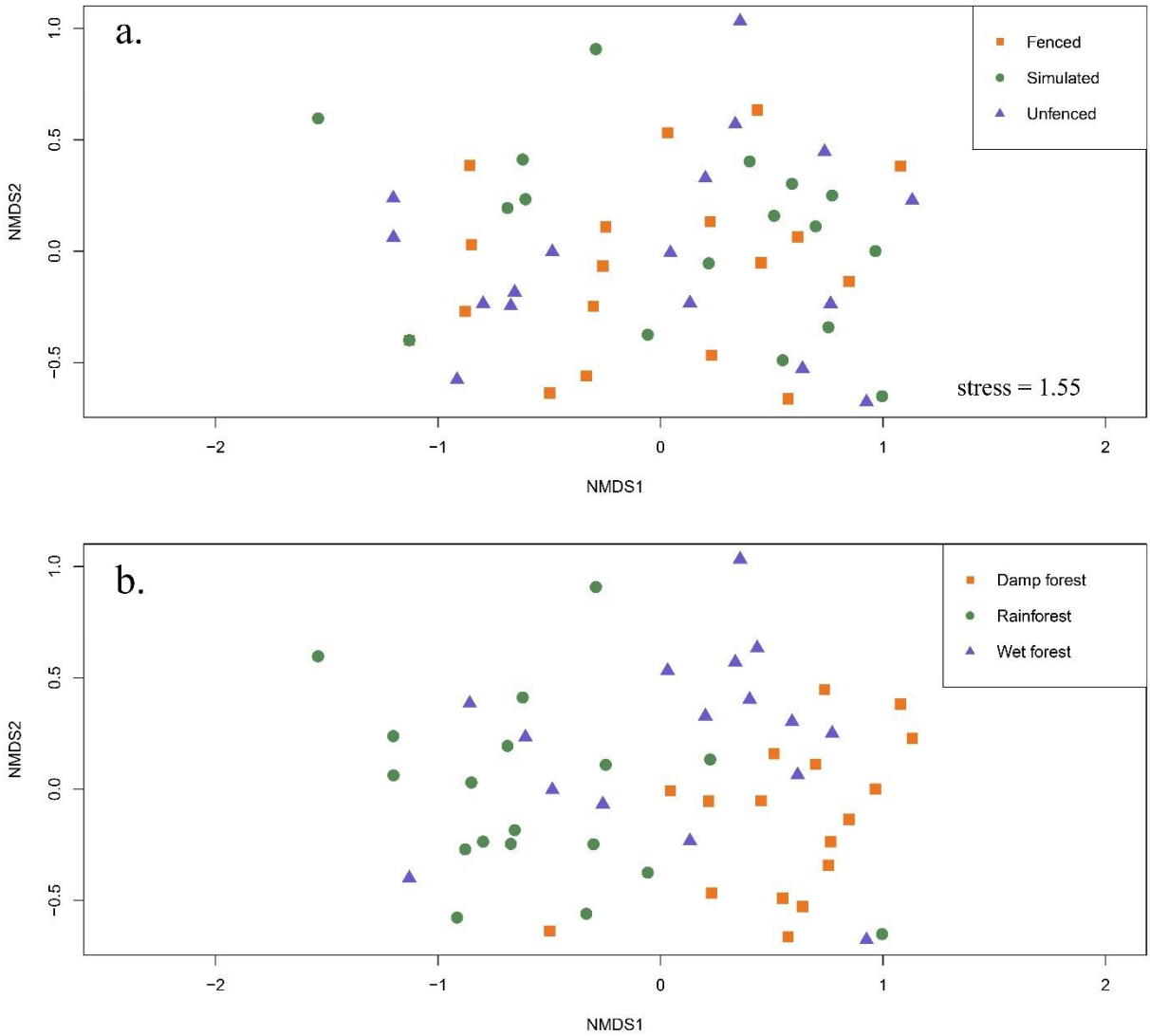


Figure 4. 3 Non-metric multidimensional scaling ordination plot comparing floristic composition at the final (24-month) sample period. The ordination is labelled by a) treatment and b) forest type.

4.3.2 Floristic richness

Measures of plant species richness (excluding epiphytes, canopy species and treeferns) increased through time in all treatments. Baseline (Oct 2015) richness measures were a mean of 3.3 species in simulated, 3.4 in fenced and 4.4 in unfenced plots; and increased through the study to mean values of 5.2, 5.4 and 5.3 species, respectively, at the final sampling period (24 months). There was a significant interaction between treatment and time for the unfenced treatment compared with the simulated treatment (Table 4.2a). That is, there was a lower increase in richness through time for the unfenced plots compared with the simulated plots (Fig. 4.4) although both experienced similar soil disturbance. This difference can be attributed to the effects of herbivory on vegetation in unfenced plots, whereas herbivores were excluded from simulated plots. Species richness in fenced plots showed a similar trend through time to simulated plots (Fig. 4.4), with no interaction between these treatments. This suggests that the physical soil engineering by lyrebirds did not impact on floristic richness during the two-year period.

4.3.3 Germinants

The number of germinants increased through time in all plots, with median baseline (Oct 2015) counts of 1 germinant in fenced, 1 in simulated and 1.5 in unfenced treatments (mean 2.8, 4.3 and 5.1 germinants respectively), increasing to 2.5 in fenced, 10 in simulated and 13.5 in unfenced treatments (mean 7.3, 15.0 and 22.4, respectively), by the final count at the end of the two-year period. A significant interaction was identified between treatment and time for the fenced plots compared with the simulated plots (Table 4.2b). The number of germinants showed little increase through time in fenced plots but increased strongly in simulated plots (Fig. 4.5a). This difference represents a positive effect on germinants of physical engineering by lyrebirds. Conversely there was no significant interaction between treatment and time for the unfenced plots compared with simulated plots: in both treatments the numbers of germinants increased strongly, suggesting potential herbivory (in unfenced plots) had little impact on germinant counts. There was also a seasonal effect: more germinants were recorded in spring and fewer in summer, than in autumn (reference category) (Table 4.2b).

Table 4. 2 Model output for the relationship between lyrebird foraging treatments over time and a) floristic richness (LMM assuming a Gaussian error distribution); and b) germinant counts and c) seedling counts (GLMMs assuming a Poisson error distribution). For all models the reference category for treatment was 'simulated', to allow for tests of engineering effects (i.e. simulated *c.f.* fenced) and herbivory effects (i.e. simulated *c.f.* unfenced). Coefficients for which the 95% confidence interval does not include zero are shown in bold. The reference category for forest type was 'Damp forest' and for season was 'autumn'. '*' denotes interactions between fixed effects.

Response	**Fixed effect**	**Estimate**	**SE**	***t* value**	$R^2_{(marginal)}$	$R^2_{(conditional)}$
a) Floristic richness (log_n-transformed)	(Intercept)	1.73	0.20	8.50	0.31	0.82
	Time	**0.18**	**0.05**	**3.36**		
	Treatment - Fenced	0.05	0.16	0.33		
	Treatment - Unfenced	0.26	0.16	1.59		
	Forest type - Rainforest	**-0.95**	**0.25**	**-3.76**		
	Forest type - Wet forest	-0.38	0.25	-1.52		
	Treatment$_{(Unfenced)}$ * Time	**-0.16**	**0.07**	**-2.12**		
	Treatment$_{(fenced)}$ * Time	-0.02	0.07	-0.21		
b) Germinant count	(Intercept)	-0.87	0.36	-2.39	0.23	0.93
	Time	**0.10**	**0.01**	**7.00**		
	Treatment - Fenced	0.21	0.37	0.57		
	Treatment - Unfenced	0.54	0.38	1.43		
	Season - Winter	-0.33	0.19	-1.72		
	Season - Spring	**0.75**	**0.17**	**4.45**		
	Season - Summer	**-0.52**	**0.21**	**-2.53**		
	Treatment$_{(Unfenced)}$ * Time	-0.01	0.02	-0.54		
	Treatment$_{(Fenced)}$ * Time	**-0.09**	**0.02**	**-4.55**		
c) Seedling count	(Intercept)	-3.13	0.57	-5.50	0.17	0.94
	Time	**0.15**	**0.01**	**14.06**		
	Treatment - Fenced	0.86	0.50	1.73		
	Treatment - Unfenced	0.90	0.48	1.86		
	Season - Winter	**-0.35**	**0.09**	**-3.72**		
	Season - Spring	**-0.75**	**0.10**	**-7.67**		
	Season - Summer	-0.22	0.11	-1.98		
	Treatment$_{(Unfenced)}$ * Time	**-0.05**	**0.01**	**-3.60**		
	Treatment$_{(Fenced)}$ * Time	-0.02	0.01	-1.78		

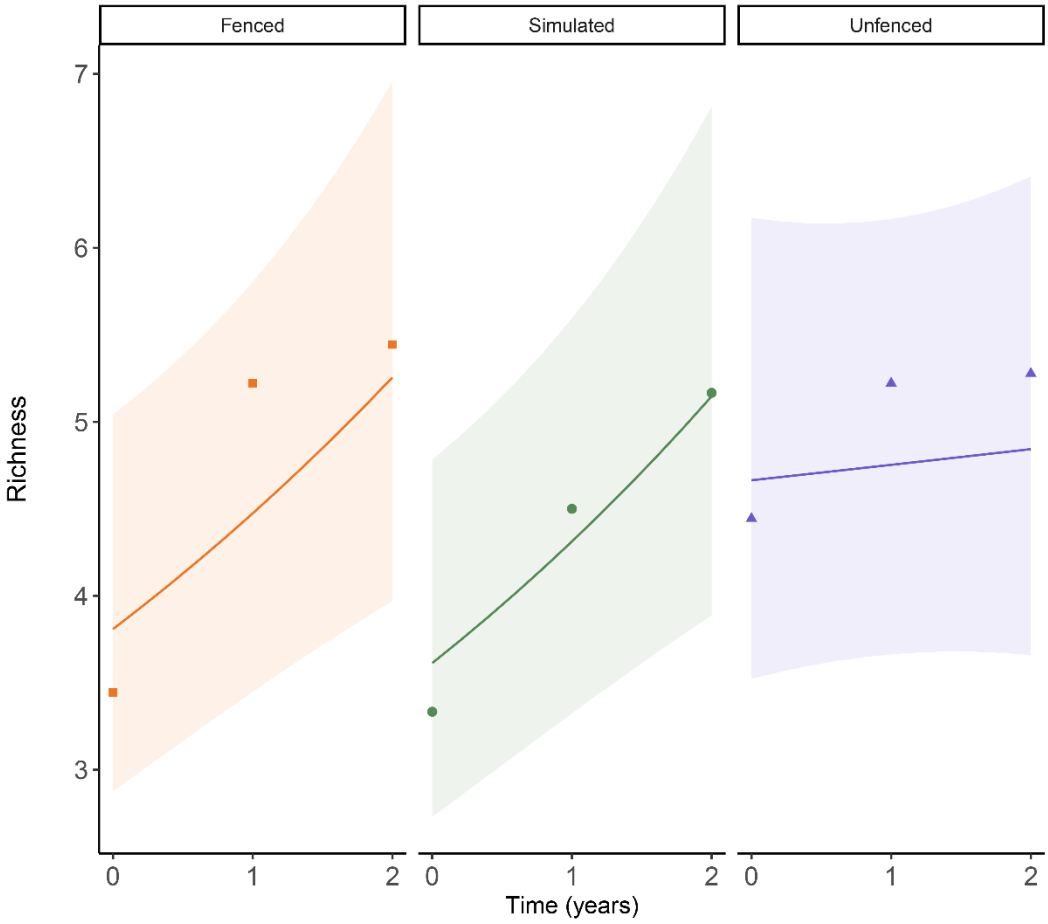


Figure 4. 4 Model prediction plots (± 95% C.I.s) for floristic species richness through time for each treatment. The three treatments are shown as separate panels for clarity. Mean richness values are plotted for each sample period and treatment.

4.3.4 Seedlings

Models showed that seedling counts increased in all treatments during the study, with median baseline counts of 0 seedlings and mean count of 0.2, for all treatments. By the end of the study, median seedling counts had increased to 1.5 seedlings in fenced treatments, 0.5 in simulated treatments, but remained at 0 for unfenced treatments (mean count of 5.5, 4.2 and 2.2 seedlings respectively). A significant interaction was identified between the unfenced and simulated plots through time, with greater increase in seedlings in simulated plots during the experiment compared with unfenced plots (Fig 4.5b). This represents an effect of herbivory on seedlings, with herbivores able to access unfenced plots but not those with simulated foraging. There was no interaction between simulated and fenced treatments through time; both showed a similar increase in seedling

counts compared with the unfenced treatment (Table 4.2c, Fig. 4.5b). There was also a significant seasonal effect, with more seedlings counted in autumn than in the other three seasons (Table 4.2c).

4.3.5 Vegetation structure

Vegetation structure in the lowest height interval (0 – 0.5 m) showed an interaction between treatment and time for the unfenced plots, compared with the simulated plots (Table 4.3, Fig. 4.6). There was a greater increase in structure (contacts with ranging pole) in simulated plots through time than in unfenced plots, consistent with a herbivory effect, suggesting herbivory by vertebrates was reducing low vegetation structure. No interactions were present for any higher strata (Table 4.3).

4.3.6 Cover of herbs and ground ferns

Model outputs revealed that herb cover increased through time in fenced and simulated treatments, but decreased in unfenced treatments (Table 4.4a). There was a significant interaction between simulated and unfenced plots, indicative of an effect of herbivory reducing cover of herbs in unfenced plots. The trajectory of increasing herb cover through time in simulated and fenced treatments did not differ (i.e. no engineering effect; Fig. 4.7). Ground fern cover did not change during the study period, with no significant treatment by time interactions (Table 4.4b).

Table 4. 3 Model outputs for the relationship between lyrebird foraging treatments and vegetation structure. Models are GLMMs (assuming a binomial error distribution). In all models, 'simulated' was the reference category for treatment to allow for comparison between potential engineering effects (simulated *c.f.* fenced) and herbivory effects (simulated *c.f.* unfenced). Coefficients for which the 95% confidence interval does not include zero are shown in bold. Autumn was the reference category for season. '*' denotes interactions between fixed effects.

Response	Fixed effect	Estimate	SE	*z* value	$R^2_{(marginal)}$	$R^2_{(conditional)}$
a) Vegetation Structure 0 - 0.5 m (touches on range pole)	(Intercept)	-2.80	0.49	-5.71	0.05	0.37
	Time	0.03	0.01	1.94		
	Treatment - Unfenced	0.21	0.56	0.38		
	Treatment - Fenced	0.48	0.55	0.88		
	Vegetation type – Rainforest	-0.13	0.48	-0.27		
	Vegetation type – Wet forest	-0.32	0.48	-0.67		
	Treatment$_{(Unfenced)}$ * Time	**-0.04**	**0.02**	**-1.97**		
	Treatment$_{(Fenced)}$ * Time	0.01	0.02	0.74		
b) Vegetation Structure 0.5 - 1 m (touches on range pole)	(Intercept)	-3.52	0.64	-5.53	0.05	0.39
	Time	-0.01	0.02	-0.49		
	Treatment - Unfenced	0.05	0.64	0.07		
	Treatment - Fenced	1.02	0.59	1.72		
	Vegetation type – Rainforest	-0.35	0.64	-0.55		
	Vegetation type – Wet forest	-0.38	0.64	-0.59		
	Treatment$_{(Unfenced)}$ * Time	-0.01	0.03	-0.29		
	Treatment$_{(Fenced)}$ * Time	-0.01	0.03	-0.24		
c) Vegetation Structure 1 - 1.5 m (touches on range pole)	(Intercept)	-4.98	0.91	-5.48	0.23	0.53
	Time	-0.13	0.07	-1.90		
	Treatment - Unfenced	1.18	0.83	1.43		
	Treatment - Fenced	0.48	0.86	0.56		
	Vegetation type – Rainforest	0.50	0.80	0.62		
	Vegetation type – Wet forest	0.15	0.82	0.19		
	Treatment$_{(Unfenced)}$ * Time	0.11	0.07	1.52		
	Treatment$_{(Fenced)}$ * Time	0.14	0.07	1.89		
b) Vegetation Structure 1.5 - 2 m (touches on range pole)	(Intercept)	-3.81	0.58	-6.61	0.16	0.41
	Time	**-0.08**	**0.03**	**-2.63**		
	Treatment - Unfenced	**1.27**	**0.55**	**2.31**		
	Treatment - Fenced	0.75	0.56	1.34		
	Vegetation type - Rainforest	**1.17**	**0.55**	**2.14**		
	Vegetation type – Wet forest	0.55	0.55	0.99		
	Treatment$_{(Unfenced)}$ * Time	0.03	0.03	1.06		
	Treatment$_{(Fenced)}$ * Time	0.02	0.03	0.70		

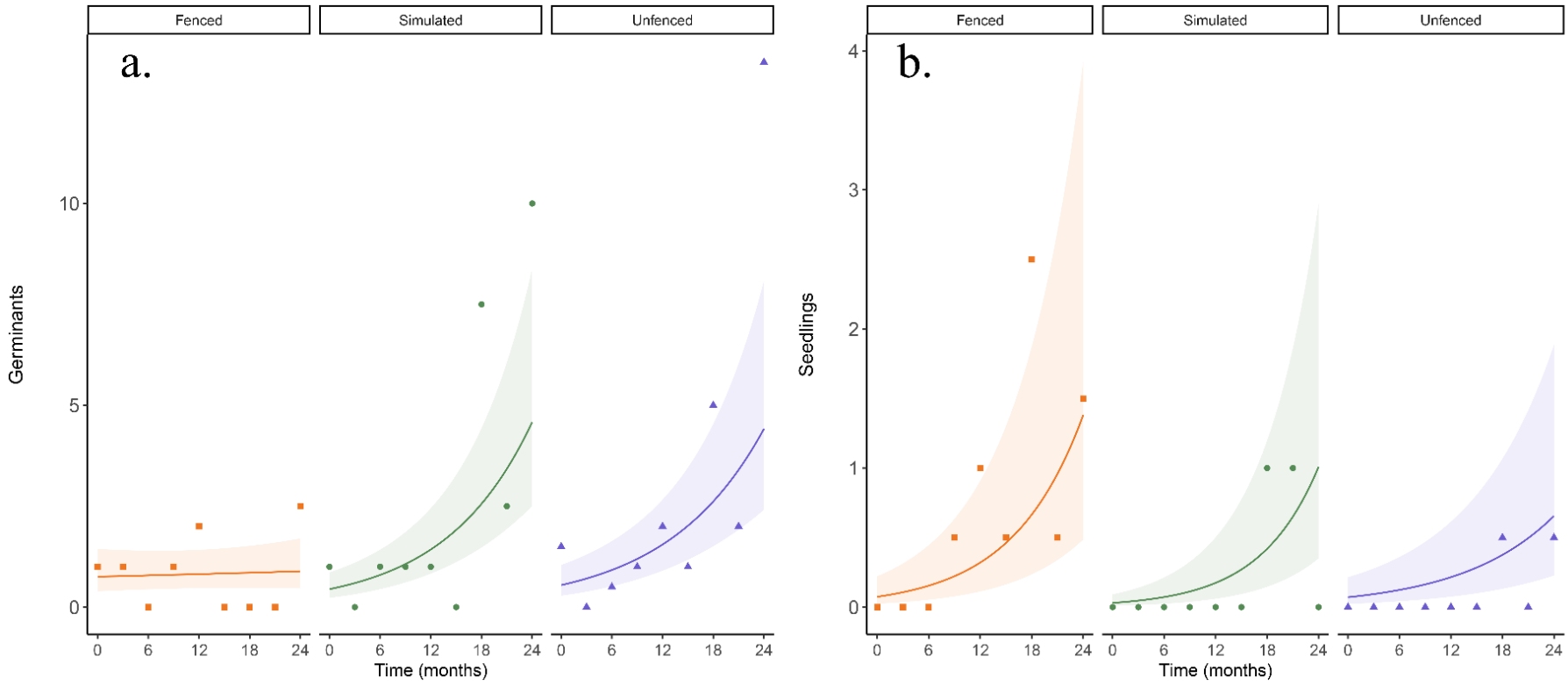


Figure 4. 5 Model prediction plots (± 95% C.I.s) from generalised linear mixed models of changes in a) germinants and b) seedlings through time for each of the three treatments (panels). Data points showing median values for each 3-monthly count are overlayed (medians are used to best represent data with a Poisson distribution).

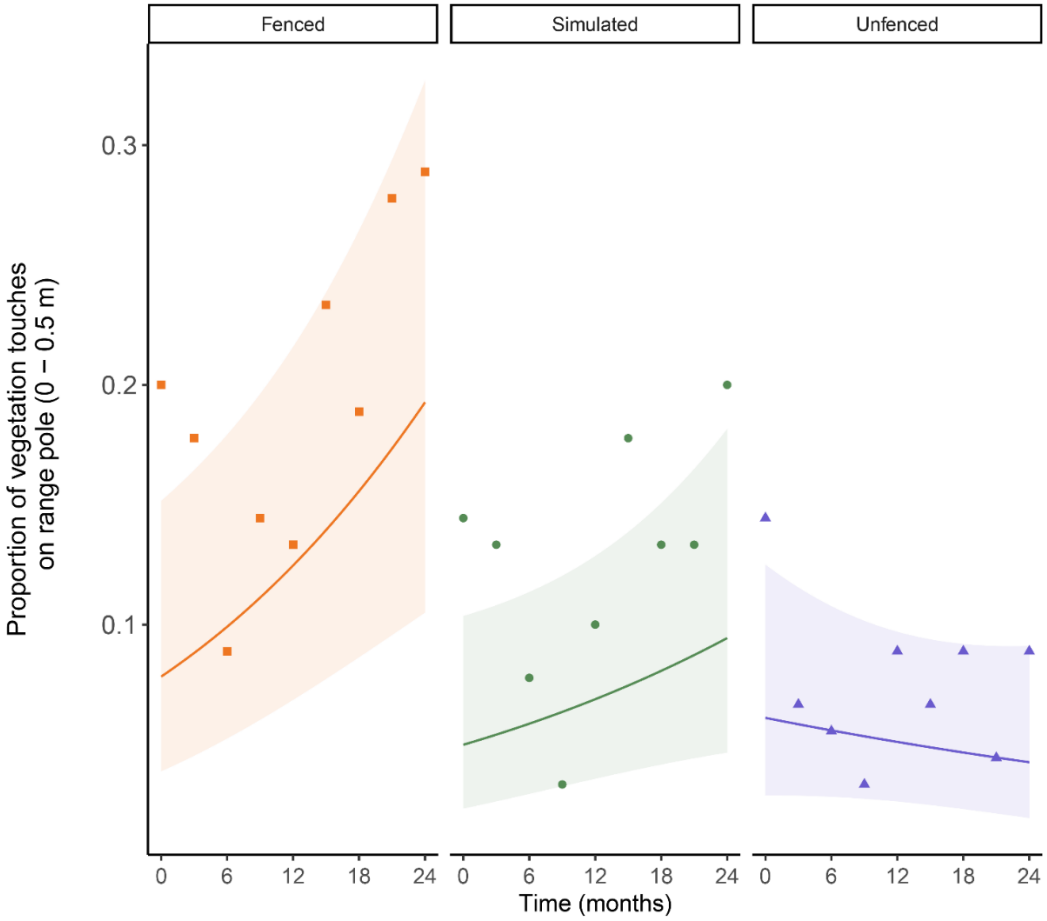


Figure 4. 6 Model prediction plots (± 95% C.I.s) from a generalised linear mixed model of changes in low vegetation structure (touches on ranging pole, 0 – 0.5 m) through time. The three treatments are shown as separate panels for clarity. Mean proportion of touches (out of five measures per plot) are plotted for each time period.

Table 4. 4 Model outputs (LMMs assuming Gaussian error distribution) for the relationship between lyrebird foraging treatments and a) herb and b) ground fern cover. 'Simulated' was the reference category for treatment, to allow for comparison between potential engineering effects (simulated *c.f.* fenced) and herbivory effects (simulated *c.f.* unfenced). Coefficients for which the 95% confidence interval does not include zero are shown in bold. '*' denotes interactions between fixed effects.

Response	**Fixed effect**	**Estimate**	**SE**	***t* value**	$R^2_{(marginal)}$	$R^2_{(conditional)}$
a) Herbs (% cover, logit-transformed)	(Intercept)	-3.54	0.44	-8.08	0.10	0.90
	Time	**0.03**	**0.01**	**4.13**		
	Treatment - Unfenced	0.21	0.32	0.65		
	Treatment - Fenced	-0.09	0.32	-0.26		
	Vegetation type – Rainforest	-0.93	0.56	-1.67		
	Vegetation type – Wet forest	-0.21	0.56	-0.37		
	Treatment$_{(Unfenced)}$ * Time	**-0.03**	**0.01**	**-3.47**		
	Treatment$_{(Fenced)}$ * Time	0.00	0.01	0.15		
b) Ground ferns (% cover, logit-transformed)	(Intercept)	-3.32	0.46	-7.22	0.03	0.85
	Time	0.00	0.01	-0.12		
	Treatment - Unfenced	-0.28	0.35	-0.80		
	Treatment - Fenced	-0.12	0.35	-0.34		
	Vegetation type – Rainforest	0.36	0.48	0.74		
	Vegetation type – Wet forest	-0.16	0.48	-0.33		
	Treatment$_{(Unfenced)}$ * Time	0.00	0.01	0.25		
	Treatment$_{(Fenced)}$ * Time	0.01	0.01	1.05		

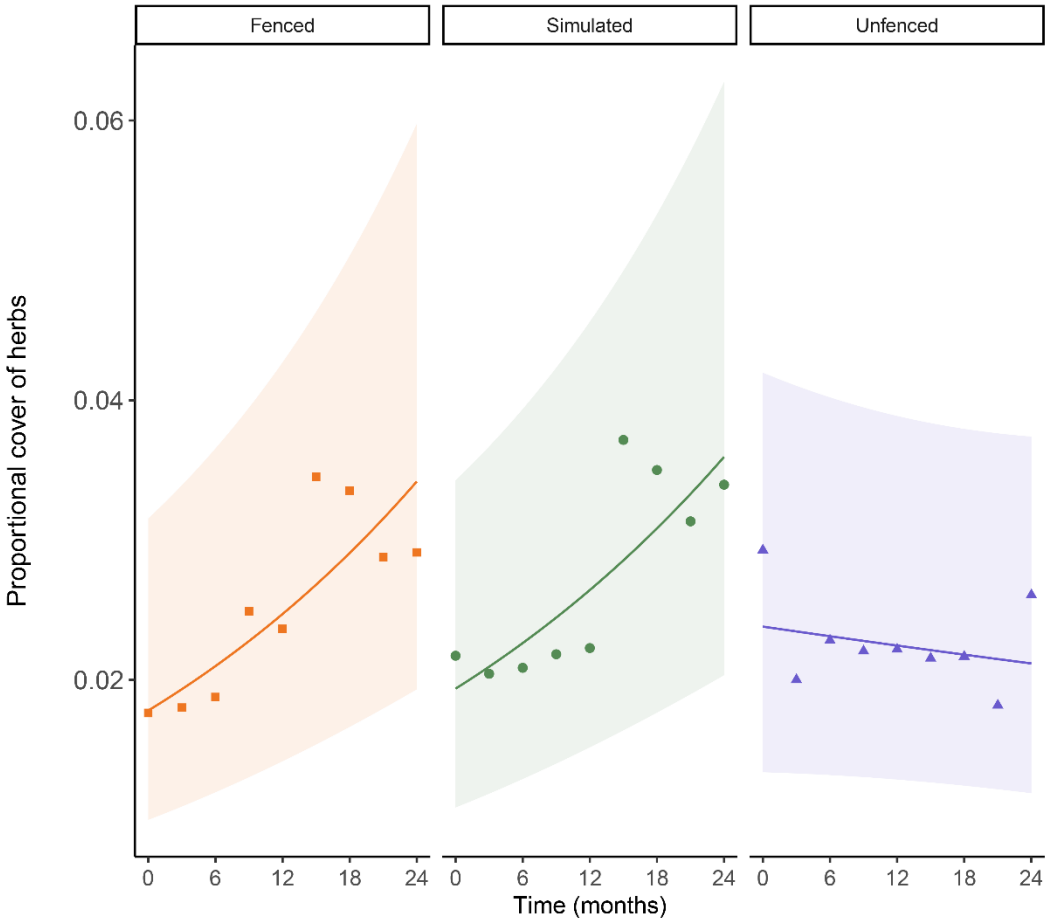


Figure 4. 7 Model prediction plots (± 95% C.I.s) from linear mixed models for change in herb cover through time. The three treatments are shown as separate panels for clarity. Back-transformed mean values are plotted for each sample period and treatment.

4.4 DISCUSSION

In recent decades, recognition of the complex interactions between herbivores and ecosystem engineers has increased (Wilby et al. 2001, Parker et al. 2007) but field studies that explicitly separate these impacts remain uncommon. Disentangling trophic impacts such as herbivory from those of engineering is challenging, yet provides nuanced insight into the population dynamics of plant communities, with potential for flow on effects to other components of the biota (Prugh and Brashares 2012, Grinath et al. 2018). This experiment was able to distinguish the trophic effects of vertebrate herbivores from the engineering effects of lyrebirds.

Two processes influencing the dynamics of plant communities in wet eucalypt forests were uncovered by this experiment. First, lyrebird foraging and the associated engineering effects of soil displacement exerted a dramatic influence over the number of germinants in plots. There were more

germinants in plots subject to either real or simulated foraging compared with fenced plots without foraging. Second, floristic richness, the number of seedlings, vegetation structure and herb cover all showed a strong response consistent with herbivory, but were not influenced by engineering effects. Other measures, including the floristic composition of the vegetation and cover of ground ferns, showed no change relating to treatments.

4.4.1 Impacts on floristic community

Vertebrate herbivores in natural systems often show neutral or negative impacts on vegetative growth (Fuller 2001, Travers et al. 2018), but may have positive effects on floristic diversity through suppression of competitive dominance (Grime 1979). During this two-year study, however, vertebrate herbivory did not increase richness, but showed the opposite trend: when herbivores (e.g., swamp wallaby and sambar) were excluded by fencing, richness of plant species increased. The lack of significant interaction between the simulated and fenced treatments suggested that lyrebird foraging activity neither increased nor decreased richness. Given the scale of soil disturbance by lyrebirds (Maisey et al. 2020), it is probable that the local elimination of some species is compensated by the creation and maintenance of niche opportunities for other plant species to exploit, maintaining overall stability of species persistence.

Conversely, floristic composition did not change as a result of the experimental treatments. This may partly reflect the use of presence/absence data that fails to capture fluctuations in species abundance through time. Nonetheless, these results suggest that while some species may respond to treatments, the full species pool was no more (or less) represented in any given treatment over a two-year period.

4.4.2 Engineering implications for germinants

Counts of germinants uncovered a strong facilitative effect of ecosystem engineering by lyrebirds. In both simulated and unfenced treatments (i.e. treatments subjected to engineering), germinants increased through time, while in the fenced plots they showed little change. When lyrebirds forage, they scrape the litter layer on the forest floor, and subsequently mix and bury much of the surface litter with mineral soil. This disturbance decreases litter depth (Maisey et al. 2020) and allows for gaps in the litter layer, promoting light-driven germination (Fig. 4.8), especially important for small seeds of many temperate forest species (Theimer and Gehring 1999). Further, by creating a finely heterogeneous litter profile, variation in depth and extent of mineral soil mixing may facilitate germination of a wider range of species that require specific litter conditions for germination and growth (Green 1999).

The observed increase in germinant counts in all treatments through the two-year experiment is most likely attributable to an increase in rainfall through this period (Bureau of Meteorology 2019). Concomitant with wetter conditions, litter decomposition rates increased on the forest floor (Maisey et al. 2020), leading to a shallower litter layer and reduced litter-smothering of seeds and seedlings. As a result, fenced plots underwent little change in litter depth and in germinant counts, rather than germinant counts decreasing (in response to deeper litter accumulation) as initially predicted.

Figure 4. 8 Image detailing native shrub and herb germinants (predominantly the shrub *Coprosma quadrifida*, but also the herbs *Viola hederacea*, *Geranium potentilloides* and *Austrocynoglossum latifolium*) in soil previously disturbed by the superb lyrebird. Note that lyrebirds typically displace soil in a downhill direction away from a structural habitat component, such as the log in the top left of the image. Image captured in the spring growing season 2019.

4.4.3 Engineering implications for seedlings

In this two-year experiment, seedling counts were impacted by herbivory, but not by engineering effects of lyrebird foraging. There were fewer seedlings in the unfenced treatments, and no difference between fenced and simulated treatments. The interpretation of this effect, however, is not straight-forward. In the fenced and simulated treatments, foraging disturbance was present when fences were constructed. As such, lyrebirds had 'primed' the ground layer for germination (i.e. a broken litter layer and exposed seed bank). In the absence of herbivores (excluded by fencing), a flush of growth occurred within these treatments; however, in fenced plots germinant counts quickly diminished as litter accumulated during the first few months of the experiment (Maisey et al. 2020). This initial pulse in germination and subsequent survival of this cohort to seedling stage in the fenced treatment represents a legacy of lyrebird foraging that remained over the duration of the study. In simulated treatments, while some seedlings were likely to have been removed or smothered, this attrition was compensated by new seedlings from seeds stimulated to grow by the simulated foraging. This was reflected in the higher germinant counts in simulated treatments compared with fenced. Overall, there was no net change in seedling counts, but importantly, high seedling turnover in the simulated treatment.

4.4.4 Vegetation structure

Vertebrate herbivory appeared to suppress low-strata vegetation structure (<50 cm) in the unfenced treatment, while the simulated treatment did not differ significantly from the fenced treatment. This suggests that simulated soil engineering did not have a strong impact on low vegetation structure during this time period. A similar pattern was evident in the analysis of herb cover, with an increase in simulated and fenced treatments, but not unfenced treatment, during the study. The same legacy effect of lyrebird foraging (at the time of exclosure) may apply to herbs, as previously described for seedlings, and obscure the true impact of lyrebird foraging activity on herbs. It is possible that a positive influence of soil engineering on herb germination and growth in simulated treatments was masked by the legacy of lyrebird foraging in fenced treatments.

The herb species most common in wet forests are mostly small and fast-growing (e.g., shade nettle *Australina pusilla*, ivy-leaf violet *Viola hederacea*), and unlikely to inhibit foraging lyrebirds. In contrast, ground ferns (e.g., *Polystichum proliferum, Blechnum wattsii*) are much larger and longer-lived. Ground fern cover, at high density, does inhibit foraging by lyrebirds (Maisey et al. 2018). Over a timescale longer than in this two-year experiment, it is predicted that lyrebird foraging would slow or inhibit widespread colonisation by ground ferns through the physical destruction of young, asexually reproduced plantlets and the uprooting of young rhizomatous species. Anecdotal evidence of dead, uprooted juveniles of mother-shield ferns *Polystichum bulbiferum* on the fringe of dense

fern colonies, suggests lyrebird activity maintains the patchwork structure of open litter areas between ground fern colonies. In addition to the restricted timescale of this study and slow life-history of fern species, this study design (see Appendix 2.3) deliberately avoided areas of high groundcover (often comprising ground ferns). As lyrebirds foraged over an average of ~11% of the unfenced plots per month the entire forest floor may be turned over in less than a year in areas suitable for foraging. While foraging permits (or may even promote) the rapid growth of herbs, slow-growing ground ferns would be unlikely to reach maturity before being destroyed by foraging activity. The interactions between lyrebirds and ground ferns are thus likely to determine forest understorey pattern over prolonged timescales.

4.4.5 Implications for ecological processes in wet forests

Wildfire is an infrequent, but profoundly important process shaping the dynamics of wet eucalypt forests (Fairman et al. 2016). Ecosystem engineering by lyrebirds potentially interacts with wildfire in several ways. First, by burying and mixing litter with soil, lyrebirds reduce fuel loads and create conditions that would reduce the intensity of a wildfire, should one occur (Nugent et al. 2014), and so indirectly influence vegetation. Second, the occurrence and extent of lyrebird foraging is likely to shape the pattern of vegetation recovery in wet forests following severe fire. Following severe wildfire, lyrebird populations are likely to be in low density in, or even absent from, early successional stages (Nugent et al. 2014). Shade-tolerant ground ferns typically recolonise from surrounding unburnt areas via spore dispersal (Ashton 2000). As lyrebirds recolonise the recovering forest, sparsely vegetated areas between fern colonies are likely to become important foraging sites. Colonies of ground ferns may harbour invertebrate communities and function as invertebrate population reservoirs (McElhinny et al. 2006), representing an important food source for lyrebirds.

As the forest matures and lyrebird activity builds, foraging activity will also intensify and the continued uprooting of small ferns may even increase the extent and complexity of the edges of fern colonies. At such a point in forest succession, a positive feedback loop may occur as lyrebirds gain greater access to their invertebrate food. Dense populations of lyrebirds may therefore maintain a mosaic of open foraging areas between fern colonies, potentially holding ground-cover vegetation structure in stasis for long periods of time. As many cool temperate rainforest species readily germinate upon the trunks of soft tree ferns, successional transition from wet forest to rainforest is unlikely to be hindered by the activity of lyrebirds (i.e. seedlings survive physical destruction by growing high above the litter layer). Moreover, Ashton and Bassett (1997) proposed that lyrebirds may increase tree fern density in forests by creating, through their foraging, germination sites on litter-free ledges of soil among tree roots and adjacent to logs. Increased treefern populations may further facilitate invasion of rainforest species. As the forest reaches a climax community, intense lyrebird disturbance and the development of a dense and shady middle-storey would lead to sparse

ground fern colonies. Thus, in a mature cool temperate rainforest, resource depletion may occur, presenting a mechanism for lyrebirds to self-regulate to lower density. This complex interaction between ground ferns and lyrebirds is worthy of further research, with the lyrebird potentially an important moderator of wet forest succession over the period of centuries.

Interactions between lyrebird foraging and the germination and survivorship of seedlings is likely to have important consequences for the evolutionary potential of plants in wet eucalypt forests. Two primary pathways are possible. First, in the presence of foraging lyrebirds, the volume of seeds afforded the opportunity to germinate is higher, stimulated by exposure to light and mechanical abrasion/disturbance (Floyd 1976, Clarke et al. 2000), thereby increasing the establishment of more individuals of more species. In turn, greater phenotypic diversity will be expressed in a highly competitive environment, over time facilitating higher fitness by retaining beneficial genes that may otherwise rarely be expressed in plant populations. Second, through burying or partial uprooting of seedlings as they grow, foraging lyrebirds may select for particular phenotypes in plant populations. For example, seedlings with strong, fast-growing roots and higher tolerance to water stress will be more resistant to such antagonistic disturbances. Both pathways may increase the resilience of plant communities to disturbance and environmental extremes.

Should lyrebirds be lost from wet forest ecosystems, plants may be less-adapted for germination in the litter-rich environment of the forest floor. In such a scenario, phenotypic expression must change rapidly, in response to a host of novel environmental conditions driving directional selection for germination, a process described as ‘contemporary evolution’ (Stockwell et al. 2003). Such impacts pose a risk to the dynamics of the forest-floor community, particularly those relating to herb diversity in wet forests.

4.5 CONCLUSION

Engineering by lyrebirds strongly facilitated seed germination, while herbivory suppressed seedling survivorship, herb cover and vegetation structure. Importantly, engineering by lyrebirds did not suppress any of the floristic measures examined over this two-year experiment. These results support the hypothesis that lyrebirds facilitate seedling germination, uncovering this process as a potentially important evolutionary driver of plant fitness in these forests. Further, impacts on vegetation by lyrebirds are likely to structure plant communities over broad timescales, and long-term studies are needed to determine these lengthy ecological processes.

Chapter Five

Ecosystem engineering and soil fungal communities in forest ecosystems

Plate 6. Three mature male lyrebirds engaged in territorial neck-snaking behaviour.

ABSTRACT

Fungi play a critical role in ecosystem function, including decomposition, vegetation growth and forest health. Soil disturbance by ecosystem engineers is common in a range of forest and wooded ecosystems and likely has an impact on soil fungi that may affect its ecosystem function. The superb lyrebird *Menura novaehollandiae* is a widely distributed ecosystem engineer in moist eucalypt forests of south-eastern Australia, turning over large volumes of litter and soil on a daily basis while foraging for invertebrates. An experimental approach was used to test the influence of lyrebird foraging on the composition, richness and diversity of the soil fungal community in three forest types (damp forest, wet forest and cool temperate rainforest) in the southern fall of the Central Highlands of Victoria. Three replicate treatments were used (fenced from lyrebirds, fenced with simulated foraging and unfenced) in each forest type to test whether lyrebird foraging influenced soil fungal communities over a two-year period. The fungal community showed a distinct composition in each forest type, with lower richness but higher diversity in cool temperate rainforest compared with the other forest types. There was no evidence that soil disturbance by lyrebirds influenced the composition or richness of the soil fungal community over this two-year timescale. Fungal communities show marked differences between forest types, apparently responding to similar environmental gradients as vascular plants, suggesting that a comprehensive and representative reserve system will best conserve the largely unknown fungal biota and its associated functions. Soil fungal communities also appear resilient to large-scale disturbance of soils by lyrebirds, with no loss or change despite intensive soil displacement annually.

5.1 INTRODUCTION

Fungal communities play a critical role in ecosystem health through multiple mechanisms (Boer et al. 2005). Saprotrophic fungi are primary decomposers that moderate nutrient dynamics and the accumulation of soil organic matter (Osono 2006, Lindahl and Tunlid 2015). Arbuscular mycorrhizal fungi benefit their plant symbionts by increasing the efficiency of water uptake during periods of drought (Dastogeer and Wylie 2017), increasing tolerance to salinity (Porcel et al. 2012), facilitating nutrient uptake (particularly phosphorus) (Smith et al. 2011) and improving soil stability (Gianinazzi et al. 2010). Fungi may interact with plant reproduction by deterring seed predators on infected seeds (Crist and Friese 1993); while fruiting bodies of epigeal and hypogeous macrofungi provide a rich food source for a diverse range of mycophagous animals (Fogel and Trappe 1978, Hammond and Lawrence 1989, Vašutová et al. 2019).

Soil and litter layers, where many fungi occur, often experience intensive disturbance from ecosystem engineers, organisms that modulate the physical environment in a manner that affects the composition or abundance of other organisms (Jones et al. 1994). Animal ecosystem engineers, particularly bioturbators, may affect soil fungal communities through their digging activities. Digging mammals and birds may directly interact with fungal communities by spreading spores via accidental or selective foraging (e.g., feeding on fruiting bodies of fungi (Vašutová et al. 2019)) and faecal deposition (Valentine et al. 2017). Mycophagous mammals, such as the Potoroidae and Peramelidae, have featured in the bioturbation literature for their tight evolutionary relationship with hypogeal fungi (Bennett and Baxter 1989, Johnson 1990), their active role in spore dispersal (Bennett and Baxter 1989, Reddell et al. 1997) and increasingly, their contribution to ecosystem health and function via other mechanisms such as impacts on soil porosity and hydrophobicity (Fleming et al. 2014, Dundas et al. 2018, Valentine et al. 2018). Birds that forage in the ground layer of terrestrial ecosystems are also likely to play an important role in the distribution and moderation of fungal communities, although this remains poorly understood (Romero et al. 2014, Coggan et al. 2018, Elliott et al. 2019, Vašutová et al. 2019).

The superb lyrebird *Menura novaehollandiae* is a large ground-dwelling passerine that occurs in wet forests in south-eastern Australia. This species is considered to be an ecosystem engineer due to the large volume of soil displaced when foraging (Eldridge and James 2009, Nugent et al. 2014, Tassell 2014, Maisey et al. 2020). Lyrebirds use their large claws and strong legs to search through leaf litter and soil for a variety of invertebrate prey. This foraging activity represents a large disturbance process, with an average of 156 t ha^{-1} yr^{-1} of litter and soil displaced (Maisey et al. 2020). Such activity assists rapid decomposition of fine twigs and leaf litter due to soil and litter piling and mixing (Nugent et al. 2014), and thus has potential to influence soil microbial communities (Tassell 2014). In a mycological study, lyrebirds were found to consume fungi (Elliott

and Vernes 2019), although their impact on fungal communities through engineering activities is entirely unknown.

Here, an experimental approach was used to: 1) test the hypothesis that lyrebird foraging will alter the soil fungal community over a two-year period; and 2) determine whether fungal communities differ between three common forest types in the southern fall of the Central Highlands of Victoria, Australia.

In this chapter, it is hypothesised that lyrebird foraging may influence fungal communities through both direct means (endozoic spore dispersal) and habitat alteration (ecosystem engineering). First, as lyrebirds consume hypogeous fungi, spore dispersal by lyrebirds may alter community structure where they forage. Second, by influencing litter depth and compaction through their foraging, lyrebirds may alter the habitat quality for fungi. To separate the consumptive and engineering impacts of lyrebirds on fungi, an experimental approach with three treatments was adopted. At each site, fenced plots were used to exclude lyrebirds from foraging, while an identical fenced plot was subjected to simulated foraging. The comparison of these two treatments represents the impact of engineering only. The third treatment was unfenced and accessible to lyrebirds. The comparison of this treatment with the simulated treatment therefore represents the impact of the consumption and excretion (dispersal) of fungi by lyrebirds.

5.2 METHODS

5.2.1 Study locations and forest types

This study was undertaken in the southern fall of Victoria's Central Highlands bioregion (Fig. 5.1). The geology of the region is characterised by Palaeozoic deposits predominantly consisting of sedimentary and granitic rock, giving rise to brown and red dermosols on the ridges and yellow or red chromosols and kurosols in valleys (DELWP 2014). In this region, lyrebirds commonly occur in three distinct forest types: damp forest, wet forest and cool temperate rainforest (Emison et al. 1987). These forest types have been classified as Ecological Vegetation Classes in Victoria (DELWP 2019).

Damp forest is common and widespread in this region (Fig. 5.1a). The canopy is comprised of messmate *Eucalyptus obliqua* and mountain grey gum *E. cypellocarpa* with a rich mix of understorey trees and large shrubs, such as hazel pomaderris *Pomaderris aspera*, musk daisy *Olearia argophylla* and snow daisy bush *O. lirata*. Ground covers include a diverse range of small herbs and forest grasses such as purple-sheath tussock *Poa ensiformis* and forest wire grass

Tetrarrhena juncea. Rough treeferns *Cyathea australis* are usually present but sparse. Damp Forest is the most resilient to fire; infrequent fires occur but result in limited tree death.

Wet forest is dominated by a canopy of mountain ash *E. regnans* (Fig. 5.1b). It often has a sparse upper mid-storey of *Acacia melanoxylon* and *A. dealbata* with a dense, rich lower strata comprised of a variety of tree species, including blanket leaf *Bedfordia arborescens*, musk daisy, austral mulberry *Hedycarya angustifolia* and prickly currant bush *Coprosma quadrifida*. The ground cover is dominated by ground ferns (*Polystichum proliferum, Blechnum watsii*) and high cover of treeferns (*Cyathea australis, Dicksonia antarctica*). This forest type is typically regenerated by infrequent, high-intensity fires that stimulate a soil-stored seed bank. Such fires sometimes are stand-replacing (Mackey et al. 2002).

Cool temperate rainforest in this region is dominated by myrtle beech *Nothofagus cunninghamii* and southern sassafras *Atherosperma moschatum* (Fig. 5.1c). The high shading by the canopy species suppresses growth of most mid-storey trees, resulting in scattered occurrence of banyalla *Pittosporum bicolor*, austral mulberry and mountain pepper *Tasmannia lanceolata*. Soft treeferns form a dense mid stratum and host a wide variety of rainforest specialists, including filmy ferns *Hymenophyllum* spp., tufted and rhizomatous epiphytic ferns (tufted: *Asplenium bulbiferum, Grammitis billardierei*; rhizomatous: *Rumohra adiantiformis, Microsorum pustulatum*). Soft treefern trunks provide germination sites for the dominant rainforest canopy species.

Three geographic locations were selected for experimental manipulation of lyrebird foraging: Sherbrooke Forest in the Dandenong Ranges; Yarra State Forest; and Yarra Ranges National Park (Fig. 5.1). Each location is at least 10 km from others, geographically isolated by sections of the Yarra Valley and considered a separate forest block. When foraging, lyrebirds are known to seasonally adjust foraging effort between the three forest types (Maisey et al. 2018); they avoid recently burnt forest (Nugent et al. 2014), and prefer mature, open forest (Loyn 1985, Ashton and Bassett 1997). Each study location supports a lyrebird population throughout all seasons, has the three vegetation types of interest, is accessible by road or tracks, and contains areas of forest unburnt for >30 years.

Sherbrooke forest is an 800 ha section of the Dandenong Ranges National Park, east of Melbourne. Elevation ranges from 400-600 m above sea level (ASL) and the forest receives approximately 1200 mm rainfall per annum. This forest is predominantly comprised of wet forest. Gullies are dominated by cool-temperate rainforest with southern sassafras the dominant species. Myrtle beech is absent in the Dandenong Ranges. The park has experienced intense historic logging: much of the wet and damp forest is even-aged and rainforest gullies are linear in form.

The Yarra State Forest near Britannia Creek has an elevation 400-800 m ASL and average rainfall exceeding 1400 mm. This area has also experienced intense logging pressure over the past century

yet retains mature stands of each of the three forest types. The cool temperate rainforest community is dominated by myrtle beech. Sections of this forest are used for recreational hunting, motorbike riding and domestic firewood collection.

Yarra Ranges National Park has a similar range in elevation (400-800 m) and rainfall >1100 mm p.a.) and comparable forest structure to Yarra State Forest. Although also intensively logged in the early 1900s, this location has been managed solely for conservation since 1995 when it was declared a national park.

5.2.2 Site selection

At each location, in each of cool temperate rainforest, wet forest and damp forest, experimental sites were selected by using randomly generated coordinates. Only sites between 40 and 300 m from access tracks were assessed for suitability. Sites were separated by > 400 m, to ensure they would not be overlapped by the territory of a single lyrebird (Smith 1988). Forest type and fire history were assessed from publicly available mapping undertaken by the Department of Environment, Land, Water and Planning (Victoria), and field visits were made to ground-truth the vegetation. In total, 18 sites were selected; two sites in each forest type, in each forest block.

At each site, three experimental plots (each 3 x 3 m) were established in October 2015. Plots were positioned along the contour of the slope, with each plot placed at a random distance between 5 and 40 m from the first established plot (Fig. 5.2). Vegetation was surveyed in the field before plot establishment to ensure the density of vegetation <50 cm height would not inhibit foraging by lyrebirds (Maisey et al. 2018). If the vegetation structure was not sufficiently open at the first randomly selected distance, the contour was followed until the vegetation was sufficiently open and each plot conformed. One of the three plots was randomly assigned to remain unfenced, allowing lyrebirds to access the plot (unfenced treatment). The two remaining plots were fenced to exclude access by lyrebirds; one remained undisturbed (fenced treatment) and the other was subjected to simulated lyrebird foraging (simulated treatment; see below) on a monthly basis between October 2015 and September 2017.

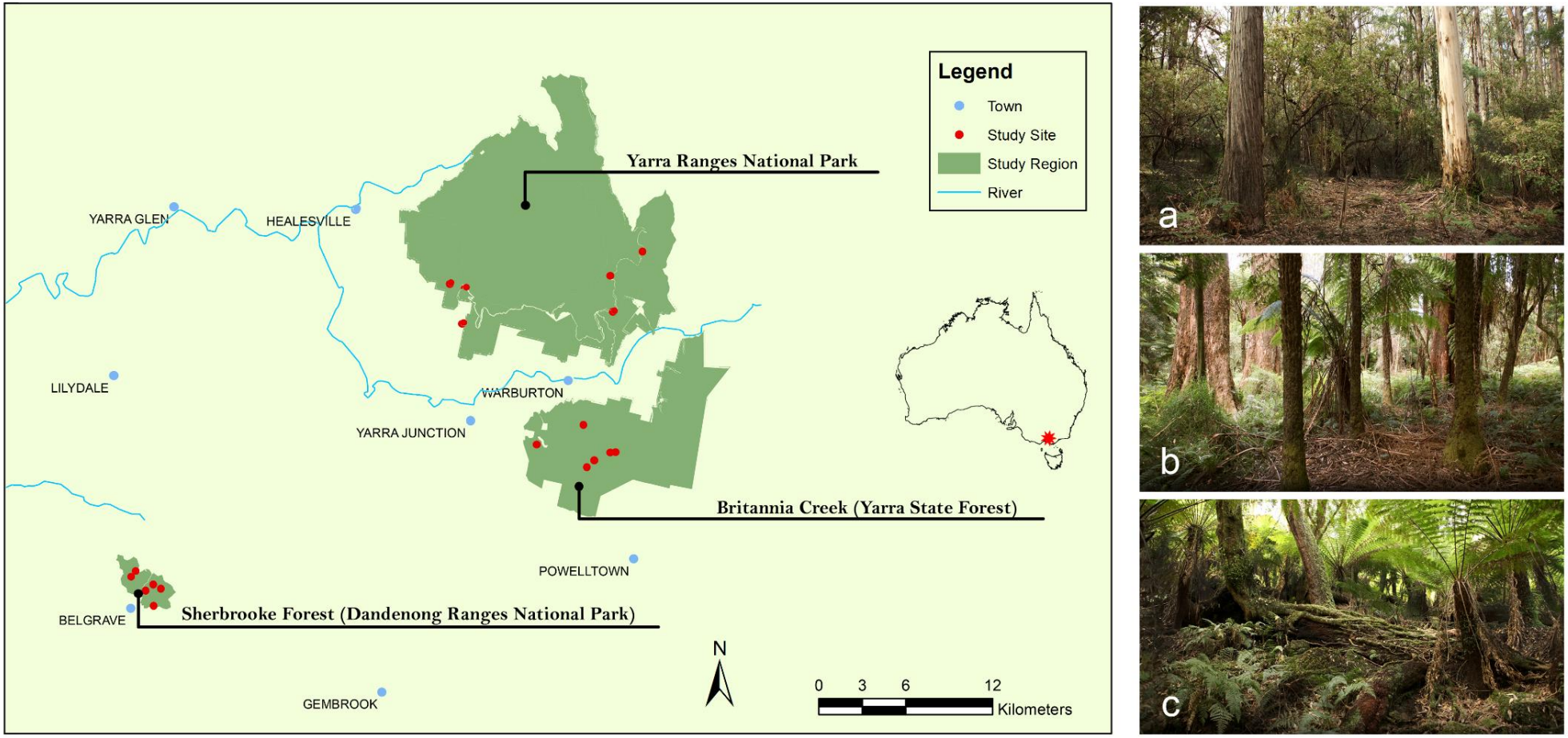


Figure 5. 1 The study region showing three forest blocks and the location of study sites within each. The panel at right provides exemplar images of a) damp forest, b) wet forest and c) cool temperate rainforest.

5.2.3 Lyrebird foraging simulations

On each monthly visit to a site, the area disturbed by lyrebirds in the unfenced plot was visually assessed and recorded as a percent cover estimate. In the fenced simulated plot at that site, foraging was then simulated using a three-pronged hand rake (the approximate width of a lyrebird spread foot, ~10 cm), to replicate the foraging cover and configuration recorded in the unfenced plot.

5.2.4 Sample collection

To sample fungal community, from each experimental plot, five soil sub-samples (~20 g each) were collected before fences were erected in October 2015 and then again in October 2017. Sub-sampling was undertaken at the centre and at each corner of a 1 x 1 m quadrat in the centre of each plot. Each sub-sample was collected in a 1 cm diameter core taken from the topsoil (leaf litter was removed to enable access to mineral soil) to a depth of 5 cm, and subsequently combined to provide a single representative sample for each plot.

Concurrent with sub-samples (above), a 200 g sample of mineral soil was collected from a randomly selected position within 1 m of the centre of each plot (see Maisey et al. (2020) for details). Samples were refrigerated and sent to the CSBP Soil and Plant Analysis Laboratory (Bibra Lakes, Western Australia). The standard soil testing package was selected to examine nutrients potentially important for fungi: ammonium nitrogen (mg/kg), nitrate nitrogen (mg/kg), Colwell phosphorus (mg/kg), Colwell potassium (mg/kg), sulphur (mg/kg) and organic carbon (%).

5.2.5 DNA extraction, library preparation and sequencing

DNA was extracted from 0.25 g of soil from each sample (five sub-samples combined) using the PowerSoil^{TM} Soil DNA Isolation Kit (MoBio Laboratories, Solana Beach, CA, USA). A negative control was included for both sampling periods (2015 and 2017). Mechanical lysis of cells was achieved using a micro-bead vortex, and DNA extracted by a series of washing and elution buffers following the standard MoBio protocol. DNA yield was quantified with the Qubit 3.0 Fluorometer (ThermoFisher Scientific; Invitrogen, MA, USA) and standardised to 5 ng/µl prior to PCR amplification. An extraction blank was included as a negative control.

Fungal ribosomal internal transcribed spacer (ITS) primers ITS1F (CTTGGTCATTTAGAGGAAGTAA) and ITS4 (TCCTCCGCTTATTGATATGC) were used to generate fungal amplicon libraries using the Nextera XT Index kit (Illumina, San Diego, CA, USA) according to the 'Fungal Metagenomic Sequencing Demonstrated Protocol' (Part #11000000064940 v01, Illumina). After indexing, amplicon size distribution was determined by using the Agilent 2200 TapeStation (Agilent Technologies, Santa Clara, CA, USA) with D1000 screentapes. Finally, the libraries were pooled (including the extraction blank) and sequenced on an

Illumina MiSeq platform (2 x 300 PE) using the MiSeq Reagent Kit v3 (600-cycle; Illumina, San Diego, CA, USA).

5.2.6 Sequence analysis

Adapter sequences, reads shorter than 125 bases and those with QC scores lower than 20 were removed by using 'cutadapt' (version 1.13) (Martin 2011). The 'trimmomatic' (version 0.32) tool (Bolger et al. 2014) was used to trim forward and reverse reads to 290 and 225 bases, respectively, to remove low-quality bases. To retain both forward and reverse reads, despite the lack of an overlapping region, a method was employed previously reported by Needham and Fuhrman (2016) where reverse reads were reverse complemented and merged with forward reads with degenerate N bases between (Needham and Fuhrman 2016). Merged reads were de-replicated and had singletons and chimeras removed with USEARCH (version 10.0.240) (Edgar 2010) *fastx_uniques* and *cluster_otus* commands, respectively. Reads were de-noised and clustered into zero-radius operational taxonomic units (zOTUs), also known as exact sequence variants (Callahan et al. 2017) by using the 'unoise3' algorithm in USEARCH. Taxonomy was assigned using the SINTAX algorithm (USEARCH) with a 97% probability threshold at genus level to search against the UNITE fungal reference database (V7.0) (Koljalg et al. 2013).

5.2.7 Statistical approach

All statistical analyses were implemented in the R programming language (R Core Team 2012) using the R Studio interface (RStudio 2012).

To investigate compositional change in fungal communities through time, the 'vegan' package (Oksanen et al. 2007) was used. PERMANOVA tests were conducted using the *adonis* function with the Bray-Curtis distance measure and 9,999 permutations. The response variables included each operational taxonomic unit and its relative abundance. Predictors included treatment, time, forest type, forest block and all soil nutrients, as these potentially influence the fungal community. Importantly, the interaction between treatment and time was examined, as this indicates whether treatments diverged through time.

Distance matrices were constructed using the *vegdist* function (with the Bray-Curtis distance measure), and the within-group homogeneity of variance (dispersion) was tested for each treatment and time period (2015 and 2017) using the *betadisper* function. Beta-dispersion tests showed no significant difference between treatments and time periods ($p > 0.05$), indicating that assumptions for PERMANOVA were met. Composition was visualised by using non-metric multi-dimensional scaling with the *metaMDS* function. Soil nutrient vectors were fitted onto the ordination space using the function *envfit* in the vegan package.

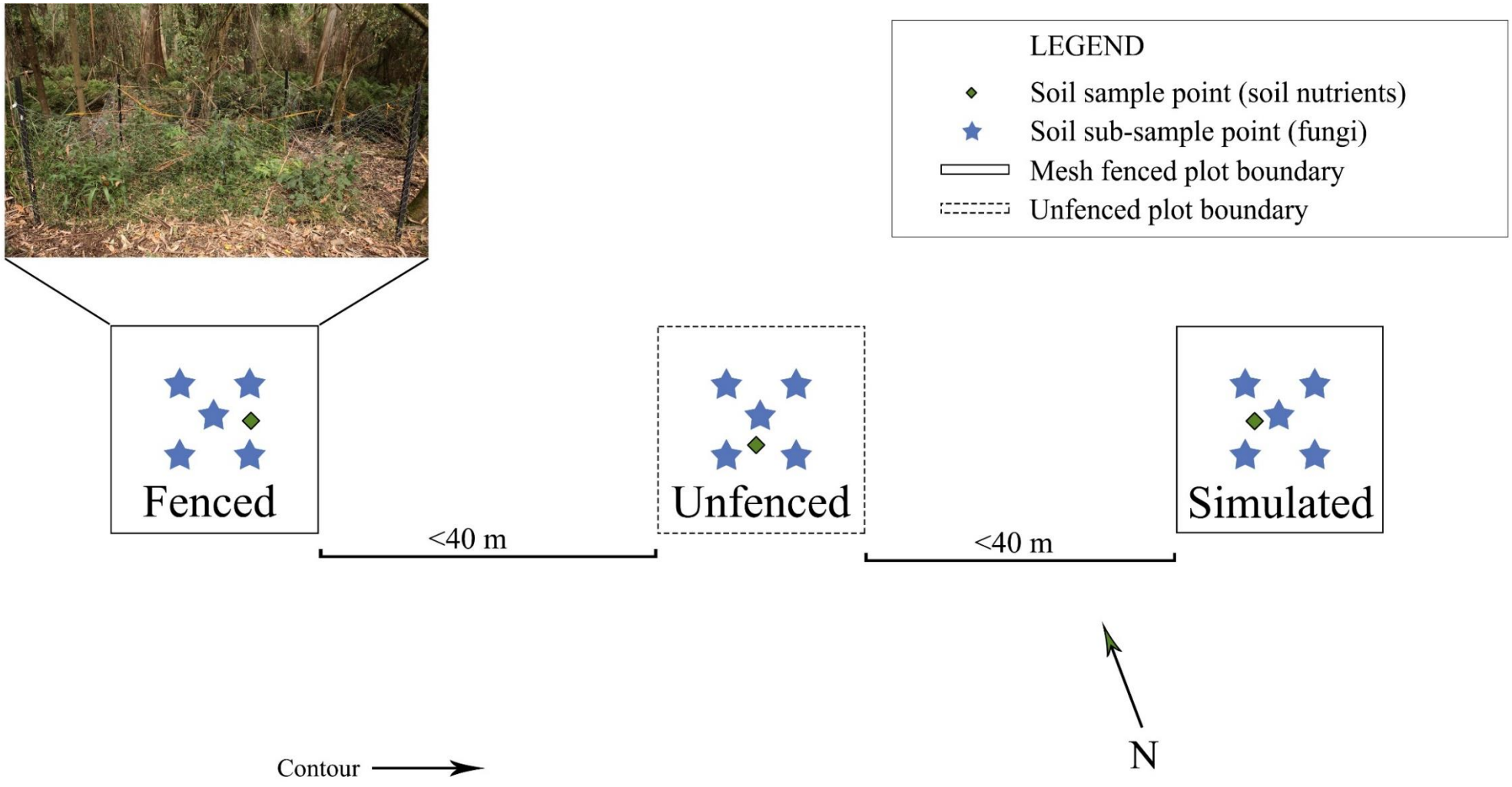


Figure 5. 2 A typical site and plot layout. Inset depicts a fenced lyrebird exclosure in Sherbrooke Forest after a two-year period, showing orange flagging tape to discourage lyrebirds from flying into the plot.

To assess the influence of experimental treatments and forest type on fungal species richness and diversity (Shannon's diversity index), linear mixed models (LMMs) with a Gaussian distribution were used. Models were generated with the 'lme4' package (Bates et al. 2014). Fixed effects in the model included treatment and time, the interaction between treatment and time, and forest type. A random term was included to nest site within forest block, to account for spatial clustering of plots. Model assumptions and fit were assessed with the aid of residual plots; model fit was quantified by using the marginal (fixed terms only) and conditional (full model) R^2 values of the global model (Nakagawa and Schielzeth 2013).

A significant treatment x time interaction between the simulated and unfenced treatments would support the hypothesis that lyrebirds affect fungal communities through trophic activities (feeding and excretion). Alternatively, a significant interaction between the simulated and fenced treatments would support the hypothesis that lyrebirds affect fungi through their engineering activities.

5.3 RESULTS

After de-noising and clustering all samples, a total of 540 operational taxonomic units (OTUs) was resolved (Appendix 2.5). Of these, the most dominant phyla were Basidiomycota (292 OTUs), Ascomycota (135 OTUs) and Mortierellomycota (72 OTUs). Less dominant phyla included Basidiobolomycota, Zoopagomycota, Mucoromycota, Glomeromycota, Entomophthoromycota, Chytridiomycota and Calcarisporiellomycota, represented by <15 OTUs in each. Collectively, these phyla encompassed 147 genera at the 97% probability threshold. The most diverse genera were Mortierella (72 OTUs), followed by Inocybe (33 OTUs), Russula (23 OTUs) and Sebacina (22 OTUs). Most other genera were represented by <3 taxonomic units (115/147 OTUs).

5.3.1 Community composition

Fungal communities differed by forest type (Fig. 5.3) and forest block, as revealed by PERMANOVA (Table 5.1), but showed no effect of treatment (Fig. 5.4) or an interaction between treatment and time (Table 5.1). Thus, there was no evidence for either a trophic or engineering effect of lyrebird foraging activity altering the composition of soil fungal communities, at least over a two-year period.

Soil nutrients, ammonium, nitrogen, potassium and sulphur, influenced the composition of the fungal community (Fig 5.3), but to a lesser extent than the variation associated with geographic location and forest type (Table 5.1).

Table 5. 1 Summary of the PERMANOVA test (using *adonis*) of variation in the composition of the fungal community in relation to experimental treatments, forest type, location and soil nutrients. Significant effects (P≤0.05) are shown in bold. '*' denotes an interaction between terms.

Response	**Factor**	**Df**	**SumsOfSqs**	**MeanSqs**	**F**	R^2	***P***
Fungal community composition	Treatment	2	0.46	0.23	1.13	0.02	0.26
	Time	1	0.37	0.37	1.80	0.01	0.03
	Forest type	**2**	**4.42**	**2.21**	**10.82**	**0.15**	**<0.01**
	Location (Forest block)	**2**	**1.83**	**0.91**	**4.48**	**0.06**	**<0.01**
	Ammonium	**1**	**0.41**	**0.41**	**2.02**	**0.01**	**0.02**
	Nitrogen	**1**	**0.47**	**0.47**	**2.29**	**0.02**	**0.01**
	Nitrate	1	0.32	0.32	1.59	0.01	0.06
	Phosphorus	1	0.21	0.21	1.01	0.01	0.40
	Potassium	**1**	**0.97**	**0.97**	**4.77**	**0.03**	**<0.01**
	Carbon	1	0.14	0.14	0.71	0.01	0.81
	Sulphur	**1**	**0.40**	**0.40**	**1.95**	**0.01**	**0.02**
	Treatment * time	2	0.22	0.11	0.53	0.01	1.00
	Residuals	91	18.58	0.20	NA	0.65	NA

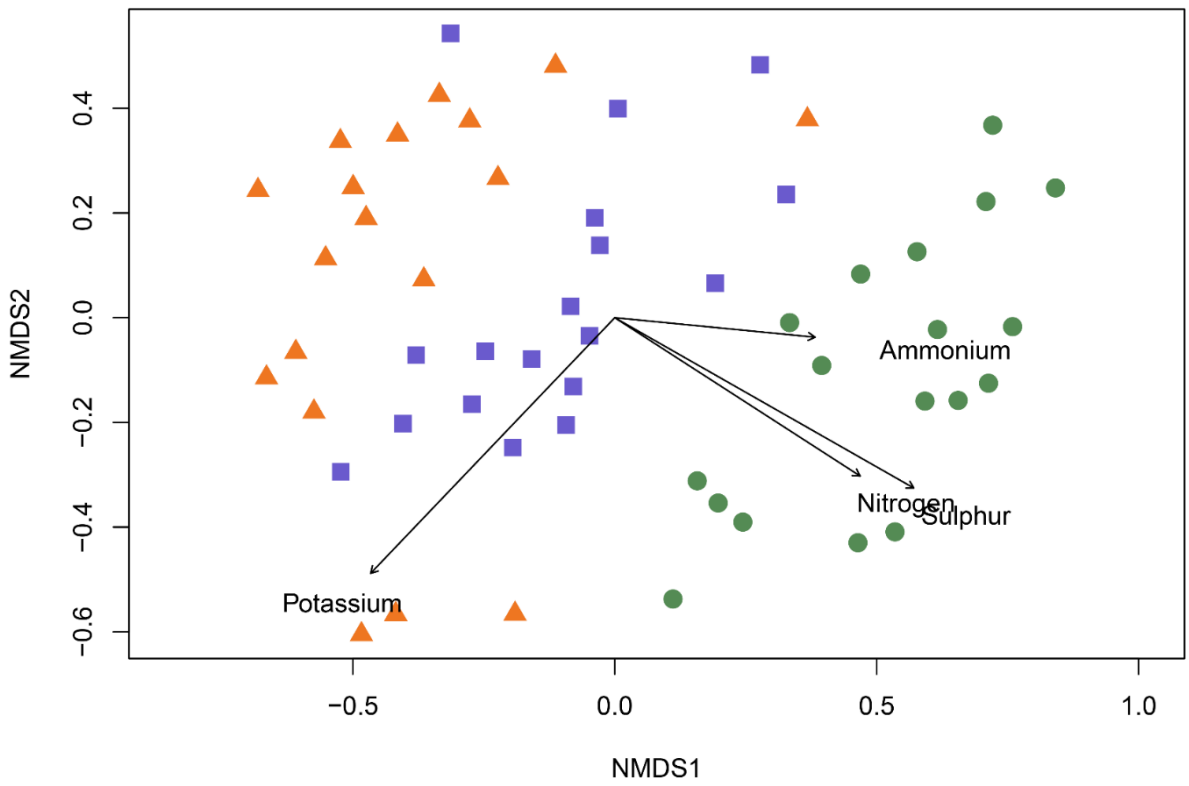


Figure 5. 3 Ordination the composition of the soil fungal community labelled by forest type. Orange triangles represent damp forest, blue squares wet forest and green circles cool temperate rainforest. Vectors are included for nutrients that were shown to drive the fungal community from the PERMANOVA analysis.

5.3.2 Richness and diversity

Results of a linear mixed model revealed that richness of fungal OTUs was significantly lower in cool temperate rainforest compared with other forest types (Fig. 5.5). There was no interaction between treatment and time, but richness increased throughout the two-year experiment (Table 5.2).

The diversity of fungal OTUs was highest in cool temperate rainforest, but did not differ between the wet and damp forest types (Fig. 5.6). There was no interaction between treatment and time for diversity (Table 5.3).

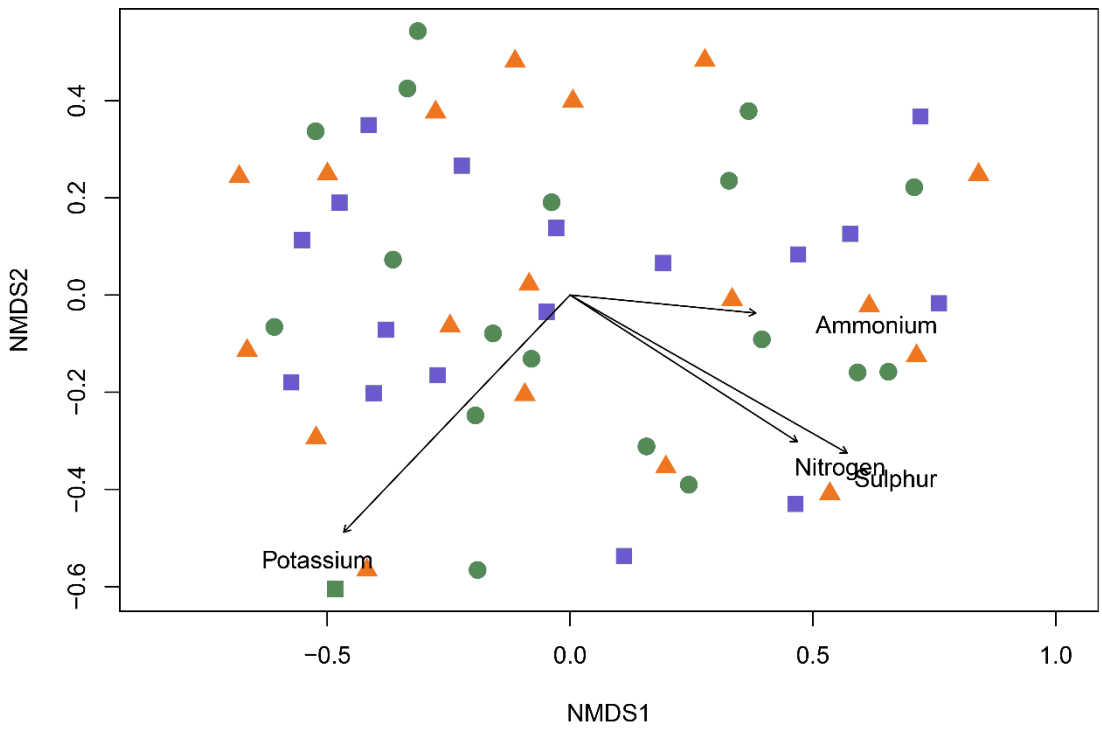


Figure 5. 4 Ordination of the composition of the soil fungal community labelled by treatment. Orange triangles represent the fenced treatment, green circles the simulated treatments and blue squares the unfenced treatment. Vectors are included for nutrients that were shown to drive fungal community from the PERMANOVA analysis.

5.4 DISCUSSION

Fungal communities are extremely diverse and so understanding their ecology is a major challenge. In contrast to an expectation that fungal communities would change in response to lyrebird-induced habitat modification, no evidence of any effect was detected. Given the strong association identified between fungi and forest type, it is possible that there would need to be changes to the floristic composition of plant communities before any significant response is triggered in the fungi. The experimental treatments caused little compositional change in plant species (see Chapter 3), therefore a similar outcome may be expected for fungi.

Table 5. 2 Model outputs (LMMs assuming Gaussian error distribution) for the relationship between taxonomic richness (the number of OTUs) of soil fungi and lyrebird foraging treatments. Coefficients for which the 95% confidence interval does not include zero are shown in bold. Damp forest was the reference category used for forest type, and 'simulated' was the reference category for treatment. '*' denotes interactions between fixed effects.

Response	Fixed effect	Estimate	SE	*t* value	$R^2_{(marginal)}$	$R^2_{(conditional)}$
a) Richness (number of OTUs)	(Intercept)	83.68	7.41	11.30	0.32	0.58
	Treatment - Simulated	11.83	9.58	1.24		
	Treatment - Unfenced	1.72	9.58	0.18		
	Time	**17.17**	**4.06**	**4.22**		
	Forest type - Rainforest	**-15.64**	**4.38**	**-3.57**		
	Forest type - Wet forest	1.44	4.38	0.33		
	$\text{Treatment}_{(Unfenced)}$ * Time	-7.28	5.75	-1.27		
	$\text{Treatment}_{(Fenced)}$ * Time	-4.00	5.75	-0.70		

Table 5. 3 Model outputs (LMMs assuming Gaussian error distribution) for the relationship between diversity (Shannon's index) of fungal OTUs and lyrebird foraging treatments. Coefficients for which the 95% confidence interval does not include zero are shown in bold. Damp forest was the reference category used for forest type, and simulated was the reference category for treatment. '*' denotes interactions between fixed effects.

Response	Fixed effect	Estimate	SE	*t* value	$R^2_{(marginal)}$	$R^2_{(conditional)}$
a) Diversity (Shannon's index)	(Intercept)	2.38	0.22	11.03	0.19	0.32
	Treatment - Unfenced	0.01	0.28	0.04		
	Treatment - Fenced	0.01	0.28	0.04		
	Time	0.19	0.13	1.50		
	Forest type - Rainforest	**0.42**	**0.13**	**3.22**		
	Forest type - Wet forest	0.13	0.13	1.01		
	$\text{Treatment}_{(Unfenced)}$ * Time	-0.01	0.18	-0.05		
	$\text{Treatment}_{(Fenced)}$ * Time	0.01	0.18	0.06		

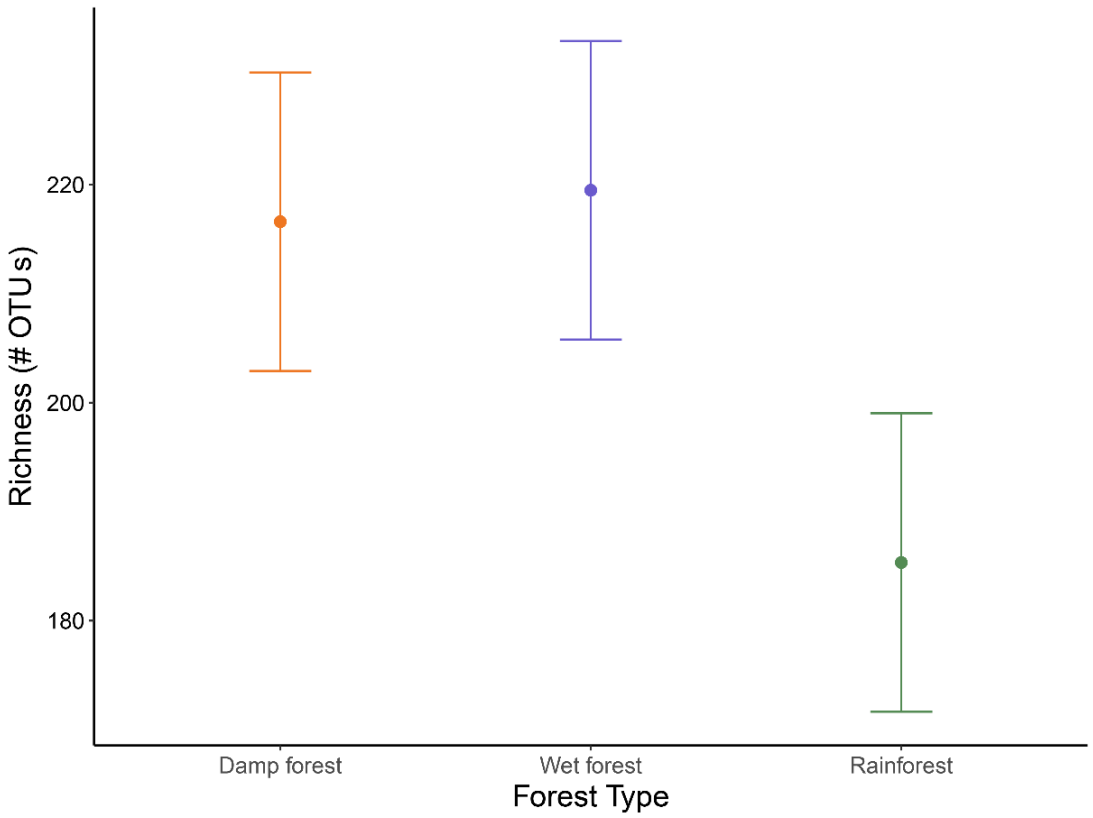


Figure 5. 5 Predicted taxonomic richness (number of OTUs) of fungi for each forest type.

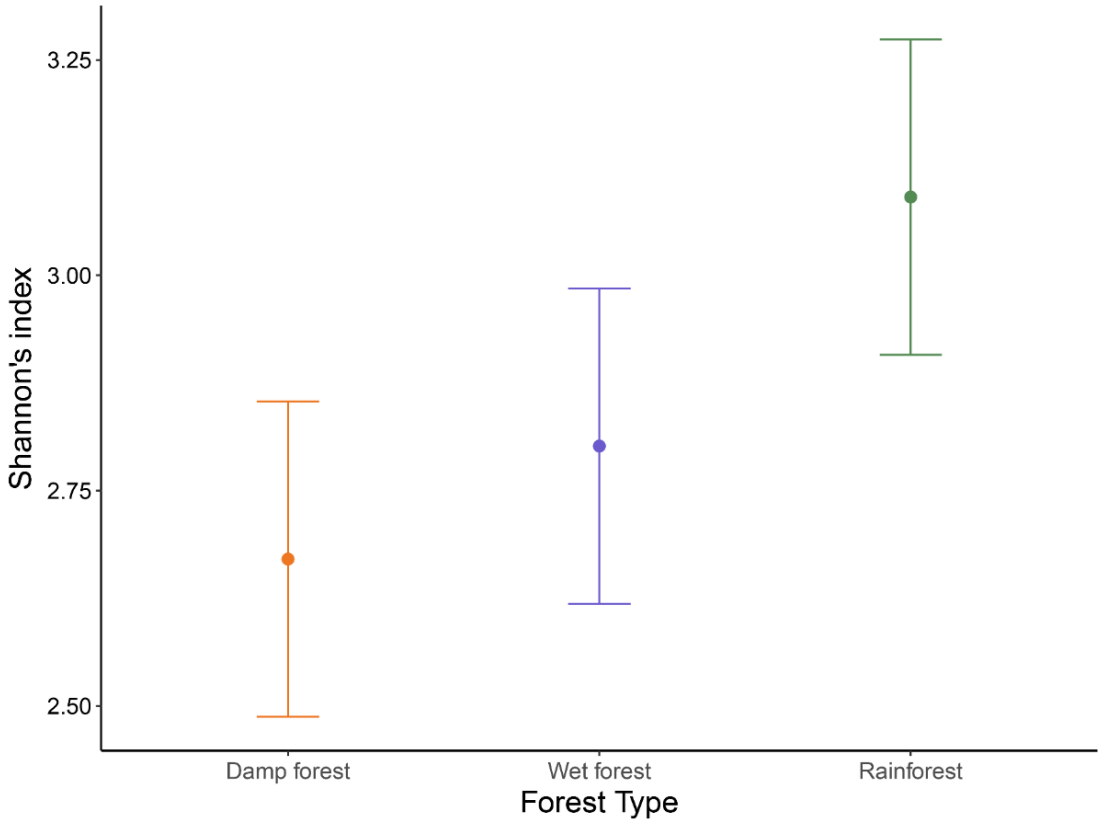


Figure 5. 6 Predicted diversity (Shannon's index) of fungal OTUs for each forest type.

As fungi respond to edaphic properties (soil nutrients), an extended time period may be required for soil nutrients to change sufficiently to influence community structure. In a study in New South Wales, Australia, Kasel et al. (2008) reported distinct fungal communities between agroforestry treatments that had diverged from a single habitat type over timescales ranging between 6 - 11 years. Similarly, in temperate Scotland, Mitchell et al. (2010) showed the fungal community had responded to experimental treatments of downy birch *Betula pubescens* after periods of >20 years. Here, the experimental manipulation was undertaken for two years, and the vegetation and soil may not have undergone divergent trajectories for a sufficiently prolonged time period to cause shifts in the fungal community. Over longer timescales, however, lyrebirds may alter the fungal community indirectly through a slower, yet sustained alteration to vegetation and soil nutrient composition.

Aridity of an ecosystem is also likely to influence the role of animal ecosystem engineers and their interactions with fungi. Some studies have suggested that engineers have greater impacts on soil in arid environments (Wright and Jones 2004, Decker et al. 2019a, Mallen-Cooper et al. 2019), although evidence for this has sometimes been conflicting (see Coggan et al. 2016). The current study was undertaken in a highly productive, wet forest. Although the amount of litter and soil displaced by lyrebirds appears greater than for any other animal engineer described (Maisey et al. 2020), changes to floristic composition and edaphic nutrient composition may be buffered by mesic conditions (Ross et al. 2020). In arid Australia, Clarke et al. (2015) documented distinct fungal communities between the inside and outside of wildlife sanctuary fences, and attributed these differences to the activities of ecosystem engineers that were reintroduced >14 years prior. Decker et al. (2019b) also found differences in decomposition rate (a proxy for fungal and bacterial activity) between the inside and outside of wildlife sanctuary fences in arid zones, however the effect was not present in sanctuaries in more temperate zones of south-east Australia.

Worldwide, vegetation has been recognised for its deterministic role in shaping fungal community composition (Gai et al. 2009, Nielsen et al. 2010, Sundqvist et al. 2011). Whether fine-scale delineations between forest types support compositionally distinct fungal communities has not yet been established, especially between forest types that are adjacent and share many plant species. In Australia, soil fungi are little known, with many species remaining undescribed and their functions poorly understood (Letcher et al. 2004, McMullan-Fisher et al. 2011). To overcome the difficulty inherent in the conservation and management of taxa of this nature, vegetation classifications such as the Ecological Vegetation Classes (DELWP 2019) used to describe forest type in this study may be a suitable ecological surrogate for soil fungi. These are ecosystem-based units that represent integrated aspects of ecological processes (Mac Nally et al. 2002), and hence more likely to provide critical resources and serve as a surrogate for poorly known biota (*c.f.* other surrogates such as umbrella species, indicator species, keystone species and many others (see Caro 2010)).

Forest types are readily identified and mapped by land management agencies, and their use as categories for biodiversity management often determines the activities that occur within them. For example, in relation to fire management in Victorian forests, land managers routinely identify minimum and maximum tolerable fire intervals when undertaking ecological fire management; and such prescriptive recommendations vary between cool temperate rainforest and eucalypt forest types (see Cheal 2010). Here, the fungal community displayed coherence within forest types, and so the use of this ecological management unit as a surrogate system for the conservation of fungi and their associated functions is supported (Mac Nally et al. 2002).

The three forest types examined in this study have only subtle differences in plant species composition, as each may occur adjacent to one another in the landscape, yet the effect of forest type on fungal composition was much larger ($R^2 = 0.15$) than that of geographic location ($R^2 = 0.06$) and edaphic properties ($R^2 < 0.02$) within forest types. This suggests that recognition of forest type captures important variation in the fungal biota in these forests, likely due to direct relationships (e.g., arbuscular mycorrhizal association) with the flora composing that community (Nielsen et al. 2010), while other microbes (e.g., archaea, bacteria) may be less affected. Kasel et al. (2008) revealed considerable plasticity in fungal community composition in response to agroforestry treatments (*Pinus radiata* and *Eucalyptus globulus* plantations) on similar soil types in eastern Australia, suggesting the fungal community was responding to vegetation community *per se*, rather than the vegetation responding to the same edaphic conditions as fungi.

Fungal community richness is correlated with plant species richness in many natural ecosystems (Peay et al. 2013, Hiiesalu et al. 2014). Floristic diversity is generally accepted to be driving such associations, with soils having a lesser or indirect effect (through mediation of floristics) on fungi (Zuo et al. 2016). In this study, there was higher fungal richness in the damp and wet forest types. These forest types (*cf* cool temperate rainforest) tend to have higher terrestrial floristic diversity, which may result in the provision of specific nutrients supporting a wider variety of fungi, especially those with ectomycorrhizal associations (Letcher et al. 2004). While many plant species occur in all three forest types (e.g., ground ferns, herbs) most of these species comprise the lower stratum, with progressively fewer shared species in the mid and canopy strata. Trees and large shrubs may be playing a major role in shaping variation in fungal communities in these forests.

5.5 CONCLUSION

Ecosystem engineering by the superb lyrebird did not appear to influence the composition, structure or diversity of soil fungal communities, at least at the timescale of this study (two years). In contrast, fungal community composition, richness and diversity varied between adjacent forest types, despite each sharing many plant species. These results suggest that by ensuring these

relatively fine-scale delineations between forest types are recognised and protected in a comprehensive and representative reserve system, fungal communities and their associated functions should also be conserved. In the case of a data-deficient taxonomic group such as the fungi, using an ecological proxy for conservation may be the most effective tool for conservation planning. The role of animal ecosystem engineers in determining the structure of fungal communities is an important emerging area of research, but may require long-term experiments to fully appreciate their ecological effects, especially in mesic environments.

Chapter Six

Synthesis: Conservation of the functional role of the superb lyrebird

Plate 7. Study of the tail plumage of a male superb lyrebird.

6.1 INTRODUCTION

This study is the first to comprehensively examine the functional role of the superb lyrebird as an ecosystem engineer. By developing a study design that explicitly separated the effects of physical habitat modification from trophic interactions, it was possible to disentangle the complex relationships between the superb lyrebird, its moderation of biotic and abiotic habitat and influence over its invertebrate prey, within an ecosystem engineering framework. Table 6.1 presents an overall summary of the objectives and key findings for each chapter. This final chapter provides a short summary for each previous chapter, then synthesises the insights and implications of this work for conservation of the superb lyrebird and its forest habitats. Finally, potential directions for future research are identified.

6.1.1 The superb lyrebird as an ecosystem engineer

Growing evidence suggests that ecosystem engineers are an important mediator of resource flows in diverse ecosystems worldwide. In pursuit of a comprehensive understanding of the ecosystem engineering process, a critical first step is to document the structural changes to engineered habitat and define the spatial and temporal pattern in the ecosystem. To this end, the structural consequences of foraging by lyrebirds was quantified (see Chapter 2, published as Maisey 2020). By gaining a measure of litter and soil displaced by lyrebirds, it was possible to place the lyrebird in the global context of ecosystem engineers, highlighting the extraordinary scale of litter and soil displaced by this species when foraging.

To quantify the effects that this disturbance has on litter and soil characteristics, a manipulative experiment was conducted with three treatments: lyrebird exclusion, lyrebird exclusion with artificial simulated foraging, and open plots that allowed wild lyrebirds to forage within them (providing a reference treatment). This allowed for rigorous assessment of the physical change to habitat qualities (e.g., litter depth, soil compaction, moisture, nutrients) from foraging activity.

Table 6. 1 Summary of the objectives and key findings of each data chapter of this thesis.

Data chapter	Objectives	Key findings
Chapter 2 - Litter and soil	To assess the impact of engineering by lyrebirds on the physical structure of litter and soil habitats, and determine the amount, pattern and drivers of litter and soil displacement by lyrebirds.	Lyrebirds were active throughout all forest types during all seasons, with small shifts in activity away from rainforest to wet forest in winter. This shift is likely to be in response to new food resources becoming available in the soil in wet forest concomitant with moist conditions during winter. Foraging activity was greatest where ground vegetation was sparse, highlighting the need for energy efficiency when foraging. Lyrebirds displaced, on average, 155.7 t ha^{-1} y^{-1} throughout the study region. This amount of material is greater than for any other terrestrial vertebrate recorded to date globally. Litter depth was strongly influenced by lyrebird foraging. Litter in fenced treatments (without lyrebird or simulated foraging) was three times deeper than open plots after two years of exclusion. Soil compaction increased in fenced treatments relative to treatments with real or simulated foraging, and was detectable to a depth of 15 cm. Soil nutrients, pH and moisture showed no change due to treatments over the two-year manipulation.
Chapter 3 - Invertebrates	To determine the influence of lyrebird engineering on invertebrate communities. Specifically, to separate the engineering impacts from trophic (predation) impacts on richness and biomass.	Engineering by lyrebirds resulted in a strong facilitative effect on invertebrate richness, suggesting that changes to litter and soil by lyrebirds provides niche habitats for invertebrates. The estimated biomass of known prey species showed a strong increase through time in the simulated foraging treatment, indicating a ‘farming’ effect by lyrebirds on their invertebrate prey. Species composition was influenced by predation effects from lyrebirds, but not by engineering effects. Different invertebrate orders responded to treatments to differing degrees. There was a consistent trend through time, across all orders, for increased biomass in response to engineering impacts.

Table 6.1 continued

Data chapter	Objectives	Key findings
Chapter 4 - Plants	To determine the engineering role of lyrebird foraging in shaping plant species composition, richness and vegetation structure.	Engineering stimulated greater germination of the soil-stored seed bank, relative to that in the fenced treatment. There was little impact of engineering on seedlings (beyond the dicotyledon stage), yet strong impacts from herbivory. Plant composition, richness and structure were all affected by herbivory effects (i.e. a different community with fewer species and lower structural complexity in the low stratum); while engineering, despite being a large disturbance process, showed no impact on these plant community measures over the two-year study.
Chapter 5 - Fungi	To determine the impact of lyrebird engineering on the litter and soil fungal community.	Fungal community composition strongly differed between forest types and was also influenced by relationships with soil nutrients. There was no evidence for an engineering effect on fungal community composition, richness or diversity over the two-year experiment.

To understand the mode and scale of ecosystem engineering, it is necessary to identify the major environmental drivers that influence the pattern of engineering. The influence of forest type, vegetation structure and landscape features on foraging activity were therefore investigated. Further, by incorporating observational data on lyrebird foraging throughout two seasonal cycles, it was possible to track foraging dynamics to gain a two-year snapshot of the temporal pattern of engineering. These components of the study describe the physical process and pattern arising from foraging by lyrebirds (see Table 6.1), providing strong grounds for the expectation that the species may act as an ecosystem engineer and influence the distribution and abundance of other species.

In Chapter 3, the effects of lyrebird foraging on invertebrates were investigated. Invertebrates comprise the bulk of the superb lyrebird's diet. As such, the aspects of the experimental design that separated 'real' from 'simulated' foraging were of primary interest. In this chapter, it was determined that the relative impact on the invertebrate population attributable to habitat alteration (represented by the difference between simulated and fenced treatments) compared with that of predation by lyrebirds (represented by the difference between simulated and unfenced treatments). This revealed an intriguing farming effect (Fig. 6.1), whereby lyrebirds, through their engineering activities, increase the predicted biomass of invertebrate prey species for any given litter depth.

In Chapter 4, the consequences of lyrebird foraging on the plant community and vegetation structure were investigated. The impacts on germination and seedling dynamics were quantified through the manipulative study design, allowing for comparison between engineering effects and herbivory. While engineering appears to strongly stimulate the germination of seeds (e.g., through breaking apart the litter layer, causing abrasion to seeds; allowing light to stimulate the soil-stored seed bank), seedling survivorship was primarily moderated by herbivory. Taken together, this suggests that the destruction of some seedlings by foraging lyrebirds is compensated by encouraging high rates of germination that would otherwise not occur. Interestingly, floristic species richness was depressed by herbivory effects, while engineering had no impact.

Animals that interact with litter and soil are also likely to both directly (e.g., through spore dispersal) and indirectly (e.g., through habitat alteration) interact with microbial communities. As such, in Chapter 5, changes to the soil fungal community under the three experimental treatments (simulated, fenced and unfenced) were tested over a two-year period. The fungal community was extremely diverse, with high levels of variability between locations. While there were community-level differences between forest types, no change could be attributed directly to the experimental treatments.

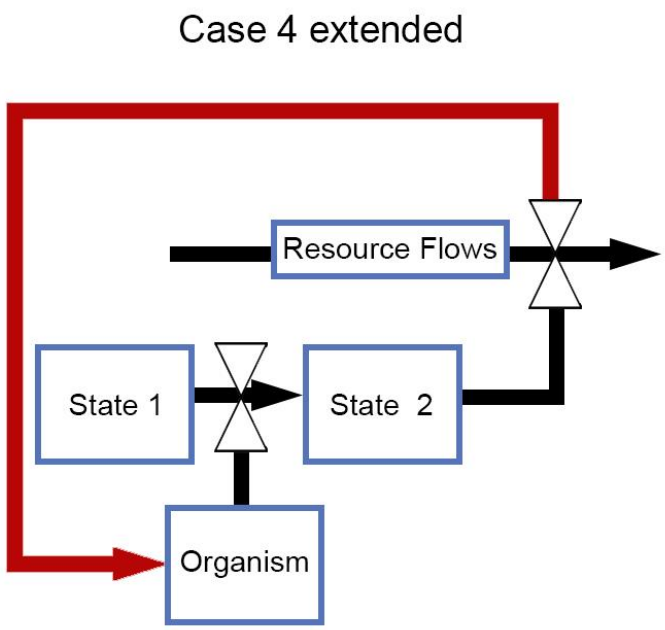


Figure 6. 1 Conceptual diagram of how ecosystem engineering by the superb lyrebird acts to 'farm' their prey, adapted from Jones et al. (1994) and extended to include a feedback mechanism on the engineer (red arrow). The '⧖' denotes a point of modulation. In this study system, the superb lyrebird is the engineering organism. Lyrebirds modulate the litter and soil from state 1 (unmodified litter and soil layer) to state 2 (foraged litter and soil with altered properties). The changed litter and soil environment interacts with resource flows to increase the biomass of the invertebrate community, thus feeding back on lyrebirds.

This study implemented a manipulative experiment over a broad spatial scale (i.e. three forest blocks, each with three forest types) to provide robust evidence and test hypotheses relating to the engineering role of lyrebirds. By randomly selecting plots throughout multiple forests in the study region, a landscape-wide understanding was gained. This was an important aspect of the experimental design, as it considered the dynamic nature of foraging by this species. Rather than focusing on local scale comparisons (e.g., between foraging pits and adjacent non-pit microsites), this study revealed a perpetual cycle of litter disturbance by lyrebirds throughout the forested landscape.

Foraging lyrebirds strip litter from the upper-slope edge of a forage site, and the ejected litter and soil is mixed and buried perpendicular to the hill contour. Where groundcover vegetation is sufficiently sparse, the foraged area undergoes a period of recovery, allowing further litterfall to cover exposed soil before a return visitation by lyrebirds recreates the disturbance. Insights described in Chapter 2 demonstrate that at the plot scale, the litter layer never returns to an unaltered state in the presence of lyrebirds.

From the combination of this understanding of physical litter and soil changes with the measured response of invertebrates and seedling plants, it was established that lyrebirds create a fine-grained heterogeneity in the litter and soil layer that promotes niche opportunities for other taxa. In addition, foraging by lyrebirds gives rise to a complex 'farming' feedback on the lyrebirds themselves (Fig. 6.1), whereby the effects of lyrebird engineering activities create favourable conditions for an increased biomass of its prey species.

6.2 INSIGHTS FOR CONSERVATION

The ecosystem engineering concept has contributed to nature conservation through its emphasis on the functional role of species. By recognising the regulatory forces that engineers confer on habitats, management actions can be focused to support and maintain these functional roles and associated ecosystem processes. When this is achieved, conservation and restoration is more likely to succeed in creating robust ecosystems that can withstand pressures from perturbations caused by climate and landscape change (Fischer et al. 2006).

6.2.1 Ecosystem management to preserve the functional role of lyrebirds

To maintain ecosystem function, the contribution of ecosystem engineers must be recognised. In forests inhabited by the superb lyrebird, litter and soil habitats are strongly modified by this species. Temperate litter and soil habitats are among the most biodiverse terrestrial communities on the planet (Anderson 1978). The extent and nature of physical disturbances by digging engineers such as lyrebirds has been shown to influence that biodiversity in several ways – including seedling regeneration, water infiltration, decomposition and nutrient cycling. Understanding how and when these important processes are likely to be influenced by an engineer will better inform conservation management.

Several factors that influence the ecological function of lyrebirds can be recognised. First, fire regimes have a profound influence on suitability of forest habitats for lyrebirds. Lyrebirds avoid severely burned forest (Nugent et al. 2014) and rarely forage in dense, low vegetation (Maisey et al. 2018). Post-burn landscapes generally represent poor habitat quality for lyrebirds for many years following a fire. Leaf litter may be slow to build to sufficient levels to support decomposer communities and in turn, food for lyrebirds, while regrowth vegetation may be structurally complex within the low strata, impeding foraging lyrebirds. This study was conducted in wet forests where fire is infrequent (Ashton 1975). Further, the tall forest types examined are not targeted for ecological or fuel reduction burns by land management agencies across the lyrebird's distribution. Much of the superb lyrebird's range, however, does carry a high risk of fire, and is indeed subject to ecological or fuel reduction burning practices. In forests that are burned regularly, the functional

role of the lyrebird is likely to become depressed. To best support the persistence of lyrebirds in such forests and maintain their functional role, land management should aim to protect wet gullies and rocky outcrops (these may concentrate resources such as litter and moisture, in addition to providing nesting structures) and long-unburnt vegetation. Where burns are conducted for conservation values, patchily burned areas will, at a landscape scale, ensure a lower loss of key resources for lyrebirds (i.e. litter and soil invertebrates).

Second, the availability of suitable habitat for nesting may limit the size of lyrebird populations. While lyrebirds use many vegetation types for foraging, nesting habitats are more likely to be limiting in post-fire or post-logging landscapes. The protection of key features such as rainforest gullies and old-growth vegetation will provide suitable breeding habitat for lyrebirds. These components of the landscape have moist litter environments, and harbour abundant invertebrate prey. Such areas tend to have well-developed mid-storey vegetation, which helps to provide protection from aerial predators (e.g., *Accipiter* hawks (Maisey et al. 2018)).

Third, management actions that address predation by feral animals (e.g., red fox *Vulpes vulpes* and feral cat *Felis catus*) will aid the conservation of lyrebirds (Lill 1980, Smith 1988). Predator control programs will be most beneficial when implemented at sufficient intensity on a broad spatial scale as part of landscape management and restoration. Landscape-scale predator control programs can provide multiple benefits for biodiversity and society. For example, the Southern Ark project in East Gippsland and the Glenelg Ark project in south-western Victoria aim to control foxes by using 1080 baits across a broad geographic area that encompasses many vegetation types. These programs have resulted in the regional recovery of some species of small mammals and ground-foraging birds, in addition to benefitting farmers by controlling pest animals on and adjacent to their land (Robley et al. 2009, Robley et al. 2013).

6.2.2 Beyond the foraging pit: scaling up our understanding of ecosystem engineers

Determining the spatial and temporal scale at which an organism acts as an engineer has been a major challenge in ecosystem engineering studies to date. Much literature on ecosystem engineering (that involves bioturbation) has compared the ‘forage pit’ with randomly chosen micro-sites within the landscape (see Bragg et al. 2005, Eldridge and Mensinga 2007, Eldridge and Whitford 2009, Louw et al. 2019, Ross et al. 2019). While these comparisons adequately characterise the engineered structure, it is difficult to determine the importance of the engineered habitat on a broader scale.

Many practical barriers stifle the implementation of experiments on ecosystem engineers at the appropriate scale. For some species, changes in species distribution (e.g., following European colonisation in Australia) may hinder consideration of landscape-scale effects of engineering. In Australia, many fossorial mammals have undergone enormous range contractions, effectively

becoming functionally extinct throughout much of the continent. Existing populations may survive only on predator-free, off-shore islands, or in fenced sanctuary environments (Johnson 2006), making it difficult to find or create replicates at a landscape scale. Further complicating this task is the issue of inadequate historical baselines and data deficiencies that hamper our ability to extend inference to natural situations. For example, while indigenous knowledge suggests that the natural density of many fossorial mammal species was high (e.g., woylie *Bettongia penicillata*; burrowing bettong *Bettongia lesueur* (Woinarski et al. 2015)), the densities maintained in fenced sanctuaries are unlikely to be 'natural', and may become over-abundant, hence depleting resources. This makes it difficult to predict how these engineers formerly functioned in the landscape, and what the consequences of losing such function might be. Despite Jones et al. (1994) drawing attention to the importance of scale in their seminal work on ecosystem engineers, problems associated with 'scaling up' experimental work have largely remained.

Further, an organism that functions as an ecosystem engineer in one environment may not do so in another, due to underlying abiotic conditions; some ecosystems may be resistant to the engineer's activity. For example, digging engineers may fail to dig foraging pits in recalcitrant soil types or the nutrient-coupling effects commonly arising from foraging pits in arid zones may be negligible in mesic climates, therefore the benefits of the engineer to biodiversity do not exist. As such, when reintroducing or managing ecosystem engineers for conservation, it is important to determine the scale and mechanism underlying the desired function carried out by the engineer.

This research has demonstrated that some ecosystem engineering processes can be captured by experiments conducted over medium timeframes (e.g., macro-invertebrates respond to altered litter and soil qualities over months or years), while others may require experiments to be carried out over prolonged time periods (e.g., the composition of soil nutrients and fungal community may respond to engineering processes over decades). Plant communities may undergo successional changes that interact with engineers on a timescale best measured in centuries. For example, if ongoing lyrebird activity influences litter structure in ways that reduce the likelihood of fire, successional development from wet forest to rainforest may follow. Transitional change of this nature is likely to occur very slowly, as the lifetime of a floristic cohort in a eucalypt forest spans several centuries. While experiments spanning centuries are unlikely to be feasible, by returning to long-term monitoring plots established by other scientists, opportunities to uncover century-scale vegetation changes can be realised (Lunt 2002). The need for long term experimental treatments to understand broad-scale and long-term successional trends is compelling. Such experiments also provide important baseline data for understanding ongoing and future changes to interactions with other processes, such as climate and fire.

As a study system, the superb lyrebird in wet forests represents a unique opportunity to examine the functional role of an engineer in a relatively natural state. Lyrebird populations have withstood European colonisation and associated changes in land use to persist at relatively high population density in this bioregion (Loyn 1985). Two aspects of the current study address some of the challenges faced by other studies of ecosystem engineers. First, randomly allocated sites within multiple forest blocks across a broad bioregion were studied. This allowed for landscape-scale inference on the impact of engineering activities (i.e. extending much beyond the foraging pit), and identified the wide-ranging extent of engineering by lyrebirds within multiple forest types. Second, this study was conducted over two seasonal cycles, providing a temporal dimension to the engineering pattern, uncovering subtle seasonal shifts in foraging activity. These aspects of study design have determined that ecosystem engineering by lyrebirds occurs on a dynamic spatial and temporal scale that is meaningful at an ecosystem level.

6.3 A FOCUS ON FUNCTION

6.3.1 Lyrebirds as key drivers of heterogeneity in the litter and soil layer of wet forests

This study demonstrates that lyrebird foraging represents a major disturbance process in the wet forests of the southern fall of Victoria's Central Highlands. Aside from severe bushfires, lyrebird foraging which turns over an average of 156 t ha^{-1} per year is likely to be the most influential natural process structuring this ecosystem. Through their foraging, lyrebirds maintain fine-scale habitat heterogeneity in open areas of the forest floor, creating a dynamic spatial and temporal disturbance regime. Freshly foraged scratching sites create complex microtopography of terraces and shallow, aerated ejecta mounds, comprised of leaf litter mixed and buried with mineral soil. Areas of exposed, bare soil are left on the upslope juncture of the forage pit. These ubiquitous foraging sites are patterned within a matrix of an unbroken-litter layer that typically is further along a recovery trajectory from previous disturbance by lyrebirds. On the scale of the 3 x 3 m plots used in this study, the litter did not return to a lyrebird-free state before re-foraging occurred. This extensive, forest-wide disturbance regime promotes the germination of seeds, while appearing to maintain niche opportunities that are exploited by litter and soil-dwelling invertebrates. Thus, foraging by lyrebirds is a key determinant of litter and soil habitat quality in these forests.

Over a longer timeframe (spanning decades), lyrebirds increase the rate of decomposition, both through the physical burial of fine litter, but also by creating niche opportunities in litter and soil habitats that in turn support a species-rich detritivore invertebrate community. Furthermore, sustained foraging in wet forest is likely to maintain a more open ground-cover (i.e. small ferns and shrubs are dug out before they establish) and further limit the build-up of fuel loads and

vulnerability to wildfire (Nugent et al. 2014). While there is little doubt that lyrebirds facilitate the germination and growth of small-bodied herbs, larger slower-growing shrubs and ferns are more likely to be dug out before they establish and are therefore maintained at low levels of complexity in the low stratum. Despite their large disturbance to litter and soil, foraging lyrebirds are unlikely to hinder successional change from wet forest to rainforest vegetation, as the rainforest community primarily develops from seedlings that germinate on the trunks of treeferns (Ashton 2000). Lyrebird foraging appears to be a key process that interacts with vegetation succession, and decreases flammability of tall wet forests as they age (Zylstra 2018).

6.3.2 Lyrebirds farm key resources

A key finding of this study was that habitat alteration by lyrebird foraging gave rise to a farming effect on invertebrate biomass. By altering litter and soil habitats to create niche opportunities, a greater diversity of invertebrates may be supported, which in turn provides further food for the lyrebird. Biomass of known prey taxa showed a greater increase through time in the simulated treatments than in fenced and unfenced treatments. Interestingly, this was not simply reflecting an increase in abundance (total invertebrate abundance did not show a strong interaction between treatments and time), but rather a change in the size distribution of prey. This may be a result of a complex trophic-engineering interaction, whereby the engineered habitat provides greater niche opportunity. For example, variable litter depths and less compact soil may create niches for invertebrate meso-predators, such as small centipedes and spiders, while disadvantaging apex predators such as larger spiders (known to associate with deeper litter depth (Bultman and Uetz 1982). Following meso-predator release, predation pressure on smaller individuals of many detritivore species may be high, while allowing larger specimens to remain in an environment rich in resources.

6.4 FUTURE RESEARCH DIRECTIONS

6.4.1 Integrating ecosystem engineering with trophic interactions

The engineering activities of organisms seldom act alone in shaping ecosystems, as all species are embedded in food webs. When assessing the function of a species as an engineer, future studies should also consider how engineering combines with trophic relationships of both the engineer and interacting species within its environment. For example, in parks where the African elephant *Loxodonta africana* is managed as an ecosystem engineer to maintain grasslands, such areas are expected to sustain more herbivores. The effects of elephant-induced changes to habitat may however also change the way in which apex predators, such as the lion *Panthera leo*, hunt those

herbivores (Ferry et al. 2020). The outcome of engineering may therefore have little or no impact on herbivores due to increased predation by lions. If either the biotic or engineering interactions are considered in isolation of one-another, management resources may be wasted and the desired function may not be realised, despite the presence or abundance of the engineer.

As the quantity and quality of litter determines dynamics of the 'brown' food web (i.e. the decomposer pathway (Zou et al. 2016)), animals like the superb lyrebird, that engineer the litter and soil environment, are likely to be key mediators between these food webs. This thesis included manipulative experiments to distinguish the outcomes of engineering effects and trophic interactions (e.g., herbivory, predation), while also considering their combined impacts. Future studies with similar designs will best address the growing need to manage species for their ecological function and predict where and when they will fulfill an engineering role.

6.4.2 Rewilding and sanctuaries: opportunities for an experimental approach

Observational studies have played an important role in the recognition of natural processes underpinned by ecosystem engineers. Nonetheless, to advance the application of the ecosystem engineering concept in real-world scenarios, manipulative experiments are needed to better inform restoration science. Worldwide, restoration projects have demonstrated that bold, large-scale experiments can be successful in restoring ecological processes (Ripple and Beschta 2012, Law et al. 2017, Perino et al. 2019), but many authors have pointed out a need for long-term monitoring and research to ensure the desired engineering functions and processes are indeed real and maintained (Smith et al. 2003, Torres et al. 2018, Schweiger et al. 2019). Some 'rewilding' projects have been criticised for their lack of monitoring and research to demonstrate the effectiveness of interventions (Torres et al. 2018), with widespread advocacy for a greater focus on ecological function and process (Corlett 2016, Torres et al. 2018).

The rise in popularity of fenced wildlife sanctuaries and island arks in countries such as Australia, South Africa and New Zealand, represent valuable opportunities for manipulative experiments. While there are many challenges in conducting research within sanctuaries (e.g., pseudoreplication, uncertainty around 'natural' vs. 'captive' population dynamics), the opportunity to experimentally manipulate the numbers of engineers (and their predators) could generate useful predictions that are broadly applicable to wild populations. Multi-sanctuary experiments have rarely been attempted (but see Decker et al. 2019a), yet provide insightful understanding on macro-geographic scales and across environmental gradients.

6.4.3 Spatiotemporal dynamics in the functional role of the superb lyrebird

This thesis provides a case study within tall wet forests, an ecosystem synonymous with the superb lyrebird, although many different forest ecosystems along the east coast of Australia are also home to this species. In regions with different geological composition (e.g., sandstone plateaus of the Blue Mountains in New South Wales or the Granite Belt in South East Queensland), lyrebird foraging may have different impacts on litter decomposition and soil compaction. Furthermore, climatic and topographic mediators of fire frequency and intensity are also likely to alter lyrebird population dynamics and foraging behaviour. In contrast, the extent to which lyrebird activity moderates fine litter accumulation may determine fire behaviour in some ecosystems. Determining these macro-geographic patterns in lyrebird activity and the mechanisms that underlie them would greatly improve understanding of the context for ecosystem engineering by lyrebirds.

This research provides new insights into the short-term dynamics of vegetation under the foraging regime of lyrebirds. Such insights provide a foundation for generating hypotheses to explain long-term forest succession in forests inhabited by lyrebirds, in particular the colonisation of rainforest plants and establishment of temperate rainforests. To what extent and in which ways do lyrebirds influence successional transition from wet forest to rainforest? What are the mechanisms and feedbacks between foraging, germination, seedling survivorship and fire? Such questions bring into sharp relief the need for long-term monitoring to uncover and test the direction of these relationships.

Climate-mediated impacts on lyrebird activity, especially breeding, are likely to be the most powerful determinant of future population structure, and therefore the persistence of the functional role of the superb lyrebird as an ecosystem engineer. In marginal habitats with low population density of lyrebirds, the engineering role of this species may be functionally depressed. Similarly, if the substratum is particularly resistant to changes induced by foraging (e.g., coarse siliceous sands derived from granite, areas of dense groundcover vegetation), engineering effects may be patchy and cover only a small proportion of the landscape. Climatic change and extreme weather events may put habitats under greater risk of severe bushfires, weed invasion and prevalence of predators, combining to create a hostile environment for lyrebirds.

6.4.4 Conservation of the superb lyrebird in the context of the 2019/20 Australian 'megafires'

The extensive bushfires of 2019/20 burned through an estimated ~12 million hectares of forest and shrubland along the Great Dividing Range in eastern Australia (Ward et al. 2020). An estimated 40% of the entire geographic distribution of the superb lyrebird was incinerated (BirdLife Australia, unpublished data), including many areas that would normally be too moist to carry fire (e.g.,

rainforest, wet gullies). This has far-reaching implications for this species, and the ecological functions it performs.

Lyrebirds are relatively adept at surviving fire fronts, with anecdotal evidence of lyrebirds sheltering in streams and rivers, taking shelter in burrows dug by bare-nosed wombats *Vombatus ursinus* and even in farm dams adjacent to bushland. Post-fire landscapes, however, present profound challenges to the long-term survival of lyrebirds. With litter and soil incinerated and few unburnt refuges in many landscapes, invertebrate biomass is greatly reduced (York 1999). Impacts of bushfires on invertebrate communities are likely to persist for many years or even decades (York and Lewis 2018, Butler et al. 2019), and together with dense vegetation structure, potentially render some habitats temporarily unsuitable for lyrebirds (e.g., serotinous wet forest regenerating primarily from seed after severe fire). Despite the persistence of the lyrebird in many post-fire landscapes, breeding is unlikely to recommence until these key litter resources return (Maisey et al. 2018). Further, it is likely that under such conditions the functional role of lyrebirds as ecosystem engineers will be depressed. This may result in the development of landscapes with high fire frequency and low lyrebird abundance, resulting in a positive feedback loop as proposed by Nugent et al. (2014). In such scenarios, lyrebirds will most likely cease to fulfill an ecosystem engineering function.

Under a changing climate, an increase in fire frequency and its associated effects on litter accumulation and decomposition are likely to exacerbate fire impacts on invertebrates (Brennan et al. 2009) and vegetation structure, therefore altering lyrebird population dynamics further. The short-term effects of wildfire on vegetation structure in many forest ecosystems inhabited by lyrebirds will be a dense flush of vegetation growth, thus impeding access for lyrebirds. Long-term vegetation trends associated with an interaction between wildfire and climate change will be an important focus for future research.

While survivorship after a fire event may initially appear high, long-term population trends may occur over longer timeframes. Lyrebirds are a long-lived species (>20 years) and population change may go undetected for many years after a large fire event. This potential lag effect makes this species of particular conservation concern, especially when common measures collected by conservation organisations and individuals (e.g., observations, reporting rate) do not represent functional persistence. Identification of fire refuges for this species, especially rainforest and wet forest breeding areas, is of paramount importance following the recent megafires.

6.4.5 A flagship for conservation of wet forests

The lyrebird has been recognised worldwide for its fascinating courtship displays featuring unrivalled mimetic abilities. These displays have captured the imagination of millions, and inspired artistic endeavours ranging from indigenous cultural dances (potentially performed for tens of

thousands of years), to the relatively contemporary works of Robert Helpmann's ballet *The Display*, produced for The Australian Ballet in 1964, or the orchestral works *L'oiseau-lyre et la ville-fiancée* by French composer Olivier Messiaen (Curtis and Taylor 2010). Yet perhaps the most important activities that the lyrebird undertakes - their foraging in litter and soil - has been mostly over-looked (but see Adamson et al. (1983) Ashton and Bassett (1997), and Nugent et al. (2014)). Working over of the forest floor in a dynamic, ongoing manner, lyrebirds maintain critical processes in the wet forests of Victoria's Central Highlands. As a highly charismatic species that also performs an important functional role, conservation programs that target the preservation of the superb lyrebird are likely to both attract public funding and popular support, while also having disproportionate benefits to ecosystem function.

Our species, *Homo sapiens*, has proved to be the ultimate ecosystem engineer, altering oceanic and atmospheric chemistry and climate, changing global fire regimes and hydrology, transporting species around the globe and dramatically reducing global forest cover (Ellis 2011). While engineering activities of our species have mostly had negative impacts on biodiversity, by applying an ecosystem engineering understanding to conservation, both through management of wild species as well as understanding how our own engineering activities interact with biota, we will be better equipped to protect biodiversity in the context of a dramatically human-altered global environment.

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APPENDIX 1.

Appendix 1. 1 Maisey, A.C.[1,2,3], Carter, N.T.[2], Incoll, J.M.[2] and Bennett, A.F.[1,3,4], 2016. Environmental influences on variation in nest-characteristics in a long-term study population of the Superb Lyrebird, *Menura novaehollandiae*. *Emu-Austral Ornithology*, *116*(4), pp.445-451.

[1]School of Life and Environmental Sciences, Deakin University, 221 Burwood Highway, Burwood, Vic. 3125, Australia

[2]Sherbrooke Lyrebird Survey Group, 30 Moores Road, Monbulk, Vic. 3793, Australia.

[3]Department of Ecology, Environment & Evolution, La Trobe University, Vic 3086, Australia

[4]Arthur Rylah Institute for Environmental Research, 123 Brown St., Heidelberg, Vic 3084 Australia

Published by: *EMU - Austral Ornithology*

Date accepted: 12 Feb, 2016

Manuscript word count: 4355

Abstract

Nests provide essential ecological services to breeding birds, and their location and architectural characteristics may be varied to maximise reproductive success. We investigated variation in nest characteristics within a breeding population of the Superb Lyrebird (*Menura novaehollandiae*) in south-east Australia over a 14-year period. Lyrebird nests take the form of a bulky, domed chamber built on a supporting platform constructed from sticks. A total of 292 nests, all successful to the nestling stage, were measured. Nest orientation differed from random, with nests predominantly facing downslope. The volume of the internal chamber (a surrogate of nest size) was smaller in high nests (nests ≥2m above ground). Mean width of the nest wall (per year) and median height above ground (per year) were positively correlated with rainfall during the nest-building period (March–June), but not with temperature; suggesting that water resistance rather than thermal insulation is a stronger influence on nest construction. Variation in nest characteristics between individuals was identified, indicating particular 'styles' of nest construction in the population. For the Superb Lyrebird, flexibility in nest location and architecture, both within and between years, likely represents a mechanism to respond to variation in environmental conditions and predation risk, which may affect reproductive success.

Introduction

Nests provide a range of essential services to birds including protection from predators (Lazo and Anabalón 1991; Weidinger 2002), insulation from the external environment (Collias and Collias 1964; Buttemer *et al.* 1987; McGowan *et al.* 2004) and a confined space for eggs and nestlings to develop. The effectiveness of these services can determine the outcome of the nesting process, and therefore influence selection pressures on breeding individuals (Lombardo 1994). Thus, the architectural characteristics of nests and their locations potentially are important to the reproduction, physiology and evolution of bird species (Sheldon and Winkler 1999; Mainwaring *et al.* 2014).

Environmental factors such as weather, seasonality and abundance of predators influence the choices made by nesting birds in relation to the micro-position of nests (Mainwaring *et al.* 2014). Characteristics such as nest orientation or height above ground can be manipulated to enhance environmental benefits. A more benign micro-climate within the nest, for example, can result in lower energy costs for brooding parents and growing nestlings (Horvath 1964). Thermal advantage has been postulated to be a strong driver of nest orientation and position, especially for hollow-nesting species (Tidemann *et al.* 1992; Dobkin *et al.* 1995; Ardia *et al.* 2006). Experimental work (Butler *et al.* 2009) demonstrated that nest boxes situated to maximise insolation maintained a significantly higher relative humidity and temperature, consistent with achieving thermal benefits.

The influence of environmental factors on the nest characteristics of non-hollow-nesting species is less well studied, but also is evident. In alpine-nesting populations of the Australian Pipit (*Anthus novaeseelandiae*), nest entrances were oriented to minimise the effects of prevailing cold fronts (Norment and Green 2005). Similarly, the Tawny Frogmouth (*Podargus strigoides*) situates nests on the lee side of nest trees, thus maximising the trade-off between shelter from inclement weather and increased exposure to the morning sun (Rae and Rae 2014). Birds may also manipulate nest characteristics or micro-position in response to temporal variation in predator guilds (Lazo and Anabalón 1991; Forstmeier and Weiss 2004). It is likely that many species display variation in nest architecture, position and orientation; this is especially true for species with prolonged nesting periods. However, such data are difficult to obtain, making long-term and comprehensive datasets invaluable to understanding the drivers of variability in nest architecture.

Here, we investigated variation in nest characteristics of the Superb Lyrebird (*Menura novaehollandiae*), a large (~975 g) ground-dwelling passerine that exhibits a paternally emancipated reproductive strategy in which the female solely constructs and defends the nest (Lill 1986). Breeding commences in mid-winter, and incubation of the single egg and nestling period are greatly prolonged (~13 weeks from laying to fledging) (Lill 1987). Consequently, nest placement and construction are likely to be a crucial aspect of the breeding biology of this species. As extended phenotypes, bird nests and the way in which they vary between individuals or between seasons (due to environmental

factors) is subject to selection pressure, thereby strongly affecting fitness of individuals (Dawkins 1978; Hansell 2000).

First, we examined variation in nest characteristics on a micro-spatial scale to describe the relationship of the nest within the environment. We tested the hypotheses that: a) lyrebirds orient their nests non-randomly to minimise the exposure to prevailing weather; and b) nests constructed in higher positions are smaller than those in lower positions. The latter pattern may represent an energetic trade-off between nest insulation afforded by a larger nest and making more flights to carry nest material. Second, we assessed nest characteristics on a temporal scale (between seasons) to investigate whether abiotic factors (rainfall and temperature) influence nest construction. Last, we compared nest characteristics between colour-banded lyrebirds to evaluate whether there are 'styles' pertaining to individual females. Such variability may assist a species to adapt to environmental change on a population level.

Methods

Study site

Nests of the Superb Lyrebird were studied in the Sherbrooke unit of the Dandenong Ranges National Park, south-central Victoria, Australia. The Sherbrooke forest is ~800 ha in size, and mostly surrounded by semi-urban land tenure. Vegetation is predominantly wet forest with an over-storey of Mountain Ash (*Eucalyptus regnans*), representing multiple successional stages due to an intensive logging history. Cool temperate rainforest dominated by Blackwood (*Acacia melanoxylon*) and Southern Sassafras (*Atherosperma moschatum*) comprises the riparian vegetation in much of the park. Two small sections of the park are classified as damp forest, with a canopy dominated by Messmate (*Eucalyptus obliqua*). Nests commonly were situated in wet forest and rainforest vegetation types, with only two nests located in damp forest.

Structure of the nest

The nest of the Superb Lyrebird takes the form of a bulky, domed chamber built on a supporting platform constructed from large (<25 mm diameter) sticks (Reilly 1970). Of the nests measured here, materials that comprised the nest platform were almost exclusively dug from the litter layer and often displayed signs of decay, such as extensive fungal mycelia, mud or debris adhering to individual sticks. Following completion of the platform, a 'cradle' nest is formed: sticks and twigs, grading from large to small, are positioned in a wreath-like fashion around the rear and sides of the nest. Nest walls are packed with moss, leaf litter and coarse fern fibre and worked into the back and sides of the cradle; often green leaves are incorporated into the interior of the nest (Reilly 1970). After the cradle stage of construction, tightly woven fern fibre is used to form an ellipsoid nest chamber with a neatly fabricated oval entry. Small twigs and often green foliage from tree ferns, eucalypts or wattles are loosely woven into the outer roof lining of the nest (Smith 1988). As lyrebirds construct their nest in

a different location each year, the position in which each nest is built is likely to be independently evaluated by the female when choosing where to nest.

Data collection

Nests of the Superb Lyrebird were located by active searches in all sections of the park, by members of the Sherbrooke Lyrebird Survey Group (SLSG), a long-term volunteer organisation. All nests included in this study were successful to at least the stage of a month-old nestling, at which stage nest measurements took place. Female lyrebirds rear a single chick during each breeding season; therefore, each nest measured in any given year represents an independent observation within that year. Some individuals in the population had been colour-banded (and thus identifiable for this study) as part of an ongoing population study undertaken by the SLSG. Lyrebirds were never recorded using the same nest site in consecutive years.

For each nest, the following characteristics were recorded: nest aspect (from magnetic North read from a compass); topographic orientation (categorised as facing downslope, upslope or level); the outer nest height, width and depth; the inner chamber height, width and depth; the nest entrance width and height; and the height of the nest above ground (measured to the nest entry platform). From these data, the nest chamber volume was estimated using the calculation for a spheroid:

$$V = {}^{4}/_{3}\,\pi abc$$

where *a*, *b* and *c* are the radii corresponding with chamber height, width and depth from front. The width of the nest wall was estimated for the walls adjacent to the nest entrance by subtracting nest chamber width from outer nest width and dividing by two. All nest measurements were taken by the authors (AM, NC, JI), or under their direct supervision.

Rainfall and temperature data were collated over the autumn nest-building period (March-June) for each year. Total rainfall and mean daily maximum and minimum temperature was sourced from the nearest weather station (i.e. Scoresby Research Institute, 10 km from the study site) operated for the study period and provided by the Bureau of Meteorology (2015).

Data analysis

Summary statistics, one way ANOVA, Pearson correlations and general linear mixed models were undertaken with the IBM SPSS Statistics package 20.0. The nest characteristics of wall width, height above ground and chamber volume were tested for normality by using a Kolmogorov-Smirnov test: nest height above ground was subsequently $\log_{10}$ transformed to normalise this variable. To examine nest chamber volume in relation to height above ground, only nests from known individuals (banded or carrying permanent physical disfigurements) were selected. These were sorted into height categories of low (<2 m from ground to platform) or high (≥2 m from ground to platform). A general linear mixed model, with individual as a random factor, was used to model the relationship between

nest volume and height category. To test whether lyrebirds orient their nests non-randomly, the first nest of each known individual was analysed (*n*=35 nests). Nest aspect (degrees from magnetic north) was stratified into 90° increments (beginning from 0°) and topographic orientation of the nest (facing uphill, downhill or level) were each analysed by using Chi-square test of independence. Pearson correlations were used to test for relationships between seasonal variation (rainfall, temperature) and nest characteristics. For yearly nest height above ground, the median was used in analysis in preference to the mean, as this was a better measure of central tendency due to a skewed distribution of this variable.

We used analysis of similarity (ANOSIM) and ordination (principal components analysis with varimax rotation) to examine the similarity in nest characteristics among nine individual, colour-banded females for which at least four nests were known. ANOSIM (with Bray-Curtis similarity measure) was used to test whether there were differences between females based on the primary characteristics measured for each nest; and ordination was employed to visually display these relationships.

Results

Data on nest dimensions, height, orientation and aspect were recorded for 292 nests of the Superb Lyrebird, from 2002 to 2015 (Table 1). The number of nests measured each year ranged from 12 to 30 (mean = 20.9). Of these nests, 86 were built by 35 individual females that were either colour-banded or had permanent physical disfigurements allowing for individual identification. The number of such identified females building nests each year ranged from 2 to 9 (mean 6.2). The identity of the remaining nesters each year was not known; it is likely that these individuals also built nests in multiple years. We selected data pertaining to the first nest of each known individual (*n*=35 nests) (i.e. a fully independent data set) and compared these measurements with those of the entire dataset (*n*=292 nests), using one-way ANOVA. For all 11 variables compared (see Table 1) there was no difference between the independent dataset for 35 known individuals and the full data set (for all characteristics $p>0.05$). Consequently, we present summary values here (Table 1) for the overall data set.

Nest height, aspect and orientation in the environment

Nests typically were positioned above ground on tree stumps, embankments, leaning treefern trunks or against the base of trees, with mean height of 1.43 m (Table 1). A small proportion of nests were located in trees (~20%, ≥ 2 m in height), usually supported in a large fork or broken trunk, up to a maximum height of 6.97 m. When controlling for the identity of the nesting female (random factor in a mixed model), the nest chamber volume of nests higher above ground (≥2 m from ground to platform) was smaller than those closer to ground (<2 m) ($F_{(1, 34)} = 7.521$ $P= 0.024$) (Fig. 1).

Table 1. Characteristics measured for nests of the Superb Lyrebird in Sherbrooke Forest, 2002-2015

Nest characteristic	*n*	Mean (cm) ± s.e.	Range (cm)
Nest height above ground	292	143.4 ± 7.8	8-697
Height of opening	291	14.9 ± 0.2	7-26
Width of opening	292	19.9 ± 0.2	7-30
Inside height	292	29.7 ± 0.2	8-45
Inside width	292	25.8 ± 0.2	16-37
Depth from front	292	34.5 ± 0.3	18-47
Chamber volume (cm^3)*	292	13926.1 ± 182	2965-25069
Nest height	292	60.8 ± 0.8	32-115
Nest width	292	48.4 ± 0.6	25-98
Nest depth	292	48.4 ± 0.6	23-85
Nest wall width*	292	11.9 ± 0.3	0-34**

* Denotes composite measurement

** Explanatory note: it was possible for nest wall width to measure zero centimetres when nests were positioned in the fork of a large tree; each trunk comprised an internal side wall of the nest chamber, thus chamber width and external nest width measured the same.

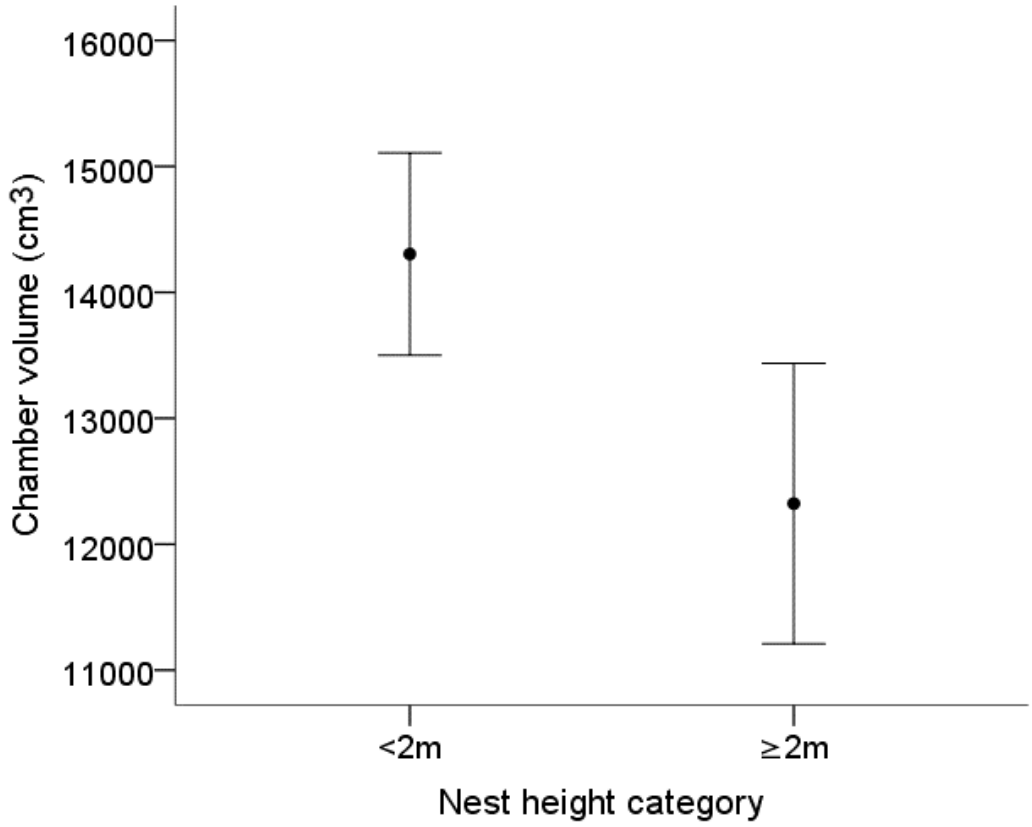

Figure 1. Mean volume of the nest chamber (± 95% C.I.) for nests close to ground (<2 m from ground to platform) and those in trees (≥2 m from ground to platform) for 292 Superb Lyrebird nests in Sherbrooke Forest.

Nest aspect (read from magnetic north) did not differ from random (χ^2 = 5.8, d.f.= 3, *P*= 0.12), but there was a marked effect of topographic orientation (χ^2= 11.886 d.f.= 2 *P*= 0.003): nests were oriented in a downslope direction more than expected (Fig. 2). Of the nests facing downhill, 11 nests (52%) were oriented to the south-east quadrant (i.e. 91-180°), but only 3 (14%) faced north-east (1-90°), 3 (14%) faced south-west (181-270º) and 4 (19%) faced north-west (271-360°).

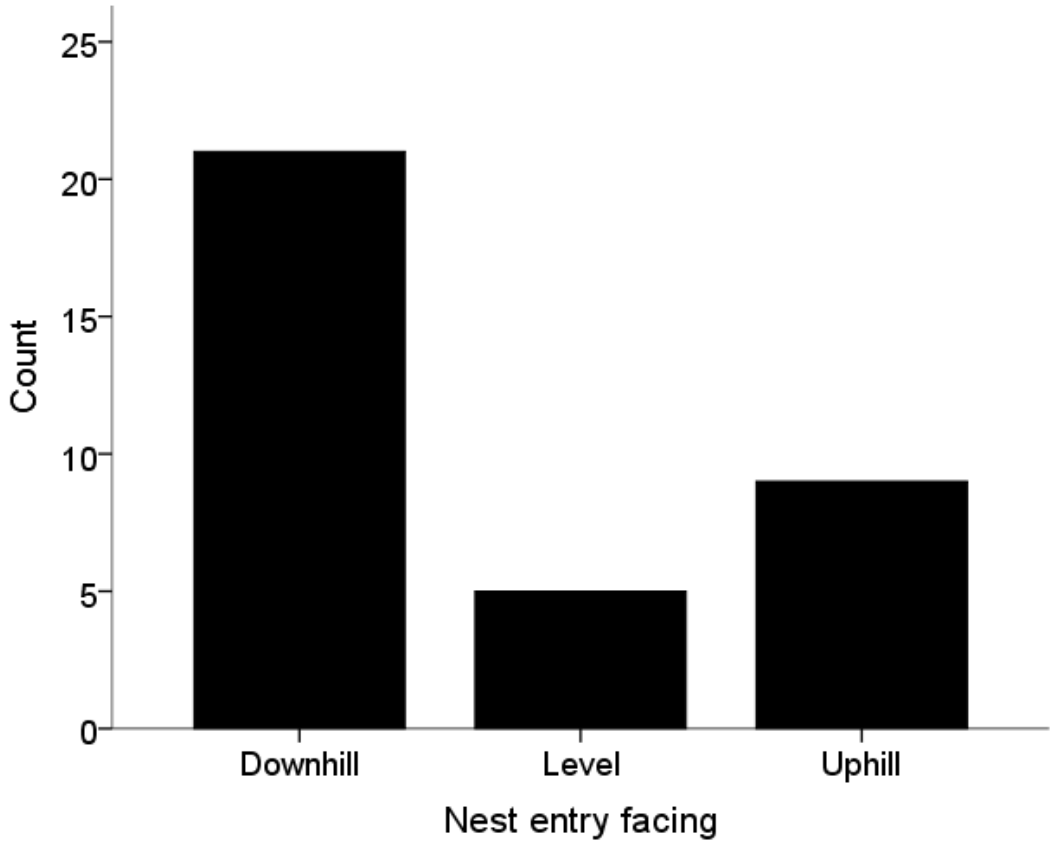

Figure 2. Topographic orientation for the first nest of 35 known individual Superb Lyrebirds in Sherbrooke Forest.

Seasonal variation in nest characteristics

The mean width of the nest wall for a given year was positively associated with rainfall during the nest-building period (March-June) ($r = 0.55$, $P = 0.044$) (Fig. 3a); as was the median nest height for a given year ($r = 0.72$, $P = 0.004$) (Fig. 3c). However, neither nest wall width, nor height, were significantly correlated with mean temperature maxima ($r = -0.219$, $P = 0.451$ and $r = -0.446$, $P = 0.110$, respectively) (Figs. 3b and d). Further, neither characteristic showed any association with mean minimum temperature for March-June for the nesting year (for both variables $P \geq 0.37$).

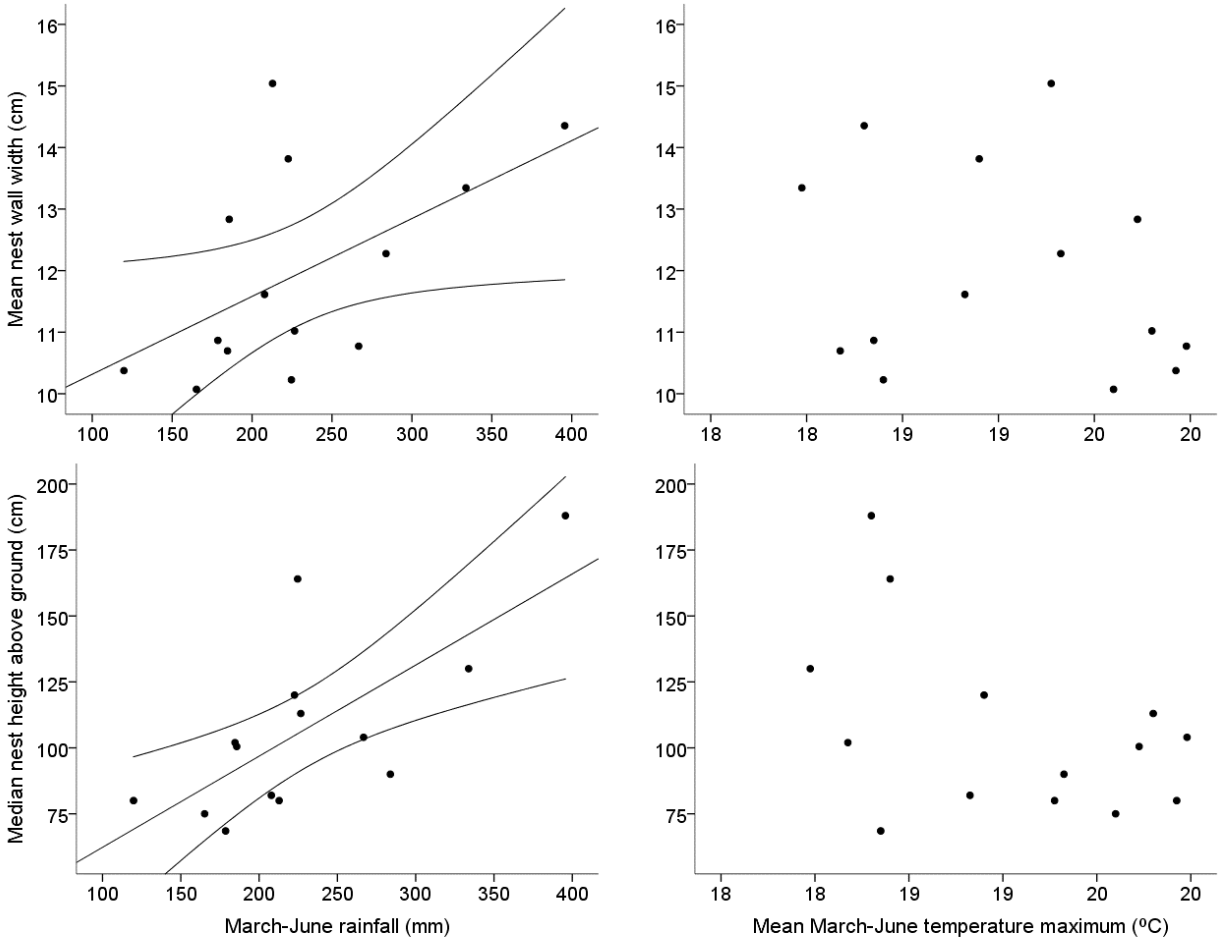

Figure 3. Mean yearly width of the nest wall (a, b) and median yearly nest height (c, d) plotted against total rainfall and mean maximum temperature, respectively, during the nest building period (March – June) in Sherbrooke Forest. The black lines represent the line of best fit ±95% CI.

Variation in nest architecture among individuals

Analysis of similarity (ANOSIM) revealed significant variation (R = 0.295, *P* = 0.001) in nest architecture between nine individually banded females (4-8 nests per female, see Appendix 1). These differences are illustrated by the clustering of nests by individual females in relation to the first two components of a principal components analysis (Fig. 4). These two components together accounted for 41.3% of the variation in the data. The first component (PC1) had positive loadings for nest chamber height, width, depth and entrance height and width, representing a gradient of increasing interior nest volume. Nest height above ground displayed a negative loading on this axis. The second component (PC2) had positive loadings for exterior nest height, width and depth (Fig. 4).

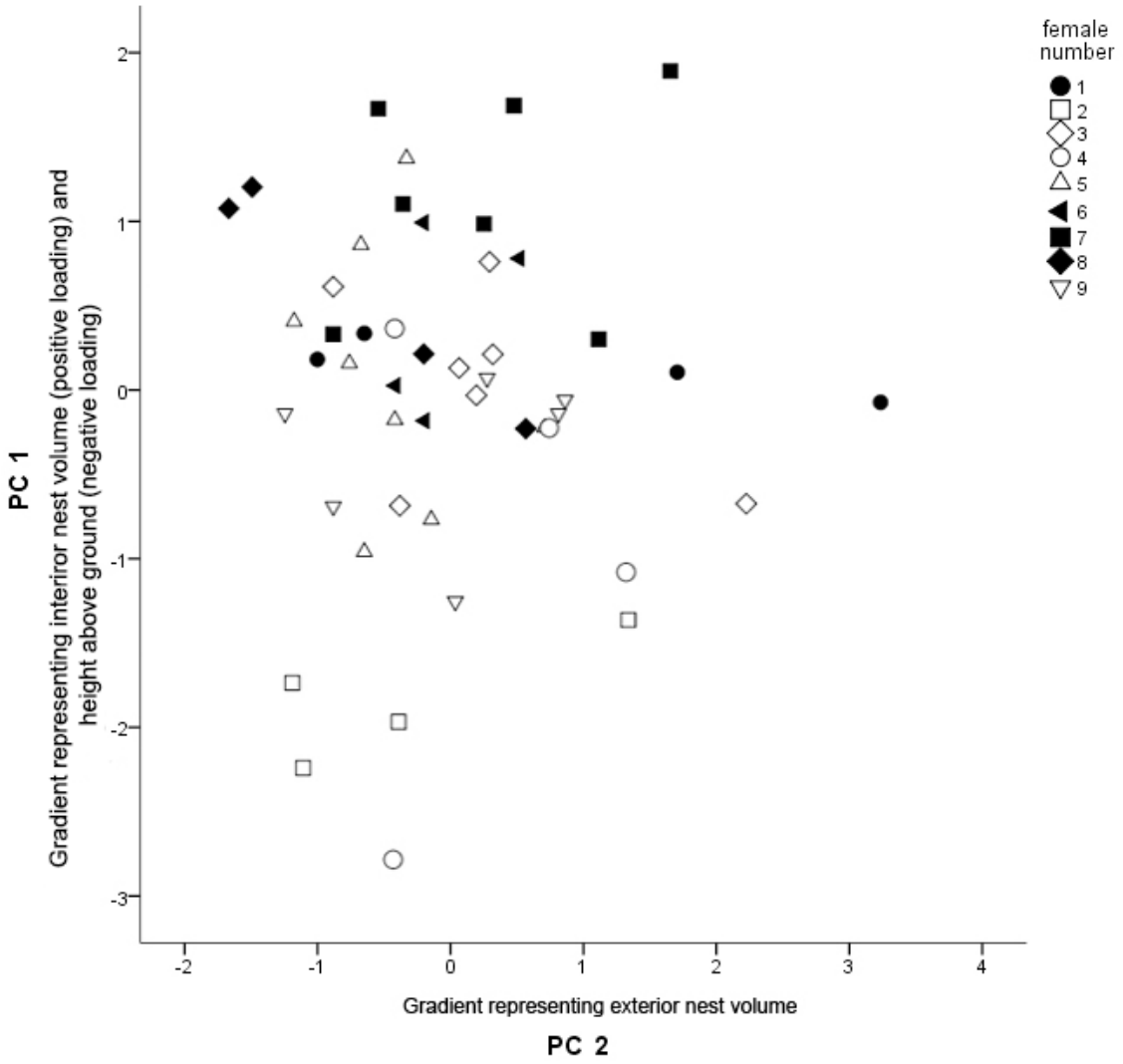

Figure 4. Principal components analysis showing the relationships among 48 nests built by nine colour-banded, female lyrebirds, based on nine measured nest characteristics, in Sherbrooke Forest.

Discussion

Environmental influences on nest orientation

By manipulating the orientation of a nest, birds can reduce the adverse effects of prevailing weather (Austin 1976; Norment and Green 2005), increase thermoregulatory properties of the nest site (Horvath 1964; Rohwer and Law 2010), or select for a trade-off between the two advantages (Rae and Rae 2014). In this study, lyrebirds did not appear to strictly conform to any of these patterns. Nests predominantly faced downhill, which in this study area is generally in a southerly direction due to south-east facing streams and gullies comprising the headwaters of the Dandenong Creek. One functional purpose for nests facing downhill is a lower risk of debris and water accumulating within the nest, especially as many nests are close to ground level. For many passerine species, nesting birds respond strongly to predation pressures when selecting a nest site and constructing a nest (Martin and Roper 1988; Götmark *et al.* 1995; Forstmeier and Weiss 2004; Eggers *et al.* 2006). By positioning nests with a down-sloping aspect, lyrebirds are more likely to be able to use their relatively weak flight to escape from predators, thus increasing survivorship of brooding birds. Further, facing the domed nest downhill would afford the brooding female a clearer view of the surroundings, and thus facilitate early detection of predators (Götmark *et al.* 1995).

Nest height

Nest building is thought to comprise the greatest energetic cost of overall reproduction in lyrebirds (Lill 1986) and so the time-energy budget may be strongly affected by the accessibility of a nest location. Indeed, when nest building, most material used in construction is sourced from within ~ 45 m of the nest (Lill 1986), consistent with lowering the distance travelled between the source of material and nest site. The negative relationship identified here between nest chamber volume and height above ground may represent an efficiency in energy expenditure associated with the number of flights required during the construction of high nests.

Positioning a nest further from the ground may also confer a reduction in risk from terrestrial predators. Some passerines display behavioural plasticity within individuals that allows nesters to manipulate nest site selection on a seasonal timescale, based on fluctuations in predator abundance (Forstmeier and Weiss 2004). Conversely, the impact on lyrebirds from aerial nest predators may increase with nest height above ground, as higher nests typically are more noticeable. The height selected by nesters may thus represent a set of trade-offs between energy efficiency and nest predation. This hypothesis requires further investigation.

Seasonal effects on nest characteristics

Variation in seasonal environmental conditions can elicit a response in nest architecture, although this has been documented for relatively few species (but see Crook (1963) Horvath (1964) Lombardo

(1994) and Austin (1976)). The positive relationship here between nest wall width and rainfall suggests that lyrebirds may enhance the impermeability of nests by manipulating the amount of absorbent moss and leaf litter packed into the nest walls, thus resulting in broader walls in years of high rainfall. Annual median nest height displayed a similar temporal pattern with rainfall during the nest-building period but not with temperature maxima. Nests built at a higher position are less likely to become water-logged; although no evidence of failure due to water-logging was observed during this study, and has only once been reported in the literature (Roberts 1922). Hilton *et al.* (2004) demonstrated experimentally with artificial nests that nest materials such as down or feathers become an extremely poor insulator when wet, suggesting that nesting birds are likely to experience strong selection pressure to minimise penetration of water into nesting materials. The benefits of physiological and behavioural adaptations for survival of eggs and nestling, such as feather-lining the nest (Møller 1991), are likely dependent on the nests ability to maintain a dry micro-environment. Thus, water resistance rather than thermal insulation appears to be a stronger driver of nest architecture in lyrebirds.

Variation between individuals

The degree of behavioural (or phenotypic) plasticity within a population is likely to influence the ability of a species to respond to temporal changes in weather, and ultimately maintain fitness within a range of environmental conditions (Nussey *et al.* 2005). This study identified distinct variation in nest characteristics of individual lyrebirds, over and above the influence of temporal variation in environmental conditions. Whether this variation is due to genetically heritable traits is not known. Climate projections for south-eastern Australia suggest the study area may experience a reduction in rainfall by as much as 13% by the year 2050 (Howe *et al.* 2005), with shifts in the timing of rainfall from winter and spring to summer and autumn (Suppiah *et al.* 2007). As such, individual females ‘styles’ represent variation on a population level that may assist the species to meet the challenge of a changing environment.

Conclusion

This long-term study of the Superb Lyrebird has documented variation in the architectural characteristics of successful nests, driven by their height above ground, environmental conditions at the time of nest building, and distinctive 'styles' of nest between individuals in the population. Such flexibility in nesting likely represents a mechanism to maintain reproductive success, involving complex trade-offs between predation risk, time-energy budgets and changing environmental conditions.

Acknowledgements

We thank the members of the Sherbrooke Lyrebird Survey Group (Kathryn Nauta, Ross Whitford, Asha Billing, Brenna Billing, Sabina Coleman, Karen Weil, John Lloyd, Sally White and Sally Bewsher) for the collection of field data and applied naturalist skills in locating and monitoring lyrebird nests. The associate editor and three referees provided thoughtful comments that improved the manuscript. This work was carried out under scientific permit No. 10006839 from the Victorian Department for Environment and Primary Industries.

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Appendix 1. Summary of nest characteristics for individually banded, female Superb Lyrebirds at Sherbrooke Forest, 2002-2015

Female identification code	# nests used in analysis	Nest chamber volume $\bar{x}$ ± s.e. (cm^3)	Nest height above ground $\bar{x}$ ± s.e. (cm)
F1	4	13415 ±1109	72.2 ±21.1
F2	4	10745 ±332	570.8 ±62.2
F3	6	11126 ±781	161.7 ±41.1
F4	8	14019 ±1068	121.0 ±34.1
F5	4	9983 ±2547	40.0 ±8.5
F6	4	14470 ±1252	215.6 ±97.5
F7	6	18195 ±759	88.4 ±11.0
F8	4	15182 ±1506	108.8 ±21.1
F9	7	12771 ±919	65.7 ±15.8

Appendix 1. 2 Maisey, A.C.,[1,2] Nimmo, D.G[3]. and Bennett, A.F.[1,2,4], 2019. Habitat selection by the Superb Lyrebird (*Menura novaehollandiae*), an iconic ecosystem engineer in forests of south-eastern Australia. *Austral Ecology*, *44*(3), pp.503-513.

[1]School of Environmental Sciences, Department of Ecology, Environment and Evolution, La Trobe University, Bundoora Campus, Vic. 3086 Australia

[2]School of Life and Environmental Sciences, Deakin University, Burwood, Vic. 3125 Australia

[3]School of Environmental Sciences, Charles Sturt University, Albury Wodonga Campus, Albury, N.S.W. 2640

[4]Arthur Rylah Institute for Environmental Research, 123 Brown St., Heidelberg, Vic 3084 Australia

Published by: *Austral Ecology*

Date accepted: 15 Oct, 2018

Manuscript word count: 7125

Abstract

Context Landscape heterogeneity is recognised as a fundamental driver of ecological pattern. The various physical features of landscapes, such as topography and vegetation, affect habitat structure and quality, and consequently the spatial distribution of resources available to species.

Objectives This study examined spatial pattern in an iconic species, the superb lyrebird (*Menura novaehollandiae*). Specific aims were to assess and quantify the a) landscape and b) local habitat influences on nest sites, male calling positions and foraging activity.

Methods Spatial pattern of the lyrebird population was evaluated with information-theoretic techniques in a multi-scale study design. We used a hypothesis-testing approach with logistic regression to generate predictive models for lyrebird nest sites, male calling positions and foraging areas in the Dandenong Ranges National Park, part of the high-rainfall forests of eastern Victoria, Australia.

Results At the landscape scale, models revealed that forest type strongly influenced all three aspects of lyrebird ecology. Rainforest, followed by wet forest, had the highest probability of occurrence for both nest placement and foraging activity, yet damp forest was largely avoided for these activities. Male calling positions were exclusively confined to wet forest. At the landscape scale, nest placement displayed a strong positive relationship with creek systems. Foraging was further influenced by edge disturbance effects and was more likely to occur with increasing distance from creeks. At the local habitat scale, nests were associated with greater leaf litter depth and structural vegetation complexity in the understorey. At this scale, foraging was influenced by only a single parameter, displaying a strong negative relationship with vegetation complexity below 30 cm in height.

Conclusions This study highlights the importance of landscape heterogeneity provided by creek systems and cool temperate rainforest patches for breeding populations of *M. novaehollandiae*. Our findings provide evidence of strong habitat selection at multiple scales. Further, different demographic units within the lyrebird population were shown to utilise different resources distributed throughout the landscape, calling for a “whole-of-landscape” approach to conservation management of this species.

Introduction

Animal and plant species rarely, if ever, occupy space evenly throughout their range (Boulangeat *et al.* 2012; Wisz *et al.* 2013). Understanding the relationship between landscape structure and the spatial patterns of animals is an increasingly important aspect of conservation ecology worldwide (Fahrig 2003). Animals make decisions about their use of space at multiple scales. At a landscape scale, variation in topography and vegetation type can strongly influence species distribution patterns (Howe *et al.* 1981; Luck 2002; Illera *et al.* 2010). Broad-scale anthropogenic disturbances, such as urbanisation or forestry, also influence and alter species' distribution and abundance (Lindenmayer *et al.* 1991; Luck 2002; Manning *et al.* 2004). Landscape context can likewise influence spatial patterns, illustrated by situations where the surrounding landscape structure moderates a species' abundance within suitable habitat patches (Graham and Blake 2001; Shanahan *et al.* 2011). Further, the effect on populations of some landscape elements may change at differing scales of investigation. Scale is therefore an important consideration when investigating the spatial patterns of species, and when seeking to identify and predict population trends in the face of broad landscape change.

On a local scale, structural complexity of habitats has a major influence on patterns of species richness and diversity, as has been documented for bird species (Macarthur and Macarthur 1961; Macarthur *et al.* 1966; Roth 1976; Ludwig *et al.* 2000; Cody 2001). For individual species, greater understanding of habitat requirements can be gained by considering local-scale habitat characteristics.

Both the broad- and fine-scale structure of landscapes exert influence over spatial patterns of entire species, yet there may also be variation within species in how individuals respond. Sex and age-class segregation between habitat types and micro-habitats has been described for some songbirds (Marra and Holmes 2001; Latta and Faaborg 2002), with habitat quality thought to influence population demography. Differences in habitat selection between sexes may occur as a result of breeding requirements, such as habitat for nesting or positions that maximise the signal distribution of advertising males (Wiley 1991; Mckibbin and Bishop 2010). Identification of such intraspecific variation in habitat preferences can assist in defining the resource requirements and drivers of population dynamics of a species, therefore facilitating effective conservation management.

Study species

The superb lyrebird (*Menura novaehollandiae*) is an international icon of the Australian avifauna. It is a large, ground-foraging passerine. Males are adorned with an ornate tail for complex sexual displays that involve dance moves accompanied by lyrebird-specific vocalisations and highly accurate mimicry (Zann and Dunstan 2008; Dalziell *et al.* 2013) for which the species is well-known.

Whilst the superb lyrebird has been studied in a range of forest types, little attention has been given to the physiognomic features of landscapes and vegetation that support the species. Landscape

structure relating to topography and vegetation type are likely to influence the way in which lyrebirds use space on a broad scale. On a more local scale, variation in vegetation structure, litter depth and soil compaction may be more influential. Further, demographic units of the species may respond differently to these influences, depending on the ecological process being undertaken. For example, nest site selection is likely to be influenced by environmental cues separate from those that influence male territory selection (Kenyon 1972).

The female lyrebird constructs a large domed nest each year within a defendable territory (Reilly 1970; Lill 1980; Robinson and Frith 1981). The construction of the nest, brooding and care for the young is undertaken solely by the female. It is likely that local habitat elements influence the suitability of nest sites, but the importance of specific habitat elements has not been resolved.

Male superb lyrebirds defend large breeding territories that may overlap with the territories of several females (Kenyon 1972). During the winter breeding season, males vocalise frequently from within their territory, especially if intraspecific competition is great (Higgins 2001). Vocalisations are thought to be directed both at females as potential mates, and competitor males in the surrounding landscape (Robinson and Curtis 1996). The positioning of male territories is therefore likely to reflect a trade-off between resource availability within the landscape and maximizing the signal distribution of territorial song and courtship vocalisations (Robinson and Frith 1981). As such, the acoustic prominence of the positioning of territory may be important. Whilst multiple factors may influence male territory position, most observations on territory placement and spacing remain speculative and further clarification is required.

Lyrebirds have been recognised as ecosystem engineers due to the extensive disturbance to the forest floor caused by their foraging activity (Song *et al*. 2012). Lyrebirds use their powerful legs and large claws to rake through the litter layer and soil when searching for invertebrate prey, generally working in an upslope direction, while soil and litter is displaced downslope. At Beenak, Victoria, in mountain ash (*Eucalyptus regnans*) forest, Ashton and Bassett (1997) calculated that lyrebirds displaced approximately 200 t ha^{-1} $year^{-1}$ of soil an average of 70 cm downslope. The spatial pattern of lyrebird foraging may be driven by multiple landscape and local habitat elements, including physiognomic features of landscapes on a broad scale, such as topography and forest type, and on fine scales by the quality of food resources and physical access through structural vegetation to the litter layer.

For this study, we used long-term data on nest locations and the mapped positions of mature males (from a winter survey in 2013) to ascertain the drivers of spatial patterns in nest site location, male calling positions and foraging, at a landscape scale and a local scale. For effective conservation management, understanding the relationships between habitat and life history is critically important, as is the understanding of differing habitat requirements of separate demographic units within a single species. As such, the specific objectives of this project were to: 1) ascertain the influence of landscape

features on nest site selection, foraging activity and male calling position of the superb lyrebird; and 2) evaluate the influence of local habitat components on nest site selection and foraging intensity by the Superb Lyrebird.

Materials and Methods

Study area

Sherbrooke Forest is an 800 ha management unit of the Dandenong Ranges National Park, located on the urban fringe of Melbourne (Victoria, Australia, Fig. 1). Vegetation within the park is predominantly comprised of tall wet forest, dominated by a mountain ash (*Eucalyptus regnans*) canopy with scattered understorey and fern-rich ground layer (Fig. 1a). Cool temperate rainforest occurs in linear strips closely following the configuration of protected gullies and creek systems. This forest type is domiated by blackwood wattle (*Acacia melanoxylon*) and southern sassafras (*Atherosperma moschatum*), and harbours a diverse fern community, yet typically displays a more open ground layer than wet forest (Fig. 1b). Two sections of the park with a westerly aspect are classified as damp forest, characterised by a canopy dominated by messmate eucalypts (*Eucalyptus obliqua*) and ground layer rich in small shrubs, grasses and sedges (Fig. 1c).

The vegetation of the study area has been mapped in detail (Clifford 1982), and represents a mosaic of forest age-classes due to an extensive history of logging. The superb lyrebirds in Sherbrooke Forest have attracted widespread attention due to their accessibility (proximity to the city of Melbourne) and their “tameness” compared to lyrebirds in other forest areas (Lill 1979).

Landscape scale analysis

To investigate landscape influences on nest site selection by lyrebirds, data were collected over a 10 year period. All nests included in this study were successful to the stage of containing a chick of at least one month of age. Nests were located by active searches throughout Sherbrooke Forest. The effect of landscape variables on the position of known nest sites were compared with 200 randomly generated points throughout the forest.

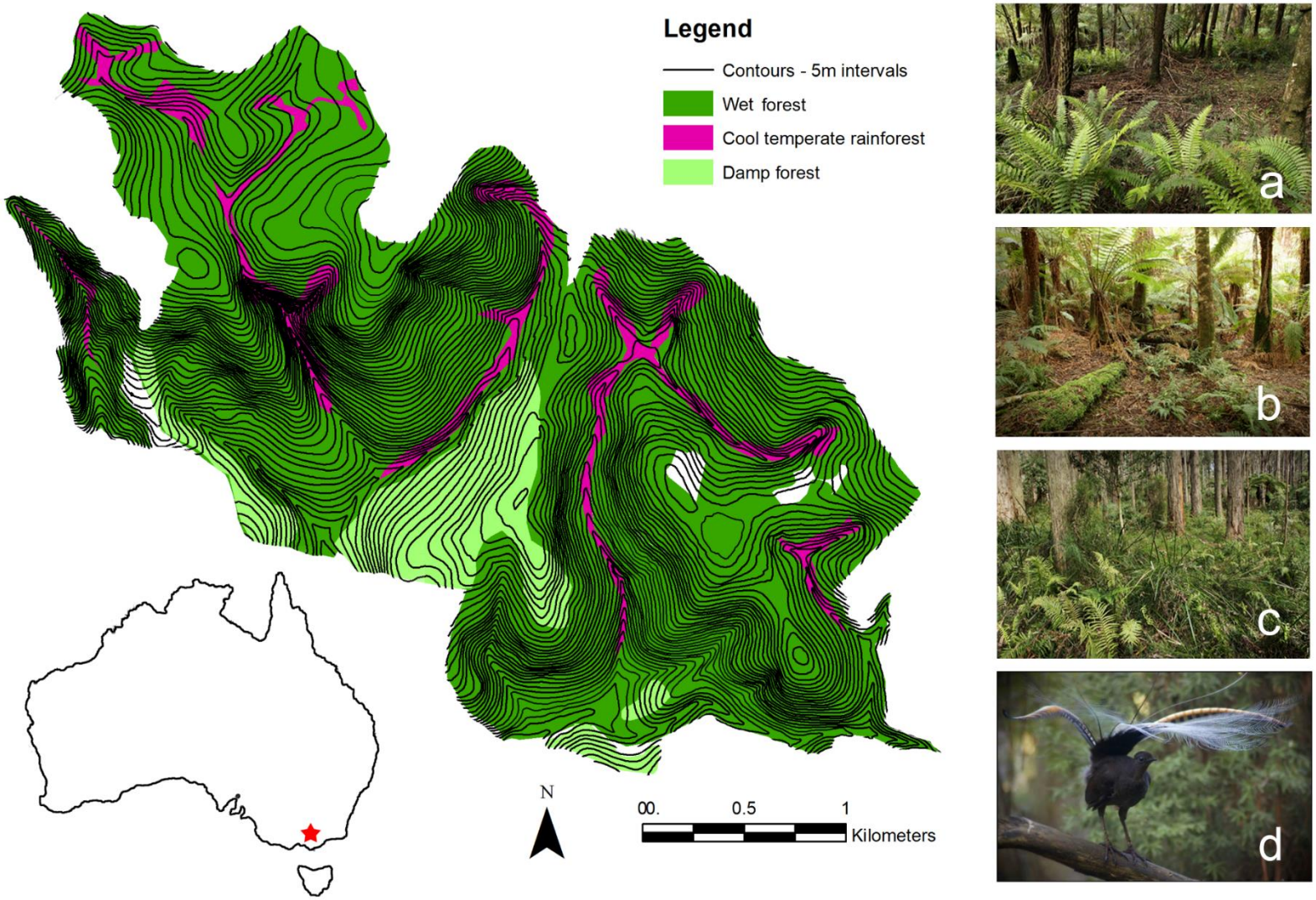

Figure 1. Topographical map of Sherbrooke Forest depicting exemplar images of wet forest (**a**), cool temperate rainforest (**b**) and damp forest (**c**). Also included is a male Superb Lyrebird in display from an elevated position (**d**). Elevation in Sherbrooke Forest ranges from 400 to 600 metres above sea level.

The coordinates of 201 known nest locations (recorded with a Global Position System (GPS)) from 2004 to 2013 were plotted over aerial imagery of the study site, along with 200 randomly located (computer generated) points. For each data point (nest site or random point), we calculated the values for a set of predictor variables relating to hypotheses that were *a priori* expected to influence lyrebird nest placement at the landscape scale (Table 1).

Response variables for the landscape-scale foraging analysis were the presence or absence of recent lyrebird foraging activity (disturbance of the litter layer) within a 5 by 5 m quadrat at 90 randomly generated sites throughout Sherbrooke Forest. Lyrebird foraging is distinct from that of other animals, and is easily recognised by their "terracette" formation (Ashton and Bassett 1997). Each site was visited during late winter to early spring, 2014. Hypotheses relating to landscape influences on foraging pattern were tested with logistic regression (assuming a binomial distribution). Sites analysed in relation to foraging pattern were a sub-set of those included in the landscape scale nest analysis.

Firstly, to categorise sites in relation to topography (categories of gully, lower slope or upper slope) each data point was assessed in relation to its distance directly uphill to the nearest ridge compared with the corresponding distance downhill to a creek to assess whether it was an upper or lower slope. We considered gully line to be within 10 m of a creek. The effect of topography was expected to reflect change in vegetation quality and thus habitat resources.

Secondly, for each data point we calculated the distance from the nearest creek. This variable represents a gradient in moisture content of soil, concomitant with food resources for lyrebirds (Robinson and Frith 1981).

Thirdly, we measured the distance from the nearest sealed road, as an indication of the influence of edge disturbance effects on nest location (Marini *et al.* 1995).

Finally, we determined the surrounding forest type. To map the forest types comprising Sherbrooke we adapted two vegetation maps, those from the Friends of Sherbrooke Forest (2000) and Clifford (1982), and used aerial imagery to validate and refine boundaries of forest types. As vegetation types are often structurally distinct, it was expected that forest type may represent the quality and availability of multiple resources (e.g., food, cover) important to nest location and foraging (Yost *et al.* 2008). For all mapping, ArcMap 10.1 (Environment Systems Research Institute 2011) was used.

Topographical position was excluded from analysis in favour of the distance from creek variable, as pairwise comparisons suggested high collinearity between the two predictors.

Local scale analysis

To examine the influence of local scale elements on nest site selection, field assessments were undertaken at 45 nest sites. This included all successful nests during the three breeding seasons prior to field work (years 2011-2013). Only these three years were included, as rainfall for these years was within the average range for the study area, and as such local habitat structure was assumed unlikely to have substantially changed between nest use and the time of sampling. Habitat assessments were conducted to measure a set of variables selected *a priori* as relating to hypotheses thought likely to influence nest placement at a local habitat scale (Table 1). As with the landscape analysis, we used logistic regression to compare known nest sites with 45 randomly generated sites throughout the forest.

Foraging pattern at the local habitat scale was assessed concurrently with habitat surveys at 45 random sites used for the local habitat scale nest analysis. The presence or absence of foraging within each quadrat was assessed, and each data point (site) was accompanied by measured habitat variables pertaining to a similar set of hypotheses as those addressed for lyrebird nest placement.

Lyrebirds have been noted to forage non-selectively for an indiscriminate range of invertebrates (Lill 1986), and so it was expected that the spatial pattern of foraging would be subject to fewer habitat influences than that of nest placement. As such, only variables relating to food resources (leaf litter depth) and vegetation structure (low strata, <30 cm; high strata, >2 m; and eucalypt canopy) were considered for analysis (Table 1). Pairwise comparisons of predictors did not show a high degree (i.e. <0.6) of collinearity.

For each data point (nest site or random site), a 5 by 5 m quadrat was set out, in the case of nest sites centred 0.5 m in front of the nest entrance. Nine sample points were marked in each quadrat in the configuration of a cross, and oriented in the cardinal directions. Firstly, at each sample point, leaf litter depth was measured, as leaf litter harbours much of the food resources on which lyrebirds rely (Lill 1996). Second, a visual assessment was made to estimate browsing of ground ferns by large browsers (such as feral Sambar Deer (*Rusa unicolor*) and the native Swamp Wallaby (*Wallabia bicolor*)). Browsing was categorised as either absent, less than 25% of fern fronds browsed, or greater than 25% of fern fronds browsed. This variable was included because loss of vegetative cover owing to large herbivores may have negative impacts on the suitability of nest sites (Olechnowski and Debinski 2008).

Third, the cover abundance of eucalypt canopy, tree ferns and understorey trees (>2m) were estimated visually for each quadrat. These habitat variables relating to vegetative structural complexity were theorised to provide benefits in lowering nest depredation rate, particularly from native birds. Vegetation structure less than 2m high was quantified by means of a vegetation structure pole at each of the nine sample points. Vegetation contacts (dead or alive) were recorded as either present or absent in 10 cm increments from ground level to 50 cm, then 50 cm increments to 2m in height, and pooled

across the nine sample points (thus achieving a possible structure reading of up to nine for any height increment). For analysis, only structure below 30 cm and above 150 cm was analysed to limit over-complicating models, especially when variables were likely to reflect similar habitat qualities. Structure measures from ground-level to 30 cm in height were pooled, as this measure of low structural complexity was considered most likely to affect the movement of lyrebirds, given the size of the species.

Male calling positions

To determine the factors that influence the location of male calling positions, data were collected during an annual survey to census the male population of lyrebirds in Sherbrooke Forest. To undertake the survey, a number of experienced volunteers were strategically distributed at designated points in Sherbrooke Forest, where participants listened for the dawn chorus of males calling from their overnight roost trees. With triangulation of call directions read from a compass, cross-referenced with start and finish call times, the location of territorial male lyrebirds can be deduced with reasonable accuracy. Immature males rarely call during the peak breeding season and the survey is conducted for only a short time past dawn to avoid repeat recordings of males that may change calling position. The resulting data on the locations of male calling positions for the winter of 2013 was the focus of analysis.

Table 1. Response and predictor variables included in models of the location of nests and foraging activity of the Superb Lyrebird at landscape and local scales.

Variable (hypothesis)	Variable type	Description	Nests	Foraging
Response				
Nest site/random site	Binary	Lyrebird nest site (presence) or random site (absence)	X	
Foraging	Binary	Foraging evidence (presence) or no foraging evidence (absence) at each random site		X
Landscape scale predictors				
Forest type	Categorical	Whether nest was located in wet forest, damp forest or rainforest	X	X
Distance from creek	Continuous	Distance that a nest was located from the nearest main road	X	X
Distance from road	Continuous	Distance that a male is located from the nearest main road	X	X
Local scale predictors				
Litter depth	Continuous	Mean litter depth from surface to mineral earth	X	X
Low strata complexity	Continuous	Structure score of vegetation complexity detected below 30 cm	X	X
Mid strata complexity	Continuous	Structure score of vegetation complexity detected from 151-200 cm	X	
High strata complexity	Continuous	Percentage cover of understorey trees (>2 m) and tree ferns combined	X	X
Canopy	Continuous	Percentage cover of eucalypt canopy	X	X
Browsing activity	Categorical	Browsing estimate (none, low or high) for ground fern	X	

Landscape scale selection of calling positions

To determine landscape influences on the location of male calling positions, the same predictor variables determined for the landscape analysis of nest sites were used. Attributes of these calling positions were compared with those of 200 random sites throughout the forest. As the male lyrebirds detected during the survey are calling from a roost tree within a larger territory and were detected by triangulation, not with a GPS, it was deemed appropriate to analyse these data at a landscape scale (i.e. not attempt a local habitat scale analysis).

A modelling approach, as described previously, was initially undertaken, but due to linear separation of the response variables (male calling positions versus random sites) by multiple predictor variables, the model failed to reach convergence, resulting in unreliable parameter and error estimates (Anderson and Burnham 2002). As all males were calling exclusively from within the wet forest type, a univariate approach was engaged to scrutinize the effect of topography on male calling positions. The proportional occurrence of male calling positions in the three topographical categories was compared with that of random sites by using Pearson's Chi square *test of independence*.

Modelling approach

We employed a hypothesis-testing approach with logistic regression to generate predictive models for lyrebird nests and foraging on a landscape and local habitat scale. We used Generalised Linear Models (GLM) assuming a binomial distribution (comparing nest sites to random sites) and logit link function to generate landscape and local habitat models.

Correlation matrices (Spearman's rank correlation) were produced to assess pairwise correlation among predictor variables. If predictor variables displayed a high degree of collinearity (Spearman's rank correlation >0.6), one of the pair was excluded from analysis, as correlated predictors may produce unreliable model parameter estimates (Quinn and Keough 2002; Symonds and Moussalli 2011).

Examination of pairwise collinearity between landscape predictors resulted in the exclusion of topographic position from analysis in favour of the distance from creek variable, as the two variables showed a high degree of collinearity. None of the predictors displayed pairwise collinearity >0.6 for any of the local habitat scale variables.

For both landscape and local habitat models, Akaike's Information Criterion (adjusted for small sample size) (AIC_c) was computed (Symonds and Moussalli 2011) to assess the relative suitability of each model in explaining the influence of landscape and habitat elements on nest site selection. Akaike weights (w_i) are used to gauge the amount of support for each model, given the sample data (Burnham and Anderson 2002). The difference between AIC_c values for each model compared with

the best-fitting model (Δ_i) allows for rapid assessment of candidate models, and only models for which Δ_i<2 should be considered to have substantial support (Burnham and Anderson 2002).

In order to rank and ascertain the relative importance of predictor variables, summed Akaike weights (Σw_i) were calculated for each predictor. This provides an indication of the likelihood that a predictor is included in the best model; thus, variables with the highest Σw_i may be considered to have the greatest influence over the response variable (Symonds and Moussalli 2011).

When there was no clearly best model (w_i >0.9) for either landscape or local habitat analyses, model averaging was employed to produce parameter and error estimates for predictors from weighted averages over all models. Multi-model inference was conducted with the MuMIn package (Barton 2011) in the R statistical program version 3.1.0 (R Core Team 2012).

Results

Nest site selection

Landscape scale

At the landscape scale, two models were generated that gained substantial support (Δ_i AIC_c <2). The most parsimonious model (lowest AICc value) included the variables of distance from creek, distance from road and forest type (Table 2). The second best model included only distance from road and forest type. Model fit (D^2) was low for both models, with a deviance explained of 10%. The absence of a clearly-best model (all models w_i <0.9) prompted a model-averaging approach to identify the relative importance of each predictor variable.

Model averaging results showed that forest type had the greatest importance in its influence on nest location at a landscape scale (Σw_i = 1.00) (Fig. 2a), with a positive effect of wet forest and rainforest (Fig. 3a) on nest placement (illustrated by a positive coefficient with 95% confidence intervals that did not overlap zero), using damp forest as the reference category (Table 3). Distance from creek also had high importance (Σw_i = 0.99), and displayed a negative coefficient, also with 95% confidence intervals that did not overlap zero (Table 3), indicating decreasing likelihood of nests with increasing distance from creek (Fig. 3b). The distance from road variable had low importance in explaining the placement of lyrebird nests at a landscape scale (Σw_i = 0.56) and for this variable the 95% confidence intervals of its coefficient did overlap zero (Table 3).

Local habitat scale

Six models gained substantial support (Δ_i AIC_c <2), all of which included the predictor variables of litter, high strata and mid strata complexity. The most parsimonious model included only the three aforementioned predictors (Table 2), although low strata complexity, herbivore browsing and eucalypt cover were included in other well-supported models. Model fit (D^2) was higher for these

local habitat scale models than for the landscape models, with almost half of the variance explained by the predictors included in the most suitable models. However, model averaging was again performed, as all models displayed low Akaike weights (w_i <0.9).

The importance of litter depth in explaining nest site location in habitat models was revealed as being well supported by model averaging, with a summed Akaike weight (Σw_i) of 1.00. Mid-strata and high-strata complexity were also important, with Σw_i of 0.76 and 0.97 respectively (Fig. 2b). The direction of effect was positive for these three predictors, and the 95% confidence interval of their coefficients did not overlap zero (Table 3). That is, nests are more likely to be located at sites with greater litter depth (Fig. 3c), and greater complexity in the mid-strata (1.5-2 m) (Fig. 3d) and high-strata (understorey >2 m) (Fig. 3e). While low strata complexity, herbivore browsing and eucalypt cover were included in at least one model receiving substantial support, the 95% confidence intervals of their coefficients overlapped zero (Table 3) and as such are not considered to be important.

Table 2. Results from landscape and local habitat scale models of the location of nest sites and foraging of the Superb Lyrebird (*Menura novaehollandiae*) in Sherbrooke Forest, Victoria. All models that gained substantial support (Δ_i AIC_c <2) are included in this table. Variables are described in Table 2. Also listed are the degrees of freedom (df), logLiklihood (logLik), AIC values (AIC_c), Delta AIC_c (Δ_i), Akaike weight (w_i) and deviance explained (D^2) for each model.

Subject	Candidate model	df	logLik	AIC_c	Δ_i	w_i	D^2
Nests - landscape	Intercept + Distance from creek + Distance from road + Forest type	5	-249.047	508.25	0.00	0.553	0.10
	Intercept + Distance from creek + Forest type	4	-250.309	508.72	0.47	0.437	0.10
Nests - local	Intercept + Litter + High strata complexity + Mid strata complexity	4	-34.389	77.3	0.00	0.159	0.44
	Intercept + Litter + High strata complexity + Mid strata complexity + Low strata complexity	5	-33.354	77.4	0.18	0.145	0.45
	Intercept + Litter + High strata complexity + Mid strata complexity + Eucalypt cover	5	-33.819	78.4	1.11	0.091	0.45
	Intercept + Litter + High strata complexity + Mid strata complexity + Low strata complexity + Eucalypt cover	6	-32.688	78.4	1.15	0.089	0.46
	Intercept + Litter + High strata complexity + Mid strata complexity + Low strata complexity + Herbivore browsing	7	-31.663	78.7	1.47	0.076	0.48
	Intercept + Litter + High strata complexity + Mid strata complexity + Herbivore browsing	6	-32.871	78.8	1.52	0.074	0.46
Foraging - landscape	Intercept + Distance from creek + EVC + Distance to road	5	-50.198	111.1	0.00	0.700	0.19
Foraging - local	Intercept + Low strata complexity	2	-22.506	49.3	0.00	0.383	0.28
	Intercept + Low strata complexity + High strata complexity	3	-22.197	51.0	1.68	0.165	0.29

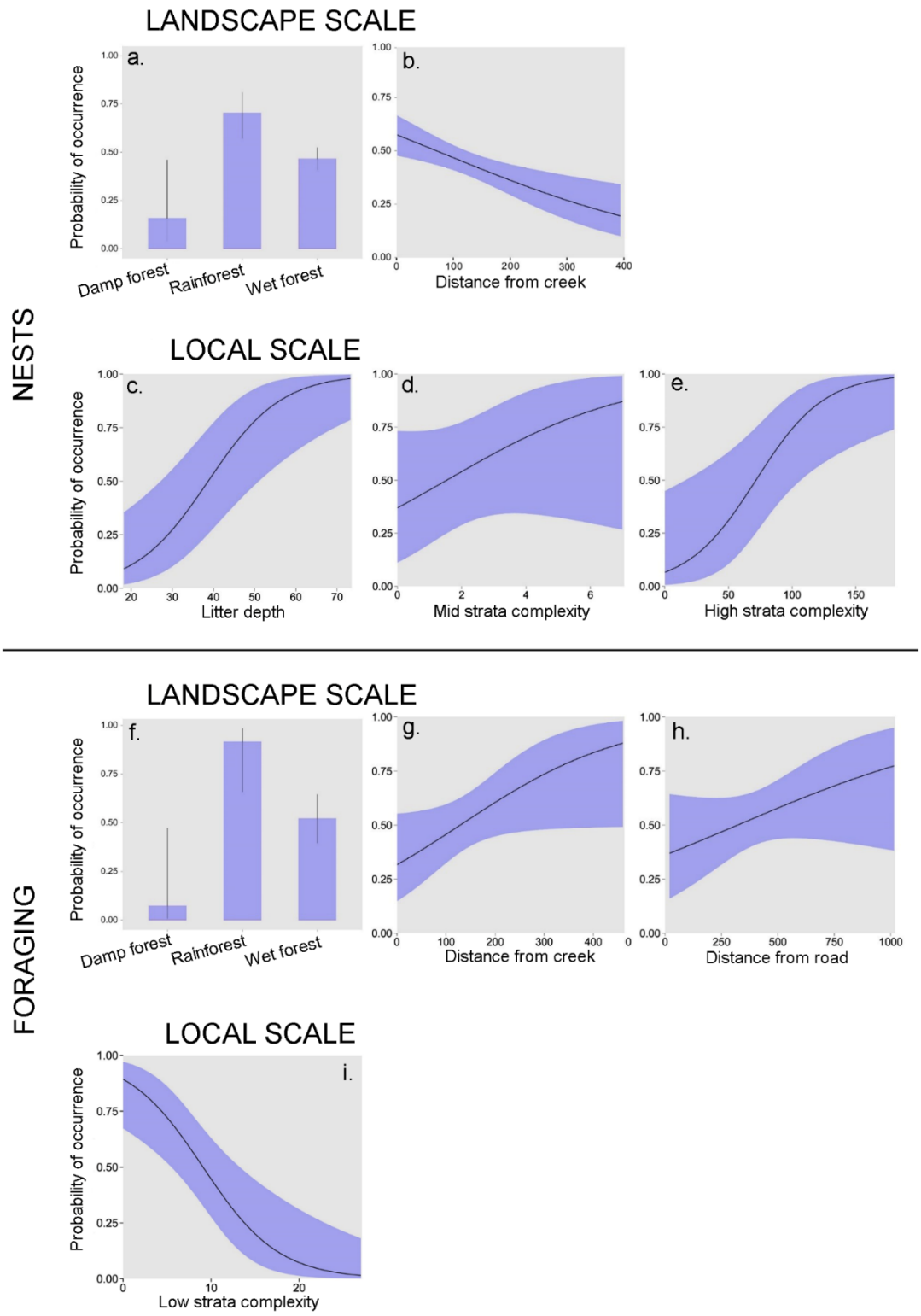

Figure 3. Modelled relationships between the probability of occurrence of either a lyrebird nest (**a-e**) or foraging (**f-i**) and corresponding landscape scale and local scale predictors.

Male calling positions

No male lyrebirds detected calling in 2013 (n=56 individuals) were located in damp forest or rainforest, with all males calling exclusively from within wet forest. The topography hypothesis was therefore of most interest in explaining the spatial pattern of male calling positions. Male lyrebirds were not detected calling from gully lines and were found only on lower and upper slopes. There was no statistically significant difference between topographical positions of male calling positions and random sites ($\chi^2 = 5.05$, d.f. = 2, p = 0.08), although there was a strong trend for male lyrebirds to call from positions on upper slopes rather than on lower slopes or gully lines (Fig. 4).

Foraging patterns

Landscape scale

A single model gained substantial support for the foraging analysis at the landscape scale (Δ_i AIC_c <2) (Table 2). The model included all three predictor variables of forest type, distance from creek and distance from road. Model fit (D^2) of the supported model was moderate, explaining 19% of the variation in foraging activity pattern at the landscape scale (Table 3).

Model averaging showed that each of the three hypotheses included in the landscape model were of similar importance in explaining foraging pattern at this scale. The summed Akaike weights (Σw_i) were high for all predictors, with forest type ranking highest ($\Sigma w_i = 0.99$), followed by distance from creek ($\Sigma w_i = 0.92$) and distance from road ($\Sigma w_i = 0.78$) (Fig. 2c). Both distance variables displayed a positive association with foraging pattern with 95% confidence intervals that did not overlap zero, although the effect size was relatively small (Table 3). Rainforest and wet forest (using damp forest as the reference category) displayed relatively large effect sizes, and again displayed 95% confidence intervals that did not overlap zero (Table 3). Thus, foraging activity was more likely to be detected in rainforest or wet forest (Fig. 3f), and with increasing distance from a creek line (Fig. 3g) or road (Fig. 3h)

T**able 3.** Model averaged results for models of nest locations and foraging activity of the Superb Lyrebird (*Menura novaehollandiae*) in Sherbrooke Forest, including coefficient, standard error and z statistic. The most influential predictors (z statistic >1.96) for each response variable are shown in bold.

Response	Predictor	Coefficient	Standard error	z statistic
Nest location				
Landscape scale	Intercept	-1.672	0.773	2.158
	Distance from creek	**-0.437**	**0.131**	**3.333**
	Distance from road	0.174	0.110	1.576
	^Forest type - Rainforest	**2.546**	**0.839**	**3.026**
	^Forest type - Wet forest	**1.541**	**0.777**	**1.979**
Habitat scale	Intercept	-7.309	2.047	3.527
	Litter	**0.113**	**0.034**	**2.894**
	Low strata complexity	-0.103	0.069	1.471
	Mid strata complexity	**0.460**	**0.227**	**2.003**
	High strata complexity	**0.038**	**0.013**	**2.894**
	Eucalypt cover	-0.013	0.013	1.036
	+Browse level - None	0.723	0.743	0.960
	+Browse level - High	-1.029	0.892	1.138
Foraging activity				
Landscape scale	Intercept	-4.050	1.458	2.743
	Distance from creek	**0.007**	**0.003**	**2.438**
	Distance from road	**0.002**	**0.001**	**2.061**
	^Forest type - Rainforest	**4.965**	**1.589**	**3.085**
	^Forest type - Wet forest	**2.644**	**1.260**	**2.070**
Habitat scale	Intercept	2.126	1.259	1.648
	Litter	-0.021	0.039	0.516
	Low strata complexity	**-0.227**	**0.074**	**2.986**
	High strata complexity	0.010	0.013	0.787
	Eucalypt cover	-0.005	0.012	0.388

^ The forest type variable is tested in the model using “Damp forest” as a reference category.

+ The browse level variable is tested in the model using “Low browsing” as a reference category.

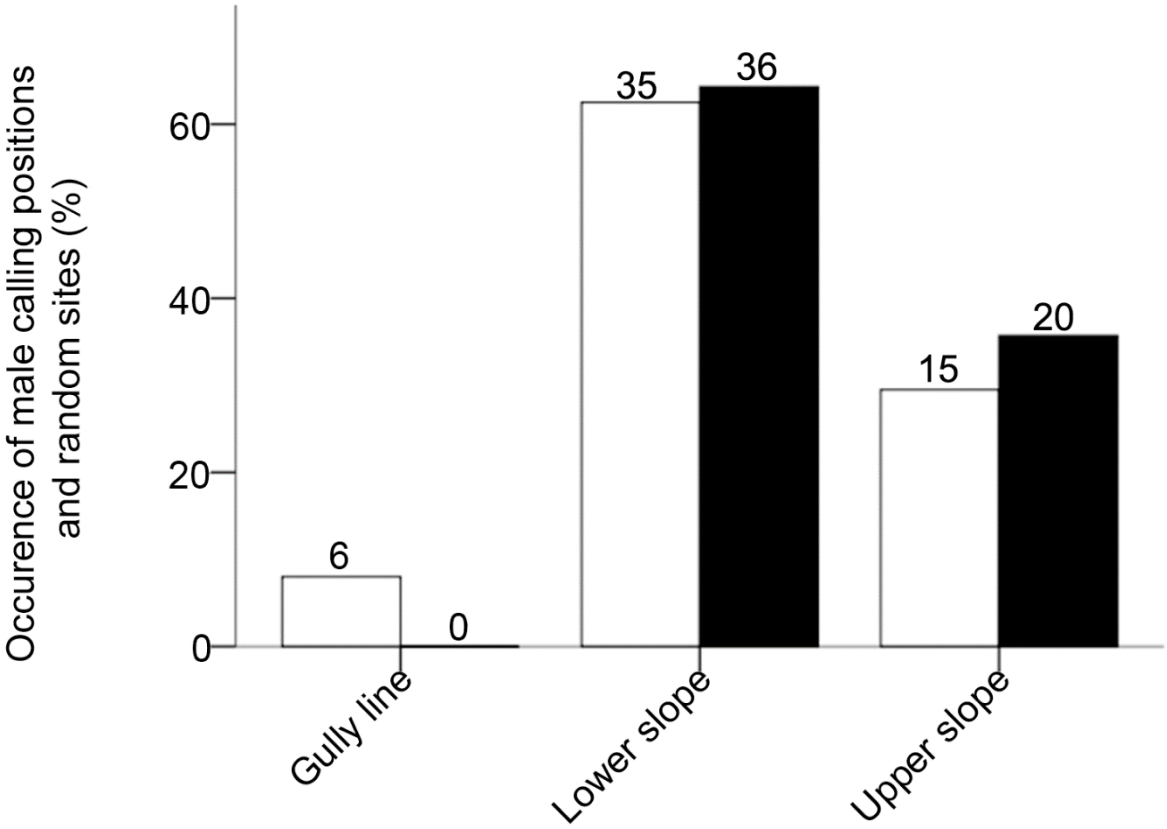

Figure 4. Topographic situation of calling positions (black bars) of male Superb Lyrebirds compared with that of random sites (white bars), in Sherbrooke Forest.

Local habitat scale

Two models gained substantial support at the local habitat scale (Δ_i AIC_c <2). The most parsimonious model included only low strata complexity, and the second-best model included both low and high strata complexity. The model fit (D^2) was similar for both candidate models at 28% and 29% respectively (Table 2).

Model averaging revealed that low strata complexity had the greatest influence on foraging activity at the local habitat scale (Σw_i = 0.99) (Fig. 2d), with a strong negative association between the probability of foraging and vegetation complexity in low strata (<30 cm) (Table 3). Other predictors had lesser support in explaining foraging activity. Lyrebirds were therefore more likely to forage in local habitats with sparse low cover (Fig. 3i).

Discussion

Nest sites

For all bird species, the decision of where to nest is vital in determining reproductive success and thus has implications for conservation management. Birds make choices on where they construct their nests at varying scales (Saab 1999). Our study demonstrates that at a broad scale, lyrebird nest sites are influenced by landscape drivers such as topography and vegetation type, whilst at the local habitat scale an array of physiognomic traits influence the suitability of habitat for nest sites.

At a landscape scale, lyrebird nest sites were associated with creek systems and gullies. Several drivers of this pattern may be inferred from this study; Firstly, an ultimate cause may be attributable to soil moisture content and the level of soil and leaf litter drying experienced on the forest floor. This drying effect would be expected to increase with distance from creeks, affecting invertebrate and particularly earthworm abundance (Presley *et al.* 1996). Earthworms are a primary food source for foraging lyrebirds (Robinson and Frith 1981; Lill 1996) and consequently variation in their relative abundance within the landscape may contribute to the spatial pattern of nests on a broad scale.

At the local habitat scale nest sites were strongly associated with deeper leaf litter. The underlying hypothesis pertaining to litter depth was that food resources in the litter would be a key aspect driving the spatial pattern of nest placement. A similar effect has been described for the ovenbird (*Seiurus aurocapillus*), for which nest sites were positioned in areas with deeper leaf litter than available at random, yielding much greater invertebrate biomass as a consequence (Burke and Nol 1998). For lyrebirds, the nesting process is prolonged with a significant energy input required from the female while rearing the nestling (Lill 1986): site selection in relation to food availability is likely to be critically important in determining the outcome of each nesting event.

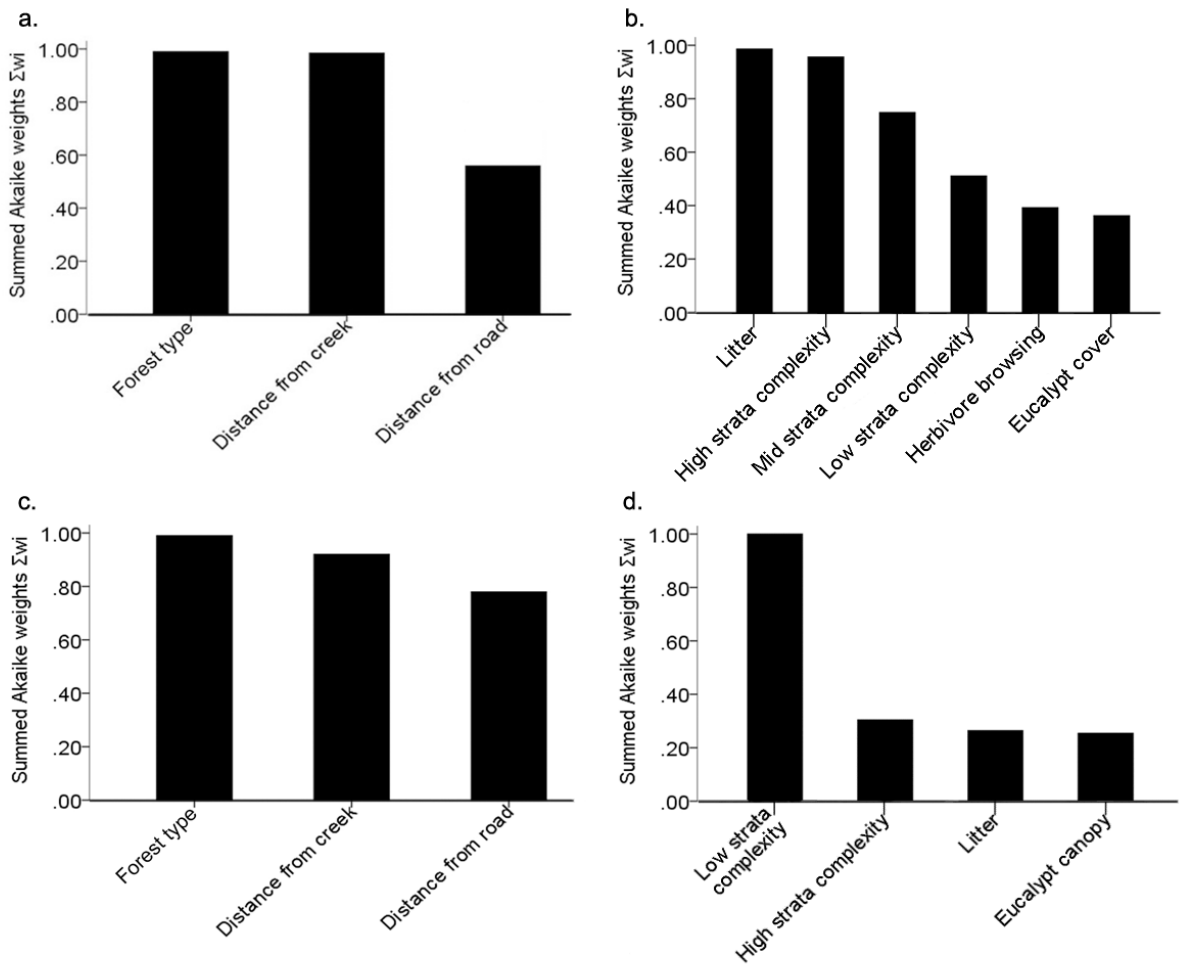

Figure 2. Summed Akaike weights for predictor variables from model averaging for Superb Lyrebird nest locations at the landscape scale (**a**) and local scale (**b**) and foraging locations at the landscape scale (**c**) and local scale (**d**) in Sherbrooke Forest.

Secondly, vegetation structural complexity would also be expected to change with distance from creeks as soil moisture influences vegetative growth. Greater structural complexity associated with creek side vegetation may confer protection and camouflage against nest predators such as corvid birds. Lyrebird nests are highly vulnerable to native predatory birds (Lill 1980) and, by selecting sites with greater vegetative concealment, nest success would be expected to be increased (Møller 1988; Rangen *et al.* 1999; Colombelli-Négrel and Kleindorfer 2009). This hypothesis is supported by the local habitat scale model, which revealed a strong positive influence of structural complexity of understorey vegetation on nest site location. Whilst this study did not specifically address the role of predators in nest site selection, our results give impetus to further investigation into predator influences on nest placement in lyrebirds. The association with creeks serves to guide management priorities in the conservation of riparian zones for breeding lyrebirds, and lends further support to the findings of other avifaunal habitat studies highlighting the importance of riparian zones in south-eastern Australia (Palmer and Bennett 2006).

Forest type also exerted substantial influence over nest placement on a landscape scale. Nesting lyrebirds avoided damp forest in preference for wet forest and particularly rainforest. Damp forest is characterised by a dense ground-storey rich in sedges, grasses and small shrubs, with a poorly developed (often absent) understorey tree layer. For lyrebirds this may translate to inhibited access to food resources, as well as poor vegetative camouflage for their nests resulting from the depauperate understorey structure. This is particularly relevant to aerial predators such as hawks in the *Accipiter* genus, members of which feature in the mimetic vocalisations utilised by female lyrebirds in nest defence (Dalziell. and Welbergen 2016). Conversely, cool temperate rainforest characteristically displays a well-developed understorey layer of tree ferns and long-lived tree species, effectively inhibiting light transmission for ground-layer plant growth and thus facilitating better access to the litter layer. Cool temperate rainforest is therefore likely to afford both greater access to food resources and high-stratum structural complexity aiding in nest concealment from aerial predators.

However, Sherbrooke Forest presents difficulties in assessing the relative influence of forest type on nest locations, as all of the rainforest in Sherbrooke occurs in protected gullies that closely follow the creek systems. Investigation into the distribution of lyrebird nests in locations where rainforest occurs away from creeks would help differentiate the relative importance of rainforest vs creek-side location as breeding habitat for lyrebirds.

The effects of herbivore browsing, low strata complexity and eucalypt cover were less pronounced on nest location. However, all three predictors featured in at least one of the well-supported habitat models. In Sherbrooke Forest, a population of sambar deer (*Rusa unicolor*) has increased dramatically over the past decade (pers. observ.), with the eastern half of the study area heavily affected by the formation of wallows, extensive erosion on creek banks and some die-back of middle-storey vegetation such as southern sassafras (*Atherosperma moschatum*), austral mulberry (*Hedycarya angustifolia*) and rough treefern (*Cyathea australis*), due to direct browsing or de-barking from use as antler rub-trees. Whilst these effects are relatively localised, continued growth in the deer population is likely to cause extensive erosion damage to creek systems (Forsyth *et al.* 2009), and die-back of understorey in rainforest sections. The feral deer population may be an increasing threat to the breeding ecology of the lyrebird population.

Foraging

The locations at which birds forage are strongly influenced by habitat quality in many species (Recher *et al.* 1985), and understanding the scale at which drivers of such spatial patterns operate is critical to predicting how a species interacts with broad and fine-scale habitat heterogeniety. Our study found that at the landscape scale, forest type, distance from creek and distance from road were all important influences on foraging pattern, whilst at a local habitat scale only low strata vegetation complexity was important.

Locations in the centre of the study area were more likely to have foraging activity than those nearer roads. As lyrebirds are a ground-dwelling species possessing only moderate flight capabilities, collisions with vehicles are a direct threat to individuals (Rose 2001). Roads may also confer detrimental edge effects associated with the peri-urban environment, including disturbance from domestic pets such as cats (*Felis cattus*) and dogs (*Canis lupis familiaris*). Additionally, foraging lyrebirds nearer roads may experience increased interactions with animals such as the red fox (*Vulpes vulpes*), a feral species known to prey on lyrebirds (Lill 1980; Smith 1988) but also associate with urbanisation (Marks and Bloomfield 1999) and habitat edges (May and Norton 1996). So whilst habitat at the patch scale may be appropriate for foraging lyrebirds (i.e. low structural vegetation complexity near ground level), at the landscape scale features of the forest and surrounding matrix may render some areas unsuitable.

Distance from creek was positively associated with foraging, during this survey in winter and spring. It is likely that this pattern varies temporally, depending on moisture levels on the forest floor. Ashton and Bassett (1997) postulated that lyrebirds may undertake foraging excursions into sub-optimal habitats including drier ridgelines in wetter months, whilst contracting their foraging activity to lower slopes and rainforest gullies in summer. By foraging in areas more distant from creeks, lyrebirds can capitalise on resources that are less accessible in summer, due to the seasonal vertical migration in the soil horizon of invertebrates, particularly earthworms (Reddy and Pasha 1993; Jiménez and Decaëns 2004).

This hypothesis suggests that resources near creeks and gullies may be exhausted over the summer months. It also raises the question of whether invertebrate populations in upper slopes remain *in situ* over summer, but largely inaccessible to lyrebirds until sufficient moisture allows for invertebrates to become more abundant nearer the surface. Further investigation of temporal patterns of resource use may help to define the way in which lyrebirds use resources in the heterogenous forest landscape with changing environmental conditions.

Foraging occurred most frequently in rainforest, followed by wet forest, but had a markedly lower probability of occurrence in damp forest. Cool temperate rainforest in Sherbrooke is relatively rare. These sections of the forest, although small, are likely to be important areas for foraging, especially in summer months when slopes become drier and near-surface invertebrate abundance is low (Ashton and Bassett 1997). Insight gained from the local habitat scale model helps to explain this preference of forest type. Vegetation structure affects the way in which many passerines forage (Maurer and Whitmore 1981) and may be attributable to the type of food resources harboured by the vegetation (Cody 1981; Recher *et al.* 1985) and the accessibility of those resources given its structural configuration. In this study, vegetation structure between ground level and 30 cm was found to influence foraging. The rainforest floor characteristically displays an open low stratum (see Fig. 1b)

with ample access to the litter layer. Conversely, damp forest and its complex low strata would make foraging in this habitat energetically expensive. Lyrebirds appear to be somewhat indiscriminate when choosing where to forage within habitats, depending on being able to do so in an energetically economical manner.

Male calling position

The location of a calling male is presumed to indicate the core area of that individual's territory, as suggested by past studies (Kenyon 1972). The number of calling males in Sherbrooke Forest, as detected by annual dawn surveys, has increased greatly over the past decade, nearly doubling in that period (Sherbrooke Lyrebird Survey Group, unpublished data). Consequently, the study landscape may be reaching a level of saturation, whereby optimal habitat is occupied and immature birds are forced to establish territories in less suitable positions, thus making spatial patterns difficult to assess. The complete absence of males calling from within gully lines suggests that they strongly avoid these positions in the landscape. Further, males tended to call from positions on upper slopes more than expected, despite most of the study site being comprised of lower slopes. This pattern, although not statistically significant, is consistent with the hypothesis that male lyrebirds call from higher positions in the landscape to maximise signal distribution (Kenyon 1972; Robinson and Frith 1981).

The spatial segregation of demographic units within populations may serve to ensure resources are available to maximum advantage for that population (González-Solís *et al.* 2007). Whether any relationship exists between nest locations and male calling positions is yet to be established, but this study suggests that over the winter breeding season some spatial segregation occurs between the sexes, primarily caused by the distribution of key resources (such as structural vegetation or acoustic prominence of a territory) in the forest landscape. We have shown that whilst female lyrebirds favour constructing nests in rainforest gullies, males appear to avoid this habitat in preference for the more open wet forest. Cool temperate rainforest at the study site is likely to be unsuitable for males for two reasons. Firstly, the rainforest occurs only in riparian zones and these areas, in deep gullies, tend to be parts of the landscape that have poor acoustic transmission properties and thus are unsuitable for males to call from. Secondly, rainforest structure limits light transmission, thus hindering the effect of display on courtship mounds (Robinson and Frith 1981). Further comparative work in areas with greater expanses of rainforest away from linear creek lines would help to define the ultimate drivers of gender-specific differences in the spatial pattern of territories.

Conclusion

The spatial distribution of the superb lyrebird is influenced by both broad landscape elements and finer habitat elements, and as such conservation planning will be most effective when these factors are taken into account. Considering this, we have specifically endeavoured to investigate influences

on spatial pattern at two scales, whilst recognizing that some of the variation seen at a habitat scale is likely to be influenced by landscape scale predictors, and *vice versa*.

We examined factors that influence the spatial pattern of the Superb Lyrebird at multiple scales. Landscape-scale influences on nest placement, male calling positions and foraging pattern were assessed, and each was shown to respond to distinct variables and in different ways at the landscape scale. On a local habitat scale, nest site location was strongly influenced by a number of parameters that showed little or no influence over foraging activity, reflecting the importance of fine-scale variability in habitats to the breeding ecology of this species. Whilst foraging was affected by a range of landscape-scale influences, very little influenced foraging at a local habitat scale.

By defining the habitat preferences of nesters and calling males, this study highlights the importance of spatial heterogeneity at both the landscape and local habitat scale, and has revealed the consequent partitioning of forest resources by demographic units within the lyrebird population. The complex relationships between physiognomic landscape features and the resources available within them determines how lyrebirds utilise their environment through multiple facets of life history. At the landscape scale, forest type, topography and edge disturbance effects are key drivers of spatial pattern, while at the local scale a range of factors reflecting habitat quality, such as litter depth and vegetation structure, become most important. This multi-scale approach to understanding the resource use of a species provides a foundation for guiding management actions to conserve species such as the superb lyrebird, by defining landscape and habitat implications on foraging and breeding ecology.

Acknowledgments

Thanks go to Asha Billing, Sally Bewsher and Don Petty for their assistance in the field. We would also like to acknowledge the members of the Sherbrooke Lyrebird Survey Group, particularly long-term members Norm Carter and Jan Incoll, for their support of this research. We extend thanks to Dr. Desley Whisson for assistance with GIS techniques and Parks Victoria for permitting the study to be undertaken in the Dandenong Ranges National Park.

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Appendix 1. 3 Maisey, A.C.,[1,2] Incoll, J.M.[2]. and White, S.M.[,2], 2019. Inflated clutch size in the Superb Lyrebird (*Menura novaehollandiae*). *Corella*, *41*, pp.63-65.

[1]School of Environmental Sciences, Department of Ecology, Environment and Evolution, La Trobe University, Bundoora Campus, Vic. 3086 Australia

[2]Sherbrooke Lyrebird Survey Group, 30 Moores Road, Monbulk, Vic. 3793, Australia.

Published by: *Corella*

Date accepted: 2 Jun, 2017

Manuscript word count: 1786

Inflated clutch size in the Superb Lyrebird (*Menura novaehollandiae*)

The factors that determine clutch size in birds remains a widely debated topic in ornithology (Hořák, Tószögyová *et al.* 2015; Ricklefs 1980). Many factors that potentially influence clutch size have been documented, including those that are intrinsic to a species (e.g., body size, mode of development (Zammuto 1986) and those of extrinsic origin (e.g., food resources, predation risk (Jetz *et al.* 2008). Pioneering work by Lack (1947) linked clutch size with resource availability, proposing that the optimal number of eggs in a clutch represents, on average, the greatest number of offspring that the parents are able to raise in a given environment. This paradigm provides an explanation for the positive relationship between clutch size and latitude (Cody 1966), because longer daylight hours in summer months in temperate latitudes allow for increased duration of daily foraging and thus greater resource provision to offspring.

An alternative hypothesis suggests that perceived vulnerability to nest predation may influence clutch size (Slagsvold 1982; Martin 2014). In environments with a high perceived risk of predation, nesting birds may undertake less frequent visits to nests, resulting in restricted provision of resources to nestlings, irrespective of the resources available within the nesters home range (Eggers *et al.* 2005).

Such extrinsic cues undoubtedly interact with intrinsic influences on clutch size, making generalisations problematic. In precocial species, clutch size tends to be larger, consistent with a small parental investment after laying; whilst in altricial species, clutch size tends to be smaller, associated with a higher parental investment after laying (Jetz, *et al.* 2008). The type of nest has also been related to clutch size; cavity nesters generally lay larger clutches compared with open nesters, and birds that build domed nests lay an intermediate number of eggs (Jetz *et al.* 2008). Even diet has been linked with clutch size, with granivores and omnivores producing larger clutch sizes than other guilds (Jetz *et al.* 2008).

Whilst many bird species exhibit variation in clutch size as an adaptive response to environmental cues, such variation can sometimes become maladaptive. The Lesser Gray Shrike (*Lanius minor*) in Slovakia has been documented to produce inflated clutches during years of high cockchafer (*Melolontha melolontha,* Coleoptera) abundance, yet fledging success was no greater than in years when cockchafers were scarce, purportedly due to the inability of brooders to successfully incubate large clutches (Hoi *et al.* 2004).

The Superb Lyrebird *Menura novaehollandiae* is a polygamous passerine that inhabits wet forests of the Great Dividing Range in south-eastern Australia. It is well known for its elaborate courtship

displays in which loud mimicry and species-specific vocalisations are accompanied by rhythmic dance-like motions (Dalziell *et al.* 2013). Male lyrebirds have no involvement with nesting, brooding or feeding of young (Lill 1986). The female constructs a large domed nest in autumn or early winter in preparation for laying in mid-June or early July (Maisey *et al.* 2016). Relative to the body mass of a female lyrebird, the egg mass (mean fresh weight = 62 g; (Lill 1987) is close to twice that expected for a passerine (Rahn *et al.* 1985), and the incubation period (43-53 days; (Lill 1987) is three times greater than would be expected for a passerine species of comparable size (Rahn *et al.* 1985). Consequently, lyrebirds follow a slow life-history strategy, with uniparental care of young and an annual clutch size of one (Lill 1987).

The Sherbrooke Lyrebird Survey Group (SLSG), a volunteer organisation, has been monitoring the movements, breeding and behaviour of lyrebirds in Sherbrooke Forest (37°53' S, 145°21' E), an 800 ha section of the Dandenong Ranges National Park, since 1958. The vegetation of Sherbrooke Forest is primarily wet forest dominated by Mountain Ash (*Eucalyptus regnans*) with a diverse understorey of small trees and shrubs. First-order streams are flanked by narrow sections of cool temperate rainforest, where Southern Sassafras (*Atherosperma moschatum*) and Blackwood (*Acacia melanoxylon*) are dominant canopy trees.

Members of the SLSG have recorded single egg clutches as the norm for the Superb Lyrebird, and occasionally two eggs present in a single nest. Overall, of 495 clutches recorded from 2002 to 2016, only five contained two eggs (representing 0.8% of all clutches). In two-egg nests, close monitoring (nest visited pre-dawn or post-dusk) suggested incubation either was not initiated or was not completed to hatching (SLSG, unpub. data). In contrast, in a multi-year study undertaken throughout the southern fall of Victoria's Central Highlands (including Sherbrooke Forest), Lill (1986) reported twin-egg clutches in 3 out of 43 nests (7%), none of which progressed to hatching.

Here, we report the first record of a three-egg clutch in the Superb Lyrebird. On 20 August 2016, we discovered a lyrebird nest containing three eggs, located approximately 20 m north-west of a tributary to Sherbrooke Creek, south of Wattle Track in Sherbrooke Forest (37°52'56" S, 145°21'10" E). The eggs and the feathers lining the nest were saturated with condensation, indicating prolonged exposure and that the nest had been abandoned some time before its discovery. One of the eggs had a small pin-sized hole penetrating the shell, causing the contents to become rancid. The eggs were of similar size, measuring (length x maximum breadth) 58.3 x 42.6mm, 60.9 x 40.2mm and 59.2 x 38.0mm.

We think it likely that the three eggs in this nest were laid by the same individual. Female lyrebirds vigorously defend their territory, and have been implicated in the destruction of the nests of neighbouring lyrebirds (Reilly 1970). Further, the colour of lyrebird eggs is highly variable between individuals (Fig.1). The three eggs in this nest were similar in colour and pattern (Fig. 2), suggesting that each was produced by the same female lyrebird.

Figure 1. Five abandoned lyrebird eggs collected from separate nests in Sherbrooke Forest, Dandenong Ranges National Park, Victoria, during the winter breeding season of 2002 (image depicts all eggs collected by the Sherbrooke Lyrebird Survey Group during 2002).

Inflated clutch size (beyond a single egg) in the Superb Lyrebird appears to be a rare occurrence that is detrimental to fecundity. Successful incubation of more than one egg has never been recorded. It is doubtful that this paternally emancipated species would be able to rear a clutch larger than a single-egg brood, because the food requirements of two or more offspring would likely be greater than that able to be met by a single parent (Lill, 1986). We do not know whether the triplet eggs were fertile, nor was this known for any of the twin egg clutches that have been reported. The cause of laying multiple eggs in a clutch may be the result of a hormonal malfunction (Ouyang *et al.* 2011). In normal circumstances, hormonal factors should lead to disruption of ovarian follicular growth and thus cessation of clutch development during a breeding attempt (Haywood 1993). It is interesting to note that in all cases observed or reported, nesters were believed to have abandoned the clutch before commencing, or in the early stages of, incubation, therefore avoiding further detrimental effects on individual fitness.

It is entirely unknown whether inflated clutch size in the Superb Lyrebird is heritable. Given the strong deleterious effect on potential offspring, inflated clutch-size appears to be either dysfunctional or maladaptive. This is further evidenced by the rarity of such events in lyrebird populations. Research investigating whether clutch size can be linked to environmental conditions would be valuable in further developing understanding of inflated clutch size in lyrebirds.

Figure 2. Image detailing the colour and pattern of the three eggs collected from a lyrebird nest in Sherbrooke Forest, Dandenong Ranges National Park, Victoria, on 20th August 2016.

Acknowledgments: We would like to acknowledge the members of the Sherbrooke Lyrebird Survey Group who dedicate their time and passion to the monitoring of lyrebird nests in Sherbrooke Forest. We sincerely thank Andrew F Bennett for his thoughtful comments on a draft of this manuscript. This research, including the collection of abandoned lyrebird eggs, was carried out under DELWP research permit #10006839.

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Appendix 1. 4 Victoria I. Austin[a], Justin A. Welbergen[a], Alex C. Maisey[b,c,d], Meghan G. Lindsay[d] and Anastasia H. Dalziell [e,f] 2019. Evidence for reproductive suppression in a female superb lyrebird *Menura novaehollandiae. Behaviour*, *44*(3), pp.1-11.

[a] Hawkesbury Institute for the Environment, Western Sydney University, Hawkesbury Campus, Penrith, NSW 2751, Australia

[b]Department of Ecology, Environment and Evolution, La Trobe University, Bundoora, VIC 3086, Australia

[c] Research Centre for Future Landscapes, La Trobe University, Bundoora, VIC 3086, Australia

[d] Sherbrooke Lyrebird Survey Group, 30 Moores Road, Monbulk, VIC 3793, Australia

[e] Centre for Sustainable Ecosystem Solutions, School of Biological Sciences, University of Wollongong, Wollongong, NSW 2522, Australia

[f] Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Cornell University Ithaca, NY 14850, USA

Published by: *Behaviour*

Date accepted: 22 Aug, 2019

Manuscript word count: 3181

Abstract

Reproductive suppression, whereby individuals decrease the reproductive output of conspecific rivals, is well-studied in mammals, but while it is suspected to be widespread in birds, evidence of this phenomenon remains rare in this class. Here we provide compelling evidence of reproductive suppression in the superb lyrebird (Menura novaehollandie), with the first audio-visual documentation of the destruction of one female's nest by another. We propose that nest destruction may be a strategy that females use in protracted territorial negotiations spanning multiple breeding seasons, and discuss how reproductive suppression could explain puzzling nesting behaviours in this species, such as the construction of multiple unfinished nests in each breeding season. More broadly, these results reveal high intra-sexual competition among female lyrebirds, and thus may provide an explanation for their elaborate vocal displays.

Introduction

'Reproductive suppression', whereby individuals decrease the reproductive output of conspecific rivals, is a severe form of competitive behaviour that may involve continued harassment, eviction of subordinates, ovicide or infanticide ((Clutton-Brock and Huchard, 2013)). Reproductive suppression of rivals is thought to increase an individual's own reproductive potential by decreasing competition ((Wasser and Barash, 1983), (Clutton-Brock and Huchard, 2013)) when reproductive efforts are improved beyond the expected costs of the suppression ((Wasser and Barash, 1983)). Whereas, males are thought to benefit from reproductive suppression when it increases their access to receptive females ((Clutton-Brock and Huchard, 2013)); females are thought to benefit when it increases access to parental care or limited resources for offspring ((West-Eberhard, 1983)), or reduces the number of future competitors that their offspring could face ((Wasser and Barash, 1983)). Reproductive suppression occurs widely in mammals of both sexes, and classic examples include infanticide by male lions Panthera leo ((Pusey and Packer, 1994)) and decreased fecundity due to intra-sexual harassment in female yellow baboons Papio cynocephalus ((Wasser and Starling, 1988)). Importantly, in mammals it is thought that reproductive suppression may select for complex behaviours and signals ((Kleindorfer and Wasser, 2004)), such as communal nursing in rodents ((Roulin and Hager, 2003)) and sexual mimicry in hyenas ((Muller and Wrangham, 2002)). However, whether reproductive suppression drives the evolution of complex social behaviours or elaborate signals in birds remains unclear.

In birds, reproductive suppression is suspected to be underrepresented in the literature ((Clutton-Brock and Huchard, 2013)). Nonetheless, there are various examples of ovicide (e.g., (Krieg and Getty, 2016)) and infanticide (e.g., (Riehl, 2016)), and one isolated example of nest destruction ((Heinsohn, 1988)). Despite this, reproductive suppression is thought to occur predominantly in

highly social species, such as cooperative breeders ((Quinn et al., 2010)) or colonial nesters ((Brown and Brown, 1988)), as in such species there is often strong competition for mates, breeding sites, or parental care ((Boves et al., 2011, Clutton-Brock and Huchard, 2013)). Yet, social breeders are relatively well-studied so that this hypothesis may simply reflect a research bias. Similarly, the belief that reproductive suppression occurs more frequently in male than female birds ((Kattan, 2016)) may be reflective of research bias towards males. Nevertheless, to our knowledge, there is no compelling evidence of reproductive suppression in solitary breeding birds with female-only parental care; and yet, in such species competition for reproductive resources for offspring can be severe, especially in those that invest heavily in a limited number of offspring.

Here we present evidence that female superb lyrebirds (Menura novaehollandiae), a solitary breeding species with very low fecundity and uni-parental care, destroy the nests of rival females. We discuss how this finding advances our understanding of female-female competition for limited resources.

Materials and methods

Study species

The superb lyrebird is a large, mainly terrestrial oscine passerine with a slow life history and a lek-like mating system, including female-only care ((Lill, 1979a, Lill, 1986), (Lill, 2004)). During the breeding season, females build a large dome shaped nest that are only laid in once and not reused ((Maisey et al., 2016a, Lill, 1979b)). While the nest is active, females defend nesting territories from other females ((Reilly, 1970a, Lill, 1980b, Kenyon, 1972), (Robinson and Frith, 1981b)). Territorial behaviour includes counter singing with rival females ((Dalziell and Welbergen, 2016a)) and may escalate to physical disputes where females are reported to fight “just as vigorously as males” ((Higgins et al., 2001b pg 153)) by “striking each other with their legs” ((Reilly, 1970a) p.g. 78). Banded females are known to return to nesting territories in successive years ((Lill, 2004)). Female superb lyrebirds lay a single egg only per breeding attempt ((Lill, 1986)). The egg is incubated for approximately seven weeks (50 days), and upon hatching the altricial nestling remains in the nest for a further six weeks (Lill 1986). Once fledged, young lyrebirds remain dependent on their mothers and may reside in their care for up to a year. Attempts to re-nest within a breeding season are rare ((Lill, 1986);). Overall, breeding requires very high levels of investment by females, and the opportunity costs associated with a failed nesting attempt are substantial.

Study site

The incident of nest destruction that we report here occurred in Sherbrooke Forest, Dandenong Ranges National Park, located on the urban fringes of Melbourne, Victoria, Australia. Many of the birds at this site are banded as part of an ongoing monitoring program by the Sherbrooke Lyrebird Survey Group ((Maisey et al., 2018a)).

Methods

A lyrebird nest with an egg inside was located on the 7th of July 2018. A Bushnell NatureView HD Essential Trail Camera (1280 x 720p video with 44 kHz audio) was placed 2 m from the entrance to the nest on the 22nd of July (Figure 1a). The camera was set to record 60 second videos (with audio) at a high shutter speed sensitivity (0.6 second trigger) and medium LED brightness. Incubation behaviour was recorded using an iButton (model DS1922L, 8K, temperature range -40 to +85) placed inside the lining of the nest underneath the egg. The iButton recorded temperature at five-minute intervals but due to iButton failure, the period after the 25th of August was not covered.

Figure 1a. The nest when found complete with egg inside on 7th July 2018.

Figure 1b. The same nest on 22nd September after marauding female DkGYR had destroyed the chamber.

Results

Incubation had commenced when the nest was found, and video footage showed that the nest was actively attended by the female from the 7th of July until the 31st of August 2018. The videos show the female entering the nest or incubating. The camera trap varied in the amount of time taken to re-set after recording a video and thus video footage was not always recorded on consecutive days. iButton data showed that the egg was incubated at least until the 25th of August, after which there was no temperature record. On that day, the egg was still present. and the attending female was observed by researchers to be unbanded. Based on an incubation period of 50 days (Lill 1986), we predicted the egg should have hatched by the 25th of August 2018. On the 20th of September 2018 at 11:30 am the camera filmed a non-resident, colour-banded female (Figure 2b: Colour bands from top left leg; Dark Green/Yellow/Red, metal band right leg; No. 18682; henceforth DkGYR). Female DkGYR was banded as a nestling in Sherbrooke Forest in 2004 (14 years old). The footage shows DkGYR landing on the nest and tearing it apart using her feet (Figure 2a-d; Supplementary Video 1). First DkGYR appears to inspect the nest closely, before moving approximately a metre away (from 0.07-0.22 minutes). At 0:23 minutes DkGYR flies onto the top of the nest and begins tearing at the nest with her feet. By the end of the 60 s clip, the top of the nest has collapsed and DkGYR is still present. The camera did not record DkGYR vocalising or entering the nest. The camera triggers again 12 minutes later (Supplementary Video 2). In this second video DkGYR cannot be seen but the nest is completely destroyed, the top caved in (Figures 1b and 2d). Two days later when researchers

checked the nest (22nd of September, at 10:14 am) it was found in the same state as filmed by the camera (Figures 1b and 2d). There was no egg or remains of an egg inside.

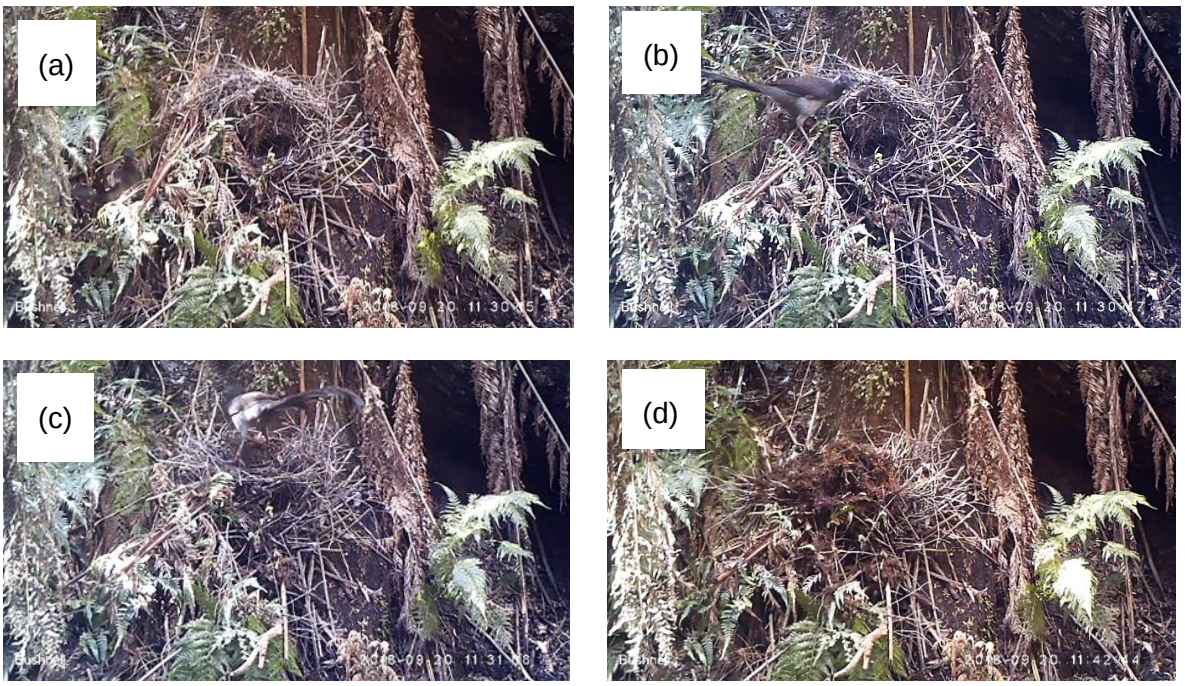

Figure 2. Stills from video footage filmed on the 20th September 2018 (a. and b.) Still shots recorded at 11:30:45am and 11.30:47 am. Female DkGYR approaches and stands on the nest. (c.) Female DkGYR begins destroying the nest using her feet. Here the nest dome is starting to collapse. (d.) Still shot from video recorded 11:42:44. Image shows the nest after female DkGYR has left. We assume the camera was triggered on her exit.

At the time the nest was destroyed, it is unclear whether the nest was active. After the 31st of August, the camera is only triggered twice before the nest is destroyed – on the 11th and 12th of September, but no female is seen in the footage. On the 12th of September, there is slight damage to the entrance of the nest, indicating that a predation event may have occurred, but this cannot be confirmed.

Discussion

In this study, we provide the first audio-visual footage of a female superb lyrebird destroying the nest of another female, which provides compelling evidence that female superb lyrebirds engage in reproductive suppression through nest destruction. To our knowledge, this is the first evidence of reproductive suppression by a female bird with female-only parental care. Our results support early suggestions that nest destruction is a regular feature of lyrebird breeding behaviour. While it is exceedingly difficult to observe nesting superb lyrebirds in the wild, Reilly (1970) described a "recognisable" (p.g. 70), banded female lyrebird destroying the nest of a rival unbanded female in September of 1968 by "scratching the dome of the nest until it was completely demolished" (p.g. 78).

Furthermore, of 525 nests monitored by the Sherbrooke Lyrebird Survey Group between 2003 and 2018, eight were found destroyed in a similar manner we report here (seven were found with the untouched egg still inside), representing 1.5% of the sample. The video shows the non-resident female engaging in a locomotion distinct from that used when foraging, thus it seems implausible that nest destruction is a by-product of foraging. Specifically, when foraging lyrebirds engage in repetitive digging with a motionless and fixed head position until they locate prey, at which point their head is lowered in a darting motion (Supplementary Video 3). By contrast the nest destruction behaviour in the video shows a female standing on the dome of the nest and pulling it apart with her feet with her head in an upright position.

Intra-sexual competition in female superb lyrebirds seems a likely driver for nest destruction behaviour. We suspect that breeding resources such as food, and food-rich territories are limited. The diet of superb lyrebirds consists largely of invertebrates that reside just below the soil's surface ((Lill, 1986)). Invertebrate based diets are considered unusual for uni-parental care breeding systems due to lower abundances compared to other food sources such as fruit or nectar (Cockburn 2006). Consequently, the effort associated with provisioning young may be especially high in lyrebirds and reproductive suppression may be an effective means of reducing competition from rivals ((Clutton-Brock and Huchard, 2013)). By destroying the nest of a neighbour, female lyrebirds are likely to secure more invertebrate- rich territory for themselves and their offspring during the breeding season. Given the extremely slow maturation rate of lyrebird young and the high investment by females in a single reproductive attempt, the benefits of opportunistic nest destruction may outweigh the energy expenditure and risk associated with the behaviour.

Reproductive suppression involving the destruction of a nest, has very rarely been reported in birds, and it is unclear why female lyrebirds appear to destroy nests, a physically taxing endeavour, rather than destroying a fragile egg (ovicide). Perhaps, given the energy that needs to be expended into building a nest which can sometimes take many months ((Lill, 1986)), its destruction may be an extreme yet absolute method of preventing a female from re-laying in an empty nest. Nest destruction has also been recorded in white-winged choughs Corcorax melanorhamphos ((Heinsohn, 1988)) and, like lyrebirds, chough nests themselves are suspected to be extremely valuable. White-winged chough nests are made from mud that is only available after rainfall, and it may take quite some time to build a new nest once one is destroyed ((Heinsohn, 1988)). Thus, opportunities to re-nest during the breeding season may be limited for white-winged choughs, like for superb lyrebirds.

In lyrebirds, nest destruction could explain other puzzling nesting behaviours. Female lyrebirds often build multiple partly constructed nests in a season before one is built to completion ((Reilly, 1970a)). This is unusual among birds (see (Berg et al., 2006)) and likely represent a significant investment in resources. However, if females are at high risk of having a nest destroyed by a rival,

building multiple partial nests may enable females to gauge the level of threat to nests within a particular location, without risking the destruction of a complete or active nest. Indeed, given that lyrebirds are long-lived and return to the same nesting territories year after year, nest destruction and multiple partial nest building may be a signalling strategy that females use in protracted negotiations over territorial boundaries spanning multiple breeding seasons.

While a definitive link between reproductive suppression and the evolution of complex behaviours and signals in birds has yet to be established, female-female competition may be driver of complex behaviours and signals ((Tobias et al., 2012)). For example, Krieg and Getty (2016) found that female house wrens Troglodyte aedon that sang more were more likely to defend against ovicide by rival wrens of both sexes, suggesting that female song in this species may function, at least in part, to defend against reproductive suppression by rivals. Female lyrebirds exhibit an impressive array of elaborate mimetic and species-specific vocalisations, suspect to play an important role in territory defence ((Dalziell and Welbergen, 2016a)), and our finding provides important evidence that female lyrebirds experience high intra-sexual competition. Given this competition, we suggest that reproductive suppression through nest destruction may act as a driver for elaborate vocalisations in this species.

Declarations

Acknowledgements - We thank the Sherbrooke Lyrebird Study Group for their ongoing support and assistance in the field, and the ABBBS for bird banding supplies.

Funding - This research was supported by a Western Sydney University Postgraduate Research Award from Hawkesbury Institute for the Environment (VIA); a Fulbright Postgraduate Scholar Award (VIA), a Holsworth Wildlife Research Endowment from the Ecological Society of Australia (VIA), LaTrobe University Postgraduate Research Award (ACM), a National Science Foundation Grant (JAW and AHD), and a University of Wollongong Vice-Chancellor's Postdoctoral Research Fellowship (AHD).

Author contributions - This study was conceived and designed by VIA, AHD and JAW. VIA wrote the manuscript with support and contributions from AHD, JAW, ACM, and MGL. Data were collected by MGL, ACM and VIA.

Permit(s) – This study was authorised by the Australian Bird and Bat Banding Authority (No.10008034: Sherbrooke Lyrebird Study Group), the Western Sydney University Animal Ethics Committee (No. A12077) and the Department of Environment, Land, Water and Planning (No.10008331).

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APPENDIX 2.

Appendix 2. 1 Examples of the diversity and functions of ecosystem engineers in Australia's wooded ecosystems. "*" denotes introduced species.

Ecosystem engineer	Interactee/s	Habitat type	Action/structure	Resource moderated	Effect	Allogenic/ Autogenic	Author/Date
*Earthworm *Lumbricus terrestris*,	Microbes, Microarthropods, grasses and legumes	Temperate /Farmland edges	Mechanical disturbance, increase soil compaction, resource competition	Soil nutrients (C, N), soil structure	Lowers microbial biomass and basal respiration, decreases coverage of legume (*Vicia americana*) and the biomass of legumes and grasses, increases abundance of *Viola canadensis*	Allogenic	Eisenhauer et al. (2007)
*European Rabbit *Oryctolagus cuniculus*	Echidna, sandswimmer and some coleoptera	Arid woodland	Construction of warrens	Burrows as refugia,	Echidnas, sandswimmers, hemipterans and coleopterans used warrens	Allogenic	Read et al. (2008)
Bare-nosed Wombat (*vombatus ursinus*)	Plants	Agricultural/Riparian forest	Construction of burrows and tracks	Growing space for plants	Short-term: lower plant cover around mounds (microsites) less canopy cover. Long term: increase habitat heterogeniety and thus plant richness (not measured here).	Allogenic	Borchard and Eldridge (2012)
Mycophageous mammals	Plants	Temperate and arid woodlands	Spread of viable fungi spores in droppings	Nutrient and water uptake of plants for growth	Increases plant health and structure	Allogenic	Claridge and May (1994)
Echidna (*Tachyglossus aculeatus*)	Seeding plants	Temperate woodlands	Dig feeding pits in soil; create ejecta mounds surrounding forage sites	Seeds, water and sediment	Couples critical resources of seed water and sediment creating small-scale heterogeneity	Allogenic	Eldridge (2011)
Mistletoe	Nesting birds	Woodland	Provision of dense vegetation for nesting	Living space	Increases incidence of mistletoe nesters	Autogenic	Watson and Herring (2012)
Mistletoe	Arthropods	Woodland	Provides patches of high nutrient in soils changing nutient flow	Nutrients and litter-rich habitat for invertebrates	Increased abundance of invertebrates	Autogenic	Mellado et al. (2019)

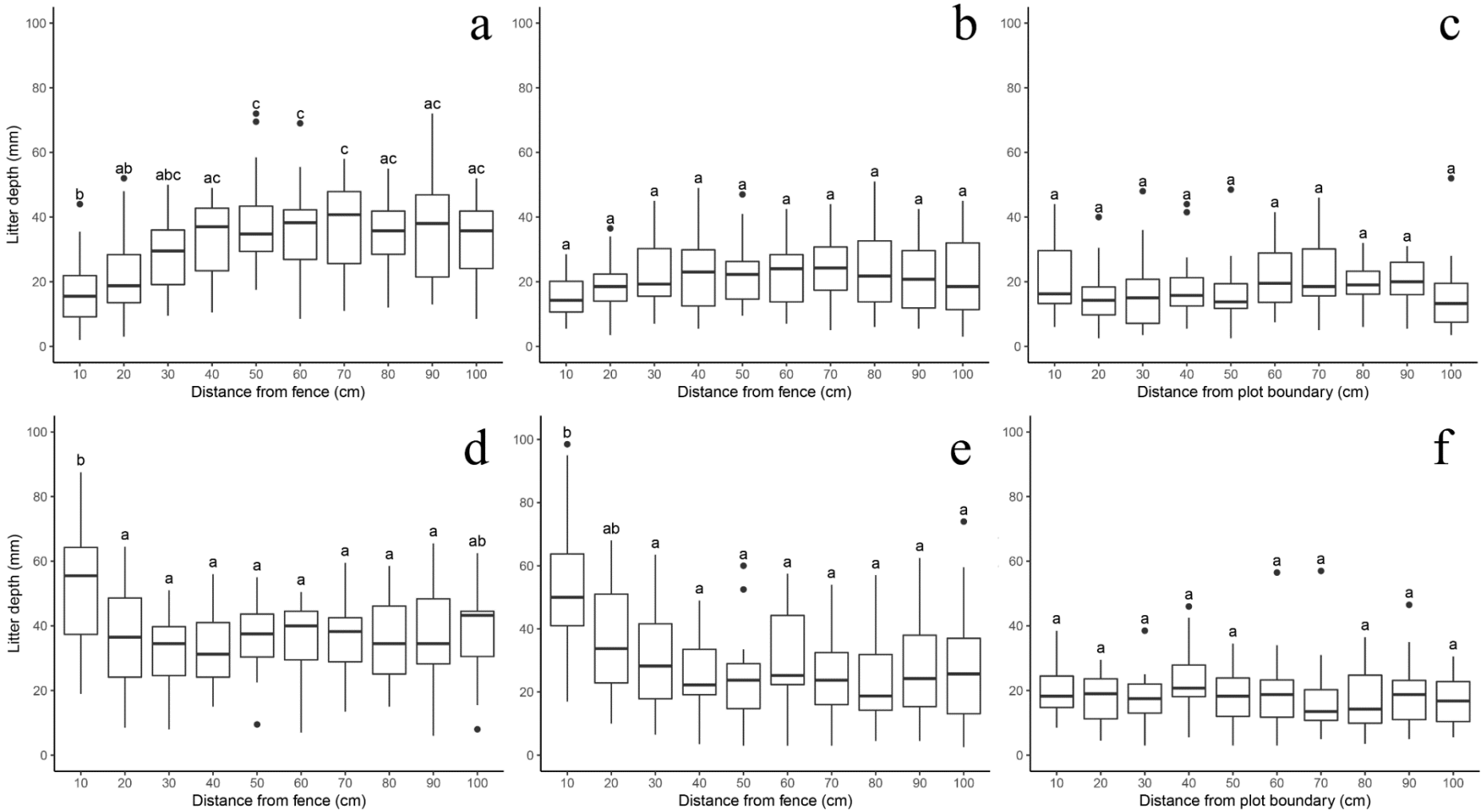
Appendix 2.1 continued

Ecosystem engineer	Interactee/s	Habitat type	Action/structure	Resource moderated	Effect	Allogenic/ Autogenic	Author/Date
Ants	Plants	Woodland	Provides patches of high nutrient in soils changing nutient flow	Nutrients for plant growth	Increases richness and abndance	Allogenic	Folgarait Folgarait (1998)
Wedge-tailed Shearwater *Puffinicus pacificus*	Introduced succulent herb *Mesembryanthemum crystallinum*	Mediterranean scrub	Bioturbation to construct borrows	Changes edaphic properties	Decreases plant richness and increases abundance of mesembryanthemum crystallinum	Allogenic	Bancroft et al. (2005)
Lamington Crayfish *Eustacus sulcatus*	Stream invertebrates (inferred only)	Sub-tropical rainforest streams	Dislodgement and displacement of materials while feeding	Nutrient level in down-stream areas	Increases nutrients available in stream	Allogenic	Furse (2010)
Arboreal termites	Palm cockatoo	Tropical savanna woodland	Hollowing out of tree limbs and trunks	Living space for breeding cockatoos	Increases nest tree availability	Allogenic	Murphy and Legge (2007)
Wood-rot fungi species	Palm cockatoo	Tropical savanna woodland	Hollowing out of tree limbs and trunks	Living space for breeding cockatoos	Increases nest tree availability	Allogenic	Murphy and Legge (2007)
*Cattle	Non-native plants	Riparian	Tracks of compacted and indented soil created by cattle movements, moving 9.28-102.7t/ha soil, trampled vegetation	Living space for native plants	33% increase in non-native plants that are resistant to trampling and grazing at high cattle use sites	Allogenic	Borchard and Eldridge (2012)
*Reed sweet-grass *Glyceria maxima*	Macro-invertebrates	Streams	Grows thick root mats that change flow dynamics of streams	Alters nutrients and changes living space	Lowers macroinvertebrate morphospecies and functional feeding group abundance and diversity	Autogenic	Clarke et al. (2004)

Appendix 2.1 continued

Ecosystem engineer	Interactee/s	Habitat type	Action/structure	Resource moderated	Effect	Allogenic/ Autogenic	Author/Date
Mound-building termites *Amitermes vitiosus, Drepanotermes perniger and Tumulitermes pastinator*	Plants	Semi-arid tropical woodland	Builds numerous large mounds	Nutrients available to plants	Increases plant-available nutrients 2-7 times that of the surrounding A1 soil horizon	Allogenic	Holt et al. (1980)
Termites and Ants	Nutrient flows/plants	Indiscriminate	Builds nests	Nutrients available to plants	Increases nutrient cycling	Allogenic	Lobry de Bruyn and Conacher (1990)
Mound-building termites *Drepanotermes tamminensis* and *Amitermes obeuntis*	Nutrient flows/plants	Open woodland	Builds nests and foraging galleries	Nutrients available to plants	Increases Organic Carbon, lowers ph, higher clay content esp. In foraging galleries	Allogenic	Lobry de Bruyn and Conacher
Woylie *Bettongia penicillata*	Soils and nutrient flows	Schlerophyll woodland	Digs foraging pits moving 4.8t per animal and 5000–16,000 new diggings ha-1 year-1.	Alters nutrient flows, changes living space for plants,	Not shown in this study	Allogenic	Garkaklis, Bradley and Wooller
Woylie *Bettongia penicillata*	Soils and water infiltration	Schlerophyll woodland	Digs foraging pits that increase water infiltration properties of the soil	Water	Increases infiltration	Allogenic	Garkaklis
Bare-nosed Wombat *(vombatus ursinus*)	Vegetation	Temperate riparian forest/agricultural land	Construction of burrows, move 5.3-258t/ha	Growing space for plants	Microsites that favour different plant cover densities	Allogenic	Borchard and Eldridge

Appendix 2. 2 Litter depth at 10 cm increments into the plot in a downslope direction for (a) fenced, (b) simulated and (c) unfenced plots; and the upslope direction for the corresponding treatments (d-f). Smaller letters above confidence intervals denote distance points with significant differences as tested with Tukey's HSD post-hoc comparisons (p<0.05).



Appendix 2. 3 Rationale for each criterion used for selection of sites for experimental treatments.

Criteria	Rationale
1. Sites had not experienced severe fire or logging within the past 30 years (mature seral stage)	The study aimed to investigate the effects of foraging by the superb lyrebird in natural ecosystems. Younger forests were avoided as these are typically young due to anthropogenic use that affects forest structure (Keith et al. 2014)
2. Sites were situated at least 40 m from a main (sealed) road or forest edge	To decrease the likelihood of both human interference and edge disturbance affecting the incidence of foraging by lyrebirds
3. Sites were no more than 300 m from an access track or road	Logistically challenging to transport fencing materials
4. Sites were located at least 400 m from one another	Ensures that a single lyrebird territory could not overlap two sites (i.e. samples are independent) (Kenyon 1972)
5. Ground vegetation (<50 cm high) is relatively less complex, assessed by vegetation intersecting a vertical structure pole at fewer than 5 of 9 points (measured in a cross centred on each plot)	Vegetation complexity above this level results in a steep fall in the likelihood of lyrebirds foraging at a location (Maisey et al. 2018)

Appendix 2. 4 Taxonomic groupings for which biomass estimates were calculated. Presented is the lowest taxonomic level to which functions were applied, the taxonomic richness identified within each group, abundance and biomass for each size class in each year and the source of the length-weight equation applied.

Taxonomic group	Taxonomic richness	Size class *	Abundance			Biomass (mg ODW)			Source of equation
			2015	2016	2017	2015	2016	2017	
O. Amphipoda	1	Medium	138	103	90	43	32	28	Gowing and Recher (1984)
		Large	918	764	698	3473	2890	2640	
O. Isopoda	1	Medium	381	376	438	204	202	235	Gowing and Recher (1984)
		Large (5.5)	50	82	62	112	183	139	
S. C. Oligochaeta	1	Medium	652	263	580	270	109	240	Collins (1992)
		Large (14)	331	443	854	150	200	386	
P. Nematoda	1	Small	498	180	1860	206	75	771	Collins (1992)
C. Gastropoda	1	Medium	50	68	44	29	40	26	Collins (1992)
		Large (6)	12	9	13	8	6	9	
O. Araneae	6	Small	8	5	14	1	1	2	Gowing and Recher (1984)
		Medium	197	182	168	276	255	235	
		Large (7)	52	74	44	547	779	463	
O. Opiliones	1	Medium	22	12	4	74	40	13	Ganihar (1997)
		Large (7)	13	30	31	85	196	203	
S.C. Acari - O. Prostigmata	1	Small	472	516	421	21	23	19	Rogers et al. (1977)
Other Acari	3	Small	25721	33883	36366	3130	4610	4425	Rogers et al. (1977)
O. Scorpiones	1	Large (15)	1	1	0	19	19	0	Höfer and Ott (2009)
O. Pseudoscorpionida	1	Medium	172	198	148	104	119	89	Höfer and Ott (2009)
C. Diplopoda	7	Medium	163	140	162	40	34	40	Gowing and Recher (1984)
		Large (12)	152	134	142	856	789	799	
C. Chilopoda	4	Medium	140	48	70	37	13	19	Gowing and Recher (1984)
		Large (7.5)	402	581	547	567	819	771	

Appendix 2.4 continued

Taxonomic group	Taxonomic richness	Size class *	Abundance			Biomass (mg ODW)			Source of equation
			2015	2016	2017	2015	2016	2017	
C. Symphyla	2	Small	61	5	33	3	<1	1	Gowing and Recher (1984)
		Medium	155	239	187	41	64	50	
C. Pauropoda	1	Small	307	329	353	25	27	29	Gowing and Recher (1984)
P. Onycophora	1	Medium	2	2	4	1	1	2	Gowing and Recher (1984)
F. Onychiuridae	1	Small	4456	4939	2326	58	64	30	Tanaka (1970)
O. Entomobryomorpha	1	Small	11398	18115	16328	372	591	533	Tanaka (1970)
O. Sminthuridae	1	Small	522	940	516	119	215	118	Caballero et al. (2004)
O. Protura	1	Small	238	125	100	19	10	8	Gowing and Recher (1984)
O. Diplura	1	Small	1	4	8	<1	<1	1	Gowing and Recher (1984)
		Medium	0	0	13	0	0	7	
O. Thysanura	1	Small	1	0	0	<1	0	0	Ganihar (1997)
O. Orthoptera	1	Large (7)	7	9	5	25	32	18	Ganihar (1997)
O. Blattodea **	1	Medium	3	3	3	2	2	2	Gowing and Recher (1984)
O. Dermaptera	1	Medium	1	0	0	1	0	0	Ganihar (1997)
O. Psocoptera **	1	Medium	10	8	11	6	5	6	Gowing and Recher (1984)
O. Mallophaga **	1	Small	1	0	0	<1	0	0	Gowing and Recher (1984)
O. Thysanoptera **	1	Small	8	50	34	1	4	<1	Gowing and Recher (1984)
		Medium	0	0	16	0	0	9	
O. Hemiptera	4	Small	79	188	218	10	14	27	Rogers et al. (1977)
		Medium	139	220	201	119	189	172	
		Large (6)	8	23	11	23	67	32	
O. Coleoptera $_{Juvenile}$	2	Small	203	222	112	64	68	56	Rogers et al. (1977)
		Medium	173	292	282	20	180	174	
		Large (7)	27	44	48	107	32	35	

Appendix 2.4 continued

Taxonomic group	Taxonomic richness	Size class *	Abundance			Biomass (mg ODW)			Source of equation
			2015	2016	2017	2015	2016	2017	
O. Coleoptera $_{Adult}$	15	Small	517	434	274	56	47	30	Gowing and Recher (1984)
		Medium	872	860	701	928	916	746	
		Large (8.5)	68	79	64	126	146	119	
O. Neuroptera $_{Juvenile}$ **	1	Medium	2	2	0	2	2	0	Gowing and Recher (1984)
		Large (7.5)	0	1	1	0	5	5	
O. Diptera $_{Juvenile}$	2	Small	1160	998	1078	47	41	44	Rogers et al. (1977)
		Medium	2880	1569	1722	240	131	143	
		Large (7)	341	324	276	99	94	80	
O. Diptera $_{Adult}$	8	Medium	113	174	113	71	109	71	Gowing and Recher (1984)
O. Lepidoptera $_{Juvenile}$	2	Small	41	32	16	1	1	<1	Rogers et al. (1977)
		Medium	77	70	83	15	14	16	
		Large (8)	50	63	66	101	127	133	
O. Lepidoptera $_{Adult}$	1	Large (8)	8	15	10	16	30	20	Rogers et al. (1977)
O. Hymenoptera - F. Formicidae	2	Small	41	98	38	2	5	2	
		Medium	565	737	840	65	306	349	Gowing and Recher (1984)
		Large (6)	41	28	23	235	45	37	
Other O. Hymenoptera	15	Small	124	140	93	10	12	10	Gowing and Recher (1984)

* Mean length (used in biomass equations) is included in parentheses for invertebrates classified as large (>5mm).

** Generic equation for class insecta applied

Appendix 2. 5 Taxonomic table displaying OTU assignments (genus match threshold set to 97%) and closest matched species for fungi referenced from the Unite database.

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
3889	Ascomycota	Archaeorhizomycetes	Archaeorhizomycetales	Archaeorhizomycetaceae	Archaeorhizomyces	Unassigned	-	
1367		Dothideomycetes	Capnodiales	Cladosporiaceae	Cladosporium	*Cladosporium aphidis*	91	SH1966719.08FU
4013				Mycosphaerellaceae	Readeriella	*Readeriella menaiensis*	45	SH1964584.08FU
1645			Pleosporales	Pleosporaceae	Pithomyces	*Pithomyces valparadisiacus*	100	SH1229625.08FU
2476				Teichosporaceae	Teichospora	*Teichospora rubriostiolata*	99	SH1552781.08FU
2651				Torulaceae	Torula	Unassigned	-	
3654			Venturiales	Sympoventuriaceae	Fusicladium	*Fusicladium amoenum*	97	SH1518138.08FU
1293					Sympoventuria	*Sympoventuria capensis*	100	SH1514002.08FU
2486						*Sympoventuria capensis*	100	SH1514002.08FU
2663						*Sympoventuria capensis*	100	SH1514002.08FU
3970						*Sympoventuria capensis*	100	SH1514002.08FU
3362					Troposporella	*Troposporella olivacea*	100	SH1514003.08FU
1117				Venturiaceae	Venturia	Unassigned	-	
2549		Eurotiomycetes	Chaetothyriales	Herpotrichiellaceae	Cladophialophora	*Cladophialophora chaetospira*	1	SH1529584.08FU
2647						*Cladophialophora chaetospira*	100	SH1529584.08FU
3086						*Cladophialophora eucalypticola*	1	SH1160325.08FU
89					Exophiala	*Exophiala equina*	99	SH1564395.08FU
413						*Exophiala equina*	92	SH1564395.08FU
1752						*Exophiala moniliae*	78	SH1529603.08FU
4047						Unassigned	-	
104			Eurotiales	Aspergillaceae	Penicillium	*Penicillium clavatus*	1	SH1156562.08FU
598						*Penicillium multicolor*	5	SH1163166.08FU
1252						*Penicillium cairnsense*	46	SH2190108.08FU
1276						Unassigned	-	
2073						*Penicillium ubiquetum*	39	SH2189938.08FU

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
2658	Ascomycota	Eurotiomycetes	Eurotiales	Aspergillaceae	Penicillium	*Penicillium wellingtonense*	59	SH1896009.08FU
530				Elaphomycetaceae	Elaphomyces	Unassigned	-	
1066						*Elaphomyces decipiens*	1	SH1587500.08FU
1421						*Elaphomyces decipiens*	2	SH1587500.08FU
1895						*Elaphomyces muricatus*	1	SH1587494.08FU
2083						Unassigned	-	
2628						Unassigned	-	
48				Trichocomaceae	Sagenomella	*Sagenomella diversispora*	42	SH1166052.08FU
771						*Sagenomella diversispora*	38	SH1166052.08FU
863						*Sagenomella griseoviridis*	38	SH1166053.08FU
1620						*Sagenomella humicola*	55	SH1163421.08FU
658					Talaromyces	*Talaromyces thailandensis*	66	SH1676221.08FU
2180						*Talaromyces atricola*	68	SH2152978.08FU
3307						*Talaromyces proteolyticus*	71	SH1557520.08FU
3337						*Talaromyces atricola*	62	SH2152978.08FU
3455		Leotiomycetes	Helotiales	Dermateaceae	Cryptosporiopsis	Unassigned	-	
1763					Pezicula	*Pezicula ericae*	85	SH1884567.08FU
1893						*Pezicula ericae*	87	SH1884567.08FU
2602				Helotiaceae	Ascotremella	*Ascotremella faginea*	93	SH1517864.08FU
630					Scytalidium	*Scytalidium lignicola*	89	SH1564465.08FU
2094						*Scytalidium lignicola*	86	SH1564465.08FU
2627						*Scytalidium lignicola*	91	SH1564465.08FU
3051					Unguiculariopsis	Unassigned	-	
276				*Incertae sedis*	Chalara	Unassigned	-	
3868				*Incertae sedis*	Leohumicola	Unassigned	-	

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
2363	Ascomycota	Leotiomycetes	Helotiales	Hyaloscyphaceae	Arachnopeziza	Unassigned	-	
294				Leotiaceae	Leotia	*Leotia lubrica*	96	SH1577065.08FU
2067						*Leotia lubrica*	99	SH1577065.08FU
210				Myxotrichaceae	Oidiodendron	*Oidiodendron chlamydosporicum*	57	SH1564442.08FU
747						*Oidiodendron chlamydosporicum*	58	SH1564442.08FU
856						*Oidiodendron maius*	2	SH1184642.08FU
968						Unassigned	-	
1750						Unassigned	-	
3761						*Oidiodendron truncatum*	48	SH1565475.08FU
3909						Unassigned	-	
237				Rutstroemiaceae	Lambertella	*Lambertella corni-maris*	100	SH1518607.08FU
4007						*Lambertella corni-maris*	94	SH1518607.08FU
4054				Vibrisseaceae	Phialocephala	*Phialocephala humicola*	98	SH1517984.08FU
623			Thelebolales	Pseudeurotiaceae	Leuconeurospora	Unassigned	-	
67		Pezizomycetes	Pezizales	Pezizaceae	Ruhlandiella	Unassigned	-	
76						Unassigned	-	
137						*Ruhlandiella limnaea*	1	SH1510542.08FU
212						Unassigned	-	
1554						Unassigned	-	
1952						Unassigned	-	
280				Pyronemataceae	Byssonectria	*Byssonectria fusispora*	98	SH1529946.08FU
3589						*Byssonectria fusispora*	99	SH1529946.08FU
1271		Saccharomycetes	Saccharomycetales	Phaffomycetaceae	Barnettozyma	*Barnettozyma californica*	64	SH1149761.08FU
1370				*Incertae sedis*	Candida	*Candida sphagnicola*	100	SH1516620.08FU
3705				*Incertae sedis*		*Candida sphagnicola*	100	SH1516620.08FU

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
69	Ascomycota	Saccharomycetes	Saccharomycetales	*Incertae sedis*	Nadsonia	*Nadsonia fulvescens*	100	SH1570250.08FU
1409				*Incertae sedis*		*Nadsonia fulvescens*	100	SH1570250.08FU
4030				*Incertae sedis*	Nadsonia	*Nadsonia fulvescens*	100	SH1570250.08FU
2145			Chaetosphaeriales	Chaetosphaeriaceae	Chaetosphaeria	Unassigned	-	
2512						Unassigned	-	
2867						*Chaetosphaeria pseudoindicum*	1	SH1720439.08FU
3124			Hypocreales	Bionectriaceae	Clonostachys	*Clonostachys divergens*	95	SH1522848.08FU
422				Clavicipitaceae	Metarhizium	*Metarhizium frigidum*	97	SH1562692.08FU
536						*Metarhizium robertsii*	99	SH2399613.08FU
873						*Metarhizium frigidum*	100	SH1562692.08FU
1211						*Metarhizium marquandii*	100	SH1561418.08FU
1212						*Metarhizium robertsii*	99	SH2399613.08FU
1430						*Metarhizium flavoviride*	48	SH1562693.08FU
1513						*Metarhizium marquandii*	100	SH1561418.08FU
2454						*Metarhizium frigidum*	80	SH1562692.08FU
3195						*Metarhizium marquandii*	100	SH1561418.08FU
270				Cordycipitaceae	Beauveria	*Beauveria caledonica*	56	SH1524436.08FU
1053						*Beauveria vermiconia*	88	SH1524464.08FU
1086						*Beauveria vermiconia*	82	SH1524464.08FU
1378						*Beauveria vermiconia*	82	SH1524464.08FU
1745						*Beauveria caledonica*	91	SH1524436.08FU
1747						*Beauveria dichromosporum*	1	SH1773219.08FU
2089						*Beauveria pseudobassiana*	78	SH1886966.08FU
2838						*Beauveria vermiconia*	87	SH1524464.08FU
3698						Unassigned	-	

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
2052	Ascomycota	Sordariomycetes	Hypocreales	Cordycipitaceae	Lecanicillium	*Lecanicillium psalliotae*	100	SH1524440.08FU
2815				Cordycipitaceae		*Lecanicillium primulinum*	89	SH1524442.08FU
2903				Hypocreaceae	Hypomyces	Unassigned	-	
3105						Unassigned	-	
717					Trichoderma	*Trichoderma moravicum*	8	SH1187999.08FU
1716						*Trichoderma oblongisporum*	11	SH1568350.08FU
2617						*Trichoderma novae-zelandiae*	33	SH1738451.08FU
2615				*Incertae sedis*	Brachysporium	Unassigned	-	
2987				*Incertae sedis*		*Brachysporium nigrum*	12	SH1151322.08FU
1465				Nectriaceae	Calonectria	*Calonectria spathulata*	42	SH2038446.08FU
3258						*Calonectria spathulata*	37	SH2038446.08FU
1436					Fusarium	*Fusarium sarcochroum*	89	SH1212153.08FU
68					Ilyonectria	*Ilyonectria mors-panacis*	100	SH1546325.08FU
321						*Ilyonectria mors-panacis*	98	SH1546325.08FU
72					Mariannaea	*Mariannaea pinicola*	99	SH1506679.08FU
1471					Volutella	*Volutella consors*	100	SH1561518.08FU
2756			Sordariales	Cephalothecaceae	Cephalotheca	Unassigned	-	
3508					Cryptendoxyla	*Cryptendoxyla hypophloia*	100	SH1553420.08FU
874				Chaetomiaceae	Chaetomium	*Chaetomium homopilatum*	5	SH1215875.08FU
4031				Lasiosphaeriaceae	Fimetariella	Unassigned	-	
757					Podospora	Unassigned	-	
2098				Sordariaceae	Diplogelasinospora	*Diplogelasinospora inaequalis*	66	SH1615726.08FU
1590				*Incertae sedis*	Dendrosporium	Unassigned	-	
933				*Incertae sedis*	Tracylla	Unassigned	-	
1350				*Incertae sedis*		Unassigned	-	

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
2032	Ascomycota	Sordariomycetes	Sordariales	*Incertae sedis*	Tracylla	Unassigned	-	
1472			Xylariales	Xylariaceae	Annulohypoxylon	*Annulohypoxylon bovei*	99	SH1178985.08FU
1800					Biscogniauxia	Unassigned	-	
383					Daldinia	*Daldinia loculata*	79	SH1507869.08FU
3391						*Daldinia loculata*	80	SH1507869.08FU
661					Xylaria	Unassigned	-	
1463				*Incertae sedis*	Ceratostomella	*Ceratostomella cuspidata*	99	SH1157004.08FU
3800				*Incertae sedis*		*Ceratostomella cuspidata*	98	SH1157004.08FU
131				*Incertae sedis*	Xyladictyochaeta	*Xyladictyochaeta lusitanica*	99	SH1569001.08FU
1331				*Incertae sedis*		*Xyladictyochaeta lusitanica*	99	SH1569001.08FU
538	Basidiobolomycota	Basidiobolomycetes	Basidiobolales	Basidiobolaceae	Basidiobolus	*Basidiobolus magnus*	93	SH1506197.08FU
1959						*Basidiobolus magnus*	94	SH1506197.08FU
2130						*Basidiobolus ranarum*	36	SH1506198.08FU
1092	Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	Agaricus	*Agaricus moelleroides*	25	SH1772383.08FU
1853						*Agaricus lanipes*	2	SH1202805.08FU
2174						*Agaricus subsubensis*	15	SH1594013.08FU
2457						*Agaricus nigrogracilis*	84	SH1594044.08FU
2775						*Agaricus nigrogracilis*	94	SH1594044.08FU
3098						*Agaricus bisporiticus*	29	SH1594043.08FU
3168						*Agaricus nigrogracilis*	87	SH1594044.08FU
3244						*Agaricus abruptibulbus*	14	SH1593903.08FU
3293						*Agaricus moelleroides*	28	SH1772383.08FU
3348						*Agaricus campbellensis*	68	SH1593972.08FU
2506					Cystoderma	*Cystoderma simulatum*	99	SH1552054.08FU
869					Leucoagaricus	*Leucoagaricus orientiflavus*	33	SH1509907.08FU

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
1039	Basidiomycota	Agaricomycetes	Agaricales	Agaricaceae	Leucoagaricus	*Leucoagaricus rubrotinctus*	3	SH1154763.08FU
2150						*Leucoagaricus rubrotinctus*	6	SH1154763.08FU
2713						*Leucoagaricus orientiflavus*	31	SH1509907.08FU
3442						*Leucoagaricus orientiflavus*	23	SH1509907.08FU
3613						*Leucoagaricus orientiflavus*	60	SH1509907.08FU
3811						*Leucoagaricus orientiflavus*	62	SH1509907.08FU
2249				Amanitaceae	Amanita	Unassigned	-	
1124				Bolbitiaceae	Descolea	*Descolea recedens*	90	SH1514066.08FU
3958						*Descolea recedens*	89	SH1514066.08FU
3463					Descomyces	*Descomyces albus*	98	SH1514060.08FU
3020					Panaeolus	*Panaeolus papilionaceus*	90	SH1648512.08FU
1357					Pholiotina	*Pholiotina gracilenta*	100	SH1556360.08FU
88				Clavariaceae	Clavaria	*Clavaria redoleoalii*	41	SH1147836.08FU
109						*Clavaria redoleoalii*	57	SH1147836.08FU
488						*Clavaria redoleoalii*	64	SH1147836.08FU
574						*Clavaria redoleoalii*	43	SH1147836.08FU
891						*Clavaria redoleoalii*	49	SH1147836.08FU
1054						*Clavaria redoleoalii*	80	SH1147836.08FU
2871						Unassigned	-	
2927						*Clavaria redoleoalii*	46	SH1147836.08FU
3067						*Clavaria citrinorubra*	4	SH1236611.08FU
3512						Unassigned	-	
3668						*Clavaria redoleoalii*	61	SH1147836.08FU
128					Ramariopsis	Unassigned	-	
171						Unassigned	-	

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
2026	Basidiomycota	Agaricomycetes	Agaricales	Clavariaceae	Ramariopsis	Unassigned	-	
145				Cortinariaceae	Cortinarius	*Cortinarius indotatus*	46	SH1504093.08FU
434						*Cortinarius rotundisporus*	85	SH1504094.08FU
665						*Cortinarius saturniorum*	1	SH1504020.08FU
743						*Cortinarius minoscaurus*	95	SH1504059.08FU
928						*Cortinarius rotundisporus*	82	SH1504144.08FU
1130						*Cortinarius lubricanescens*	2	SH1503898.08FU
1225						*Cortinarius austrovaginatus*	80	SH1222154.08FU
1391						*Cortinarius minoscaurus*	100	SH1504059.08FU
1562						*Cortinarius periclymenus*	2	SH1141916.08FU
1744						*Cortinarius erythraeus*	90	SH1142875.08FU
1945						*Cortinarius indotatus*	37	SH1504093.08FU
2350						*Cortinarius viscincisus*	66	SH1504239.08FU
2901						*Cortinarius viscincisus*	67	SH1504239.08FU
2932						*Cortinarius thaumastus*	47	SH1504088.08FU
3141						*Cortinarius minoscaurus*	100	SH1504059.08FU
3959						*Cortinarius hinnuleus*	17	SH1545293.08FU
4155						*Cortinarius memoria-annae*	87	SH1504063.08FU
2895					Gymnopilus	*Gymnopilus lepidotus*	99	SH1626112.08FU
3074						*Gymnopilus junonius*	97	SH1626114.08FU
3510						*Gymnopilus ferruginosus*	100	SH1221836.08FU
1925				Crepidotaceae	Crepidotus	Unassigned	-	
3045						Unassigned	-	
3671						*Crepidotus caryotis*	1	SH1503893.08FU
477				Entolomataceae	Clitopilus	*Clitopilus kamaka*	77	SH1746622.08FU

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
2197	Basidiomycota	Agaricomycetes	Agaricales	Entolomataceae	Clitopilus	*Clitopilus kamaka*	74	SH1746622.08FU
1335					Entoloma	*Entoloma conferendum*	76	SH1569064.08FU
1525						*Entoloma conferendum*	12	SH1569064.08FU
2112						*Entoloma sericeum*	10	SH1569065.08FU
2365						*Entoloma piceinum*	21	SH1569115.08FU
3003						*Entoloma piceinum*	36	SH1569115.08FU
3185						*Entoloma minutum*	11	SH1569110.08FU
3571						*Entoloma quellarense*	1	SH1179202.08FU
3815						*Entoloma piceinum*	13	SH1569115.08FU
1547				Hydnangiaceae	Laccaria	*Laccaria kanuka*	2	SH1553015.08FU
2183						*Laccaria canaliculata*	83	SH1553030.08FU
92				Inocybaceae	Inocybe	*Inocybe calamistrata*	14	SH1638627.08FU
146						*Inocybe kapila*	1	SH1183850.08FU
151						*Inocybe lasseroides*	37	SH1527313.08FU
200						*Inocybe torresiae*	82	SH1235245.08FU
262						Unassigned	-	
441						*Inocybe serrata*	67	SH1569541.08FU
465						*Inocybe serrata*	6	SH1569544.08FU
720						Unassigned	-	
987						Unassigned	-	
1167						*Inocybe torresiae*	87	SH1235245.08FU
1423						*Inocybe calamistrata*	15	SH1638619.08FU
1427						Unassigned	-	
1540						*Inocybe serrata*	12	SH1569544.08FU
1579						*Inocybe serrata*	48	SH1569541.08FU

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
1842	Basidiomycota	Agaricomycetes	Agaricales	Inocybaceae	Inocybe	*Inocybe serrata*	4	SH1569544.08FU
1877						Unassigned	-	
1942						*Inocybe spuria*	11	SH2184135.08FU
2011						*Inocybe serrata*	8	SH1569544.08FU
2046						Unassigned	-	
2147						*Inocybe assimilata*	1	SH1527384.08FU
2346						*Inocybe serrata*	58	SH1569545.08FU
2360						*Inocybe lasseroides*	32	SH1527313.08FU
2380						*Inocybe mendica*	6	SH1171179.08FU
2505						*Inocybe pseudodestricta*	86	SH1562257.08FU
3182						*Inocybe torresiae*	84	SH1235245.08FU
3198						*Inocybe mendica*	5	SH1171179.08FU
3271						*Inocybe pseudodestricta*	80	SH1562257.08FU
3372						*Inocybe fibrillosibrunnea*	70	SH1649868.08FU
3724						*Inocybe nitidiuscula*	4	SH1155144.08FU
3876						Unassigned	-	
3911						*Inocybe nitidiuscula*	1	SH1155144.08FU
3923						*Inocybe viscata*	93	SH1646269.08FU
3981						Unassigned	-	
787				Lyophyllaceae	Lyophyllum	*Lyophyllum pulvis-horrei*	1	SH1200366.08FU
4104						*Lyophyllum striipilea*	1	SH1236436.08FU
834				Marasmiaceae	Marasmius	*Marasmius ochroleucus*	43	SH1171759.08FU
2459				Omphalotaceae	Rhodocollybia	*Rhodocollybia purpurata*	100	SH1646591.08FU
567				Physalacriaceae	Armillaria	*Armillaria novae-zelandiae*	29	SH1510659.08FU
1456						*Armillaria novae-zelandiae*	24	SH1510659.08FU

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
1698	Basidiomycota	Agaricomycetes	Agaricales	Pleurotaceae	Nematoctonus	*Nematoctonus pachysporus*	99	SH1651215.08FU
385				Pluteaceae	Pluteus	*Pluteus floccipes*	19	SH1208508.08FU
1062						*Pluteus cinereofuscus*	16	SH1604318.08FU
2022						*Pluteus floccipes*	15	SH1208508.08FU
2251						*Pluteus atromarginatus*	87	SH1551997.08FU
4129						*Pluteus floccipes*	15	SH1208508.08FU
786				Psathyrellaceae	Coprinopsis	*Coprinopsis phlyctidospora*	26	SH1566133.08FU
3457						*Coprinopsis candidolanata*	91	SH1566179.08FU
4159						*Coprinopsis phlyctidospora*	50	SH1566133.08FU
2379					Lacrymaria	*Lacrymaria lacrymabunda*	72	SH1566139.08FU
354					Psathyrella	*Psathyrella echinata*	100	SH1144813.08FU
1016						*Psathyrella sphagnicola*	18	SH1513479.08FU
1155						*Psathyrella cortinarioides*	98	SH1148439.08FU
1249						*Psathyrella scanica*	35	SH1148448.08FU
1566						*Psathyrella trinitatensis*	87	SH2095902.08FU
1700						*Psathyrella orbicularis*	27	SH1508508.08FU
1730						*Psathyrella scanica*	90	SH1148448.08FU
2066						*Psathyrella echinata*	100	SH1144813.08FU
2461						*Psathyrella sphagnicola*	19	SH1513479.08FU
3068						*Psathyrella scanica*	25	SH1148448.08FU
3296						*Psathyrella kellermanii*	25	SH1148450.08FU
3320						*Psathyrella echinata*	57	SH1144813.08FU
3872						*Psathyrella impexa*	20	SH1513442.08FU
934				Strophariaceae	Galerina	*Galerina patagonica*	100	SH1563883.08FU
2192						Unassigned	-	

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
561	Basidiomycota	Agaricomycetes	Agaricales	Strophariaceae	Hypholoma	*Hypholoma brunneum*	94	SH1639455.08FU
805						*Hypholoma fasciculare*	63	SH1639421.08FU
2120						*Hypholoma australe*	74	SH1639464.08FU
2315						*Hypholoma fasciculare*	73	SH1639462.08FU
4095						*Hypholoma fasciculare*	56	SH1639421.08FU
532				Tricholomataceae	Fayodia	*Fayodia gracilipes*	100	SH1553066.08FU
1849						*Fayodia gracilipes*	1	SH1553066.08FU
2441						*Fayodia gracilipes*	100	SH1553066.08FU
710					Mycena	*Mycena rebaudengoi*	79	SH1542295.08FU
754						Unassigned	-	
1711						*Mycena rebaudengoi*	58	SH1542295.08FU
3853					Ripartites	*Ripartites tricholoma*	50	SH1551979.08FU
2795					Tricholoma	*Tricholoma fulvum*	3	SH1520326.08FU
2328				Typhulaceae	Tygervalleyomyces	Unassigned	-	
3027						Unassigned	-	
809			Boletales	Boletaceae	Octaviania	*Octaviania tasmanica*	98	SH1547313.08FU
3904						*Octaviania tasmanica*	99	SH1547313.08FU
308					Phylloporus	Unassigned	-	
3012				Coniophoraceae	Coniophora	*Coniophora opuntiae*	8	SH1142636.08FU
3300				Pisolithaceae	Pisolithus	*Pisolithus microcarpus*	50	SH1519539.08FU
2695				Sclerodermataceae	Scleroderma	*Scleroderma areolatum*	2	SH1172048.08FU
4024						*Scleroderma areolatum*	4	SH1172048.08FU
2618				Tapinellaceae	Tapinella	*Tapinella panuoides*	100	SH1572461.08FU
3720			Cantharellales	Ceratobasidiaceae	Ceratobasidium	Unassigned	-	
42				Clavulinaceae	Clavulina	*Clavulina subrugosa*	11	SH1546126.08FU

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
162	Basidiomycota	Agaricomycetes	Cantharellales	Clavulinaceae	Clavulina	*Clavulina subrugosa*	25	SH1546126.08FU
217						Unassigned	-	
230						*Clavulina subrugosa*	41	SH1546126.08FU
373						*Clavulina subrugosa*	27	SH1546126.08FU
926						*Clavulina subrugosa*	28	SH1546126.08FU
1978						*Clavulina subrugosa*	27	SH1546126.08FU
2640						Unassigned	-	
3041						*Clavulina subrugosa*	12	SH1546126.08FU
3420						*Clavulina subrugosa*	38	SH1546126.08FU
3434						*Clavulina subrugosa*	23	SH1546126.08FU
3491						*Clavulina subrugosa*	17	SH1546126.08FU
790			Geastrales	Geastraceae	Geastrum	*Geastrum fornicatum*	1	SH1217545.08FU
2654						*Geastrum fornicatum*	1	SH1217545.08FU
3088			Jaapiales	Jaapiaceae	Jaapia	*Jaapia ochroleuca*	78	SH1571451.08FU
3847			Polyporales	Fomitopsidaceae	Laetiporus	Unassigned	-	
4087					Obba	*Obba valdiviana*	100	SH1519686.08FU
87				Ganodermataceae	Ganoderma	*Ganoderma australe*	98	SH1555639.08FU
390						*Ganoderma australe*	93	SH1555639.08FU
783						*Ganoderma australe*	97	SH1555639.08FU
2404						*Ganoderma australe*	20	SH1555639.08FU
3794				Meruliaceae	Bjerkandera	*Bjerkandera adusta*	100	SH1615228.08FU
106					Ceriporia	*Ceriporia reticulata*	10	SH1180546.08FU
1506						*Ceriporia reticulata*	8	SH1180546.08FU
688				Xenasmataceae	Xenasmatella	*Xenasmatella vaga*	6	SH1554040.08FU
3609						*Xenasmatella vaga*	9	SH1554040.08FU

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
4052	Basidiomycota	Agaricomycetes	Polyporales	Xenasmataceae	Xenasmatella	*Xenasmatella ardosiaca*	100	SH1554042.08FU
792			Russulales	Russulaceae	Lactarius	*Lactarius imperceptus*	22	SH1632890.08FU
1801						*Lactarius chichuensis*	48	SH1632889.08FU
2176						*Lactarius eucalypti*	78	SH1632888.08FU
1660					Lactifluus	*Lactifluus atrovelutinus*	2	SH1151527.08FU
103					Russula	*Russula crustosa*	1	SH1633448.08FU
119						*Russula cyanoxantha*	1	SH1567120.08FU
228						*Russula heterophylla*	90	SH1633421.08FU
329						*Russula acrolamellata*	29	SH1188932.08FU
426						*Russula acrolamellata*	11	SH1188932.08FU
606						*Russula acrolamellata*	5	SH1188932.08FU
799						*Russula delica*	11	SH1509938.08FU
1001						Unassigned	-	
1358						*Russula crustosa*	11	SH1633448.08FU
1528						*Russula kermesina*	42	SH1212579.08FU
1544						*Russula crustosa*	2	SH1633448.08FU
1807						Unassigned	-	
1906						*Russula acrolamellata*	5	SH1188932.08FU
1929						*Russula violeipes*	13	SH1527635.08FU
1968						*Russula atroviridis*	14	SH1181769.08FU
2068						Unassigned	-	
2389						*Russula anthracina*	6	SH1569618.08FU
2490						*Russula acrolamellata*	6	SH1188932.08FU
2719						Unassigned	-	
2941						*Russula tawai*	17	SH1558619.08FU

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OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
3094	Basidiomycota	Agaricomycetes	Russulales	Russulaceae	Russula	*Russula atroviridis*	13	SH1181769.08FU
3526						*Russula crustosa*	4	SH1633448.08FU
3884						*Russula violeipes*	17	SH1527635.08FU
63			Sebacinales	Sebacinaceae	Sebacina	*Sebacina incrustans*	3	SH1615392.08FU
75						Unassigned	-	
133						Unassigned	-	
211						Unassigned	-	
215						Unassigned	-	
243						*Sebacina dimitica*	5	SH1561893.08FU
455						*Sebacina incrustans*	6	SH1561970.08FU
460						Unassigned	-	
635						Unassigned	-	
667						*Sebacina dimitica*	3	SH1561893.08FU
676						Unassigned	-	
1190						Unassigned	-	
1239						Unassigned	-	
1375						*Sebacina incrustans*	1	SH1561979.08FU
2053						*Sebacina dimitica*	2	SH1561893.08FU
2126						Unassigned	-	
2265						Unassigned	-	
2474						Unassigned	-	
2725						Unassigned	-	
3106						Unassigned	-	
3235						Unassigned	-	
3565						*Sebacina incrustans*	8	SH1561979.08FU

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OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
1748	Basidiomycota	Agaricomycetes	Sebacinales	Serendipitaceae	Serendipita	Unassigned	-	
739			Thelephorales	Thelephoraceae	Tomentella	*Tomentella bryophila*	1	SH1502792.08FU
1390						*Tomentella ferruginea*	1	SH1528432.08FU
3968					Tomentellopsis	Unassigned	-	
1728			Trechisporales	Hydnodontaceae	Luellia	Unassigned	-	
2198						Unassigned	-	
2480						Unassigned	-	
3777						Unassigned	-	
1531					Trechispora	*Trechispora invisitata*	11	SH1544423.08FU
2009						*Trechispora invisitata*	2	SH1544423.08FU
2525						*Trechispora invisitata*	12	SH1544423.08FU
2626						*Trechispora stevensonii*	1	SH1517540.08FU
2637						Unassigned	-	
2696						*Trechispora invisitata*	9	SH1544423.08FU
2743						Unassigned	-	
2884						*Trechispora invisitata*	13	SH1544423.08FU
3229						Unassigned	-	
3345						*Trechispora cohaerens*	19	SH1180898.08FU
3361						*Trechispora caucasica*	2	SH1180896.08FU
3452						Unassigned	-	
3842						*Trechispora cohaerens*	23	SH1557424.08FU
3039		Agaricostilbomycetes	Agaricostilbales	Chionosphaeraceae	Cystobasidiopsis	*Cystobasidiopsis lophatheri*	68	SH1522728.08FU
429		Geminibasidiomycetes	Geminibasidiales	Geminibasidiaceae	Basidioascus	*Basidioascus magus*	68	SH1722769.08FU
1287						*Basidioascus undulatus*	89	SH1555408.08FU
4182						*Basidioascus undulatus*	99	SH1555408.08FU

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OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
182	Basidiomycota	Geminibasidiomycetes	Geminibasidiales	Geminibasidiaceae	Geminibasidium	*Geminibasidium donsium*	1	SH1563154.08FU
359						Unassigned	-	
555						Unassigned	-	
602						Unassigned	-	
1093						Unassigned	-	
1114						*Geminibasidium hirsutum*	4	SH1563158.08FU
1771						*Geminibasidium hirsutum*	4	SH1563158.08FU
2082						*Geminibasidium hirsutum*	6	SH1563158.08FU
2528						*Geminibasidium donsium*	54	SH1563154.08FU
2836						*Geminibasidium hirsutum*	9	SH1563158.08FU
2857						Unassigned	-	
3011						*Geminibasidium hirsutum*	2	SH1563158.08FU
3230						*Geminibasidium hirsutum*	4	SH1563158.08FU
624		Microbotryomycetes	*Incertae sedis*	Chrysozymaceae	Udeniozyma	Unassigned	-	
1291			*Incertae sedis*			Unassigned	-	
2144			*Incertae sedis*	*Incertae sedis*	Colacogloea	*Colacogloea falcata*	100	SH1522643.08FU
1157			Sporidiobolales	Sporidiobolaceae	Rhodosporidiobolus	*Rhodosporidiobolus fluvialis*	20	SH1558735.08FU
1024					Sporobolomyces	*Sporobolomyces johnsonii*	100	SH1575130.08FU
1232		Tremellomycetes	Cystofilobasidiales	Cystofilobasidiaceae	Cystofilobasidium	*Cystofilobasidium capitatum*	84	SH1650088.08FU
1096				Mrakiaceae	Tausonia	*Tausonia pullulans*	99	SH1650607.08FU
3858			Filobasidiales	Piskurozymaceae	Piskurozyma	Unassigned	-	
9					Solicoccozyma	*Solicoccozyma terricola*	100	SH1649268.08FU
278						*Solicoccozyma terrea*	55	SH1649269.08FU
588						*Solicoccozyma terricola*	100	SH1649268.08FU
765						*Solicoccozyma terricola*	100	SH1649268.08FU

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
1372	Basidiomycota	Tremellomycetes	Filobasidiales	Piskurozymaceae	Solicoccozyma	*Solicoccozyma terrea*	60	SH1649269.08FU
1770						*Solicoccozyma terrea*	57	SH1649269.08FU
4190						*Solicoccozyma aeria*	95	SH1649270.08FU
2425			Tremellales	Tremellaceae	Tremella	Unassigned	-	
4167						Unassigned	-	
2216	Calcarisporiellomycota	Calcarisporiellomycetes	Calcarisporiellales	Calcarisporiellaceae	Calcarisporiella	Unassigned	-	
2906	Chytridiomycota	Chytridiomycetes	Chytridiales	Chytridiaceae	Dendrochytridium	*Dendrochytridium crassum*	100	SH1553914.08FU
2699		Lobulomycetes	Lobulomycetales	Lobulomycetaceae	Lobulomyces	*Lobulomyces poculatus*	1	SH1160020.08FU
3575						*Lobulomyces poculatus*	81	SH1160020.08FU
1138		Rhizophlyctidomycetes	Rhizophlyctidales	Rhizophlyctidaceae	Rhizophlyctis	*Rhizophlyctis rosea*	96	SH1149333.08FU
514		Rhizophydiomycetes	Rhizophydiales	Rhizophydiaceae	Rhizophydium	Unassigned	-	
895						Unassigned	-	
1150						Unassigned	-	
2584						Unassigned	-	
2925						Unassigned	-	
3365						Unassigned	-	
3961						Unassigned	-	
349				*Incertae sedis*	Operculomyces	*Operculomyces laminatus*	100	SH1538470.08FU
3171		Spizellomycetes	Spizellomycetales	Powellomycetaceae	Powellomyces	Unassigned	-	
2157	Entomophthoromycota	Entomophthoromycetes	Entomophthorales	Ancylistaceae	Conidiobolus	*Conidiobolus coronatus*	28	SH1548452.08FU
3288						*Conidiobolus coronatus*	1	SH1548453.08FU
3363	Glomeromycota	Glomeromycetes	Diversisporales	Diversisporaceae	Diversispora	Unassigned	-	
2933			Glomerales	Glomeraceae	Glomus	Unassigned	-	
3419						Unassigned	-	
3507						Unassigned	-	

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
2	Mortierellomycota	Mortierellomycetes	Mortierellales	Mortierellaceae	Mortierella	*Mortierella minutissima*	1	SH1607998.08FU
4						*Mortierella elongata*	9	SH1557020.08FU
7						*Mortierella pseudozygospora*	95	SH1529195.08FU
8						Unassigned	-	
17						*Mortierella sarnyensis*	99	SH1557018.08FU
21						Unassigned	-	
25						Unassigned	-	
30						*Mortierella gamsii*	24	SH1557013.08FU
34						*Mortierella zonata*	10	SH1557019.08FU
37						*Mortierella alpina*	51	SH1650283.08FU
46						Unassigned	-	
47						*Mortierella amoeboidea*	87	SH1557037.08FU
73						*Mortierella fimbricystis*	2	SH1608140.08FU
78						*Mortierella gamsii*	17	SH1557011.08FU
108						*Mortierella jenkinii*	71	SH1629839.08FU
127						Unassigned	-	
149						Unassigned	-	
268						Unassigned	-	
272						*Mortierella gemmifera*	83	SH1557014.08FU
277						Unassigned	-	
327						Unassigned	-	
357						Unassigned	-	
363						*Mortierella beljakovae*	56	SH1554355.08FU
393						*Mortierella fimbricystis*	88	SH1608140.08FU
459						*Mortierella sarnyensis*	99	SH1557018.08FU

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
507	Mortierellomycota	Mortierellomycetes	Mortierellales	Mortierellaceae	Mortierella	*Mortierella ambigua*	85	SH1573330.08FU
516						*Mortierella elongata*	3	SH1557020.08FU
523						*Mortierella jenkinii*	79	SH1629839.08FU
533						Unassigned	-	
543						*Mortierella globulifera*	100	SH1557569.08FU
565						*Mortierella hyalina*	14	SH1557031.08FU
571						*Mortierella amoeboidea*	95	SH1557037.08FU
578						*Mortierella alpina*	63	SH1650283.08FU
722						*Mortierella amoeboidea*	89	SH1557037.08FU
749						Unassigned	-	
936						*Mortierella chlamydospora*	44	SH1556954.08FU
975						*Mortierella jenkinii*	5	SH1629839.08FU
1030						*Mortierella kuhlmanii*	52	SH1724700.08FU
1049						*Mortierella amoeboidea*	100	SH1557037.08FU
1106						*Mortierella fimbricystis*	1	SH1608140.08FU
1172						Unassigned	-	
1229						*Mortierella sarnyensis*	73	SH1557053.08FU
1244						*Mortierella elongata*	1	SH1557020.08FU
1500						Unassigned	-	
1563						*Mortierella jenkinii*	70	SH1629839.08FU
1582						Unassigned	-	
1624						*Mortierella jenkinii*	82	SH1629839.08FU
1692						Unassigned	-	
1760						*Mortierella jenkinii*	82	SH1629839.08FU
1779						*Mortierella jenkinii*	1	SH1629839.08FU

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
1819	Mortierellomycota	Mortierellomycetes	Mortierellales	Mortierellaceae	Mortierella	Unassigned	-	
1872						*Mortierella ambigua*	79	SH1573330.08FU
2007						*Mortierella amoeboidea*	92	SH1557037.08FU
2080						Unassigned	-	
2301						Unassigned	-	
2406						*Mortierella sarnyensis*	1	SH1557018.08FU
2565						*Mortierella globulifera*	100	SH1557569.08FU
2573						*Mortierella alpina*	100	SH1650283.08FU
2783						*Mortierella minutissima*	1	SH1607998.08FU
2868						*Mortierella ambigua*	88	SH1573330.08FU
2877						*Mortierella jenkinii*	70	SH1629839.08FU
2882						Unassigned	-	
2893						*Mortierella amoeboidea*	97	SH1557037.08FU
3018						Unassigned	-	
3287						Unassigned	-	
3305						*Mortierella pseudozygospora*	93	SH1529195.08FU
3569						*Mortierella gamsii*	21	SH1557011.08FU
3642						Unassigned	-	
3812						Unassigned	-	
3955						*Mortierella amoeboidea*	90	SH1557037.08FU
3972						*Mortierella gamsii*	13	SH1557013.08FU
4025						*Mortierella amoeboidea*	1	SH1557037.08FU
1348	Mucoromycota	Endogonomycetes	Endogonales	*Incertae sedis*	Densospora	Unassigned	-	
2215				*Incertae sedis*		Unassigned	-	
3206				*Incertae sedis*		*Densospora laevis*	1	SH1525386.08FU

Appendix 2.5 continued

OTU#	Phylum	Class	Order	Family	Genus	Species	% match	Unite accession code
4006	Mucoromycota	Endogonomycetes	Endogonales	*Incertae sedis*	Densospora	Unassigned	-	
1245		Umbelopsidomycetes	Umbelopsidales	Umbelopsidaceae	Umbelopsis	*Umbelopsis angularis*	52	SH1557754.08FU
1710						*Umbelopsis ramanniana*	78	SH1522257.08FU
1777						*Umbelopsis angularis*	76	SH1557754.08FU
1904						*Umbelopsis dimorpha*	98	SH1522247.08FU
1996						*Umbelopsis ramanniana*	65	SH1557751.08FU
2303						*Umbelopsis angularis*	40	SH1557754.08FU
2577						*Umbelopsis isabellina*	43	SH1522249.08FU
2852						*Umbelopsis isabellina*	32	SH1522249.08FU
3350						*Umbelopsis angularis*	83	SH1557754.08FU
3707						*Umbelopsis isabellina*	88	SH1522249.08FU
4000						*Umbelopsis isabellina*	1	SH1522248.08FU
1935	Zoopagomycota	Zoopagomycetes	Zoopagales	Piptocephalidaceae	Syncephalis	Unassigned	-	
3277						Unassigned	-	
3801						Unassigned	-	

SUPPLEMENTARY MATERIAL

S1. Litter and soil displacement by the superb lyrebird. https://youtu.be/vMPc5ikhXZQ