BIOTIC INTERACTIONS AFFECTING THE REPRODUCTIVE SUCCESS OF ANTARCTIC BEECH (*NOTHOFAGUS MOOREI)*
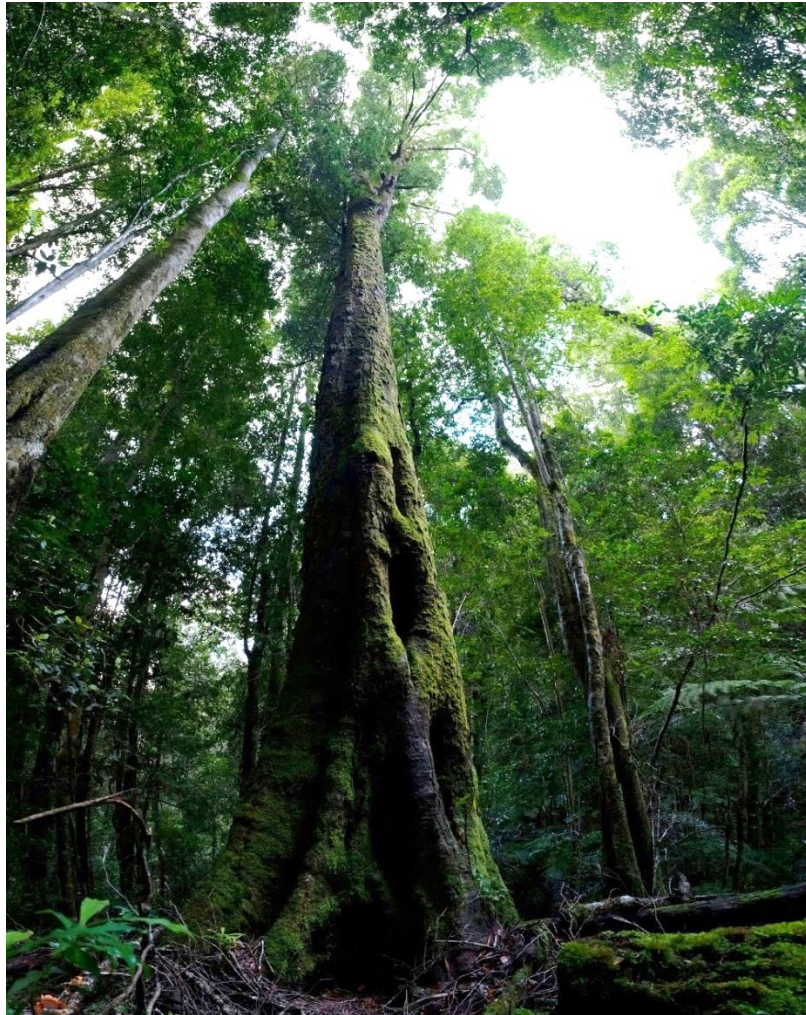
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DECLARATION

I wish to acknowledge the following assistance in the research detailed in this report:

Andrea Westerband assisted with the statistical analysis of all components in this thesis.

Dominique Homberger provided valuable knowledge into the behaviour and ecology of parrots.

Ian Wright assisted with the organisation of the project as a whole and finalisation.

Ross Peacock provided the long-term regeneration, climate and vertebrate exclusion data that this thesis is largely based on.

All other research described in this report is my own original work.

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ABSTRACT

Nothofagus moorei (Antarctic Beech) is the dominant canopy tree of many remaining fragments of cool temperate rainforests of northern NSW and south-eastern Queensland. Despite being an iconic species there is a paucity of information (especially quantitative data) concerning life history stages and processes that together determine reproductive success. In this thesis I made significant advances towards closing this knowledge gap. First, pre-dispersal fruit/seed predation by birds and insects was quantified, revealing a decreasing amount of predation later in the masting season – in accordance with the "predator starvation/satiation" hypothesis. Second, the proportion of juveniles that were derived from seed or vegetative regeneration was quantified, both for *N. moorei* and co-occurring tree species. While there was a higher abundance of seedlings, juveniles of vegetative origin exhibited superior relative height. Third, I quantified the influence of soil-litter disturbing vertebrates on juvenile tree success. While, overall, survivorship and growth were higher in the presence of soil disturbing vertebrates, Antarctic Beech juveniles exhibited enhanced survival when protected from physical disturbance. These findings provide a greater understanding of the mechanisms underpinning stand dynamics and canopy renewal of Antarctic Beech and co-occurring tree species in an ecologically unique vegetation type under increasing threat from climate change.

1. INTRODUCTION

This thesis primarily concerns biotic interactions affecting the iconic species *Nothofagus moorei* in one area – Werrikimbe and Willi Willi National Parks – of its native habitat in northern NSW, Australia. Secondary emphasis concerns juveniles of the tree species which co-occur with *N. moorei* at my study sites. This Introduction (Chapter 1) is comprised of two components: first, a general literature review regarding the genus *Nothofagus*, its biotic interactions and its regeneration strategies, largely written before the thesis research was undertaken; and second, an overview of the research questions and associated hypotheses addressed in this thesis. Three studies were conducted as part of my thesis work, focusing on: Pre-dispersal seed predation on *Nothofagus moorei* (Chapter 2); Regeneration modes of cool temperate rainforest trees (Chapter 3); and The effect of vertebrate exclusions on rainforest juveniles (Chapter 4). Each of these chapters includes a Methods and a Results section. A general Discussion follows (Chapter 5), allowing consideration of the three studies together. An Appendix section placed after the bibliography contains supplementary results.

Literature Review

Strategies and Biotic interactions of Nothofagus

Nothofagus is an ancient Cretaceous genus with a distribution that has attracted considerable interest from biogeographers investigating the vicariance versus long-distance dispersal controversy, and is a major component of the southern hemisphere fossil record (Hill, 1992, Hill et al., 2015). *Nothofagus* had a much greater distribution and diversity in the past than it currently has, indicating the extant distribution and relatively small number of living species represents the remnants of a once remarkably dominant genus (Hill et al., 2015).

Fossil records indicate that the genus *Nothofagus* occurred throughout cool temperate rainforests that spread across most of Gondwana prior to the breakup of the continent (Heenan and Smissen, 2013). *Nothofagus* is currently found in the Patagonian region of South America, in select areas of eastern Australia and throughout the islands of New Zealand, New Caledonia and New Guinea (Hill et al., 2015).

Nothofagus species are long-lived, with *N. moorei* estimated via tree ring analysis at Werrikimbe NP (pers. comm. Peacock) to live at least to 300 years. *Nothofagus* trees often dominate the canopy in temperate rainforest, but are generally highly limited in their distribution, restricted by climate and geography (Hill and Dettmann, 1996). Most species have very slow

growth, only gaining 1-2 mm in diameter growth each year (pers. comm. Peacock). These traits make this genus vulnerable to biotic interactions in the early stages of its life cycle.

This review will outline the reproductive strategies of *Nothofagus* species, and some of the biotic interactions this genus incurs. I will cover two types of biotic interactions that occur within the genus *Nothofagus* and associated species in cool temperate rainforests. Firstly, I will look at the trophic interactions that occur prior to seed dispersal, identifying a potential tri-trophic interaction. Secondly, I will investigate the effects of native ecosystem engineers on the different regeneration strategies pursued by *Nothofagus*, i.e. seedlings and vegetative growth. Lastly, I will address gaps in our knowledge regarding the Australian species *Nothofagus moorei* with particular reference to a site in northern New South Wales (NSW).

Sexual reproduction and pre-dispersal biotic interactions

All species of *Nothofagus* are monecious, with male flowers occurring prior to female flowers (Veblen et al., 1996). Flowering occurs during the same few months of the year dependent on location, with the exception of tropical species located in New Guinea and New Caledonia which have been recorded flowering at different times between January and August (Read and Hope, 1996). The occurrence and quantity of mast flowering (the large synchronous seed season) in southern beech trees is highly variable each year (Allen et al., 2014), with masting years thought to correspond to the preceding spring being unusually dry (Veblen et al., 1996), although a number of other hypotheses have been proposed (Bahamonde et al., 2016).

Masting behaviour occurs with a periodicity of between two and eleven years (Marchelli and Gallo, 1999, Ogden et al., 1996, Read, 1989). Nothofagus species are anemophilous (Riveros et al., 1995), with pollen transfer between individuals relying on wind, however, in the closed rainforest canopies pollen is unlikely to be spread far by wind currents. There is currently no published information on self-compatibility in Australian species therefore this may be an important constraint on the species dispersal and consequentially, the ability to expand its range.

The seeds of Australian *Nothofagus spp.* are also thought to be primarily wind dispersed (Read and Brown, 1996) although there are no empirical studies to support this. Studies have shown that the majority of fruits with seeds fall within 20 m and up to 150 m away from the parent tree (Read and Hope, 1996, Read and Brown, 1996, Ogden et al., 1996, Hickey et al., 1983, Veblen et al., 1996). This poor dispersal is due to the small wings of the fruit relative to the weight and size of

the fruits. However, some have suggested seeds may be dispersed long distances in water (Preest, 1963 in Read and Hope, 1996); Wardle 1984 in Read and Brown, 1996). There is also the possibility of dispersal in the fur of arboreal mammals such as possums, as the cupules containing the fruits are covered in small sticky hair-like appendages (pers. obs. Peacock).

Two chief hypotheses have been proposed to explain the selective advantages of masting: pollination efficiency (Schauber et al., 2002), and starvation/satiation of predators (Kelly et al., 2001, Kon et al., 2005, Janzen, 1971). Firstly, pollination success is believed to be increased during high flowering years due to a higher diversity of pollen being available (Kelly et al., 2001). This hypothesis is supported by Kon et al (2005) whose study found pollination failure was as high at 75% in a non-mast year, whereas during a mast season it was as low as 43%. This failure is likely due to the decreased genotypic diversity with only a few trees flowering as well as higher predation rates (Marchelli and Gallo, 1999).

The second hypothesis ("starvation/satiation") suggests that seed predator populations will decrease due to starvation in non-mast years, such that population sizes decrease and become satiated more quickly in the next masting season, allowing a larger proportion of seeds to survive (Crawley and Long, 1995, Kon et al., 2005, Nilsson and Wastljung, 1987). In the cool temperate rainforests of Japan, Kon et al (2005) found seed predation of Japanese beech (*Fagus crenata)* to be a larger cause of seed mortality than pollination failure.

Pre-dispersal seed predation
Similar to other masting taxa, masting events in *Nothofagus* attract a range of seed predators. Pre-dispersal seed predation is limited to species that can fly or live in the canopy, such as parrots and insects. The loss of viable seeds due to predation may be significant considering that only a small proportion of undamaged fruits contain viable seeds (Graeme Errington, pers. obs).

Insects
Predation by insects may result in reduced flowering and seed production. Various insects, such as those occurring in the orders Diptera, Lepidoptera, Coleoptera and Hymenoptera feed on the seeds and flowers, adversely affecting the reproductive output of the plant (Schoonhoven et al., 2005). While some insects specialise in seed-boring (feeding occurs inside the seed or seed pod (Price, 2011), many insects also parasitise the plant, depositing eggs into flower buds, where the eggs will then hatch and develop into larvae (Schoonhoven et al., 2005). Some species of moths in the

Gelechiidae family are known to bore into fruits and flowers as larvae, where they pupate (Zborowski and Edwards, 2007). There are approximately 800 species belonging to this family in Australia, many of which are unidentified (Zborowski and Edwards, 2007). This family of insect has been found in *Nothofagus truncana* and *Nothofagus menziesii* in New Zealand (Alley et al., 1998).

Evidence of pre-dispersal insect predation is also present in *N. glauca* of Chile. Previous studies have found that 57% of seeds contained Microlepidopteran larvae, *Perzelia spp.* (Burgos et al., 2008). *Perzelia* adults emerge from August to November, similar in timing to the flowering of *N. glauca* (Morales 1993 and Rojas 1996 in Burgos et al., 2008). It is likely that adults parasitize female flowers with their eggs in early spring at the moment of flowering. Larval stage lasts approximately 2 months, during which time the larvae grow inside the developing fruits, feeding on the seeds. The larvae then emerge when seeds fall, and once on the ground they enter the pupal stage (Burgos et al., 2008, Marchelli and Gallo, 1999). Marchelli and Gallo (1999) found more than 80% of *N.nervosa/alpine* seeds showed evidence of insect damage.

In New Zealand, a similar insect-plant interaction may occur between a moth and *N. truncata.* Shortly after the emergence of male flowers in *N. truncata,* large amounts of *Tingena* moths have also been observed emerging (Ogden et al., 1996).

Parrots

Species of parrot are known to forage on *Nothofagus* species over the world, particularly during a masting season. For example, parakeets have been observed feeding on flowers and fruits in both South America and New Zealand (Diaz and Kitzberger, 2006, Ogden et al., 1996). However, the parrots may not just be feeding on the plant structures.

Parrots and other species of birds were originally thought to have specialised diets: they would be classified as either frugivorous (fruit eaters), granivorous (seed eaters), nectivorous (nectar eaters), or insectivorous (insect eaters). Over time, research has shown many birds display opportunistic feeding behaviours with seasonal dietary switches that indicate several types of food may be consumed. The Austral Parakeet *(Enicognathus ferrugineas)* of South America, for example, will feed upon the pollen grains of *N. pumilio*, but then in late summer it switches to only eating seeds (Diaz and Kitzberger, 2006). Dietary shifts may also be more diverse than changing the plant structure which is fed on. In times of decreased plant growth, some species are known to switch to a more insectivorous diet (Boyes and Perrin, 2013, Selman et al., 2002). The switch to insects may also occur as an active choice, such as when birds have a higher nutritional need for

protein in breeding season, for example house sparrows (*Passer domesticus*) (Klvanova et al., 2011).

Many parrot species are canopy feeders and are believed to be highly granivorous (Diaz et al., 2012). Even though the majority of their diet consists of seeds, these birds are not limited to this diet and will actively forage for fruits, nectar and invertebrates (Bollen and van Elsacker, 2004, Contreras-Gonzalez et al., 2009, Diaz et al., 2012, Renton, 2001). This varied diet allows parrots to survive when particular food resources are limited. For example, Rüpell's Parrot (*Poicephalus rueppellii*) feeds primarily on seeds from December-August and nectar from January-May, but switches to flowers and invertebrates during September-November when seeds are less abundant (Selman et al., 2002).

Many parrot species throughout the world have been observed feeding on insects, despite being thought of as highly granivorous or frugivorous (Boyes and Perrin, 2013, Diaz and Peris, 2011, Galetti, 1993, Homberger, 2003, Long, 1984, Magrath and Lill, 1983, Martuscelli, 1995, Sazima, 1989, Selman et al., 2002, Symes and Perrin, 2003, Taylor and Perrin, 2006, Warburton and Perrin, 2005). Similar to sparrows, parrots will not only consume invertebrates when opportunity occurs, but they will actively search for them in preference of plant material (Boyes and Perrin, 2009, Boyes and Perrin, 2013, Derbel et al., 2007, Rowley and Chapman, 1991, Selman et al., 2002). Invertebrate consumption provides the bird with a greater amount of protein and fat compared to a purely plant-based diet (Levey and Karasov, 1989, Magrath and Lill, 1983).

Parrots have been observed foraging on a variety of invertebrate orders (Coleoptera, Lepidoptera, Hemiptera, Hymenoptera), showing a preference for larvae and nymphs located in galls, tree bark, and leaves, but also for cryptic invertebrates within seeds and fruit (Boyes and Perrin, 2013, Diaz and Peris, 2011, Homberger, 2003, Magrath and Lill, 1983). The morphological features of the psittaciforme bill and highly movable tongue allow parrots to easily deshell seeds as well as extract any invertebrates from within plant structures (Homberger, 1988, Homberger, 1994, Homberger, 2017, Homberger, 2003, Mudge, 1902). This specialised bill and tongue are likely being used to extract invertebrates when there are observations of large amounts of food dropped by parrots. The lesser vasa parrot (*Coracopsis nigra*) of Madagascar, for example, known to feed on seeds, fruits, and nectar, is also known to be a highly 'wasteful' species, dropping seemingly excessive amounts of uneaten food to the ground (Bollen and van Elsacker, 2004). This food wastage is also observed in South America, where research has shown that fruits dropped by parrots

have evidence of invertebrate larvae once inhabiting them (Diaz and Peris, 2011, Martuscelli, 1995).

Considering the research above, it is likely that the parrots observed foraging on *Nothofagus* flowers and fruits may in fact have been foraging for invertebrates (pers. comm, Homberger.). This potential tri-trophic interaction involving *Nothofagus*, invertebrate larvae and parrots requires additional research.

Seedling recruitment and biotic interactions

Masting seasons lead to prolific seedling germination; however, seedlings from masting events are often short-lived. Seedlings of *N. gunnii* and the Victorian *N. cunninghamii* rarely survive more than one year (Read and Brown, 1996). The reasons for their short lifespan include, but are not limited to, high shade intolerance (Read and Hill, 1985b) and difficulty establishing themselves in a loose soil layer created by ground-disturbing animals (Read and Brown, 1996). Most seedling mortality is caused by biotic interactions (self-thinning, pathogens, fungi, effects of herbivores, litter burial). However, physical disturbance by animals may also increase seedling mortality. Animals that alter their surroundings intentionally or unintentionally are known as ecosystem engineers.

Ecosystem engineers physically modify the environment, altering the availability of resources available to other taxa (Jones et al., 1994, Jones et al., 1997). Ecosystem engineering occurs at multiple temporal and spatial scales. Coggan et al (2017) describes three levels of ecosystem engineering: 1. The obligate engineer who has large impacts on the ecosystem structure and function; 2. The facultative engineer whose impacts are only detectable under certain conditions; and 3. The non-engineer who has minimal influence on ecosystem and whose actions may only affect very few species.

There are very few vertebrates that could be considered ecosystem engineers in rainforests dominated by *Nothofagus moorei*. The main species known to modify the landscape in this ecosystem is the Australian Brush Turkey (*Alectura lathami*). Brush turkeys use their large feet to scratch up the soil and litter layer whilst they forage for invertebrates and when they are building mounds in which to incubate their eggs. Brush turkey mounds measure up to 5 metres in diameter, are about 1 m high (Jones, 1988) and weigh between 3-4 tonnes (Vleck et al 1984). These mounds are the sole reproductive resource used to incubate their eggs and will be maintained by the birds for approximately seven months (Jones, 1988).

Another potential ecosystem engineer (Ashton and Bassett, 1997, Maisey et al., 2019) is the superb lyre bird *(Menura novaehollandiae)*, which are endemic to temperate forests (Tassell, 2014). These birds are known to move up to 200 tonnes per hectare per year of soil-litter in sclerophyll forests (Ashton and Bassett, 1997) and have been seen moving rocks weighing up to 2 kg (Tassell, 2014). Similar to brush turkeys, lyre birds scratch up the soil-litter layer to forage for invertebrates. Additionally, the males will scratch over a bare patch of soil about 1 m in diameter as part of their courtship display (Adamson et al. 1983 in Tassell 2014). Females may build nests on the ground or in low trees (Lill, 1996).

Both the Australian brush turkey and superb lyre bird frequent northern NSW rainforests, with a slight preference during the October to January breeding season of the brush turkey. Brush turkeys occur in low altitude subtropical rainforest, and superb lyre birds in high altitude rainforest and open forest (Osborne, 1991). These soil-disturbing behaviours can have both positive and negative effects on the surrounding seedlings (Dunham, 2011), including many seedlings becoming uprooted or buried. One reproductive strategy that may help decrease plant mortality is vegetative regeneration.

Vegetative regeneration

Vegetative regeneration is a form of asexual reproduction where clones arise from roots or stems of living plants. It allows plants to remain present for long periods of time, a valuable trait especially if seedlings have specific establishment requirements, such as high light conditions. In addition, vegetative growth allows the colonisation of new ground when seedling establishment may fail due to stressful or changing conditions. Many temperate angiosperms exhibit different types of vegetative regeneration. Two types of vegetative growth have been identified by Tredici (2001): "sprouting", which is the repair and eventual replacement of damaged trunks, and "clonality", which is the appearance of additional trunks without initial damage. However, it is difficult to distinguish between the two origins of a vegetative shoot in the field.

Sprouting, the more common form of vegetative growth, can occur in four ways: collar or basal sprouts, sprouts from specialised underground stems (rhizomes), sprouts from roots (root suckers), and opportunistic sprouts from layered branches or the trunk (Tredici, 2001). More importantly than the origin of the sprout is how it responds to its surroundings. The behaviour of sprouting by plants has proven to be advantageous in the arboriculture and silviculture industries. The technique of coppicing, where tree stems and trunks are regularly cut, has been used in forestry

as a way to encourage secondary growth in plants (Beach, 1974). Northern Red Oak (*Quercus rubra*) sprouts (resulting from coppicing) have been shown to have higher photosynthetic rates, higher stomatal conductance, increased growth rates, and a lower leaf area to root surface area ratio than those that were un-coppiced (Kruger and Reich, 1993b, Kruger and Reich, 1993a). Sprouting in *N. cunninghamii* has been demonstrated to produce leaves with increased stomatal conductance compared to canopy leaves, i.e., the leaves of vegetative sprouts are more responsive to diffuse sunflecks (Tausz et al., 2005).

Sprouting is known to occur in all three Australian species of *Nothofagus*. Evidence of epicormic sprouting has been observed in both *N. cunninghamii* and *N. moorei* following fire (Howard, 1973). Layering, where low hanging branches send roots to the ground, has been observed in *N. gunnii* (Read and Brown, 1996). High amounts of vegetative reproduction have been observed in closed, undisturbed forests of *N. moorei* (Johnston and Lacey, 1983, Read and Hill, 1985a, Read and Hope, 1996, Read and Brown, 1996). However, sprouting from mature canopy trees in undisturbed forests is rarer, therefore these trees are more likely to be clonal (Tredici, 2001).

Clonality, such as sprouting, produces genetically identical copies of the parent tree and can originate in the same ways (rhizomes, root suckering, layering) albeit without the initial damage to the parent tree. Peterson and Jones (1997) state that there are two main benefits of clonality in woody species. Firstly, it increases the stability of the parent tree, and secondly, it reduces the risk of damage to the parent tree. Among angiosperms in temperate forests, root suckering is one of the most common techniques, for both monocot and dicot taxa (Jenik, 1994, Peterson and Jones, 1997).

While vegetative reproduction appears to enhance survival and colonisation where seedling regeneration is not effective, these communities are genetically limited (Schultz, 2008). However, not all multi-stemmed clusters are genetically identical, as some species have found a way to gain the benefits of vegetative reproduction while still maintaining diversity. Genetic diversity within a clonal population can occur with niche specialisation (Skalova et al., 1997) and by somatic mutations (Antolin and Stroback, 1985). For example, clonality was detected in *N. pumilio* clusters on the edges of second growth forests, usually following fire disturbance (Till-Bottraud et al., 2012), but each cluster comprised at least two different genotypes (Till-Bottraud et al., 2012). By visual inspection alone it had been expected that these clusters had been formed by a type of vegetative reproduction, but it was also suspected that seedlings may have merged to withstand the high winds of the forest edge (Fajardo and McIntire, 2011).

Cool temperate rainforests in Australia

There are three species of Australian *Nothofagus.* They are often the dominant species of cool temperate rainforests. All three species are confined to areas with high rainfall and high atmospheric humidity, which are occasionally supplemented by ground water (Read and Brown, 1996).

Nothofagus gunnii is endemic to the cool montane regions of Tasmania. *Nothofagus cunninghamii* has the widest distribution in Australia and is found both in Victoria and Tasmania. The flowering seasons of *N. gunnii* and *N. cunninghamii* often coincide with each other and with other masting angiosperms, which suggests that flowering is strongly affected by climate (Read and Hill, 1989). After flowering in October-December, the fruits of both species are released in late summer, depending on climatic conditions (Read and Brown, 1996).

Nothofagus moorei is the most northern species of *Nothofagus* and is found only at altitudes above 500 metres and primarily above 900 m in north-eastern NSW and south-eastern Queensland. Rainfall seems to be the main confining factor in this species' distribution, limiting it to areas with 50 mm of rainfall in the driest month and a total of at least 1800 mm per year (Read and Brown, 1996). Flowering in *N. moorei* begins in August and ceases in October, while fruits are released from December to March (Floyd, 1990).

Even though *N. moorei* and *N. cunninghamii* occur in the east of mainland Australia, they are not co-occurring. Read and Hill (1989) suggest that one of the reasons is that *N. cunninghamii* is more tolerant of frost. While less frost tolerant, *N. moorei* may not spread into warmer areas because of its lack of shade tolerance and inability to compete with species adapted to a combination of warmth and shade (Read and Hill, 1985a). The divergence of these two species is likely to have occurred in the late Tertiary and into the Quaternary when there were large climatic changes (Adam, 1992).

Floyd (1990) lists two chief types of cool temperate rainforest in NSW, one dominated by *N. moorei* in the north,* and the other by *Eucryphia moorei* in the south. In many areas, other co-dominant species are often associated with *Nothofagus moorei* stands. There are five recognised alliances with *Nothofagus moorei* in NSW: *Nothofagus-Quintinia sieberi-Doryphora, Nothofagus-Ceratopetalum, Nothofagus-Callicoma-Tristaniopsis, Nothofagus-Doryphora-Orites-Caldcluvia,* and *Nothofagus-Elaeocarpus holopetalus* (Floyd, 1990). Most of these alliances are disjunct from

one another and occur at different altitudes (Fig.1; Table 1). A more detailed overview of the floristic associations of *N. moorei* rainforests in NSW is provided by Bale and Williams 1993.

Table 1. The known altitudes and locations of each *N. moorei* alliance.

Alliance	Altitude	Location
Nothofagus-Quintinia sieberi-Doryphora	750 m – 1 450 m	Border Ranges NP, New England NP, Cunnawarra NP
Nothofagus-Ceratopetalum	800 m – 1 240 m	Lamington NP, Dorrigo NP, Cunnawarra NP, Werikimbe NP, Willi Willi NP
Nothofagus-Callicoma-Tristaniopsis	Over 1 000 m	Mt Nothofagus NP, Limpinwood NR, Kiwarrak SF, Ulidarra NP
Nothofagus-Doryphora-Orites-Caldcluvia	700 m – 1 000 m	Barrington Tops NP (Gloucester to Paterson Rivers)
Nothofagus-Elaeocarpus holopetalus	1 150 m – 1 500 m	New England NP, Barrington Tops NP
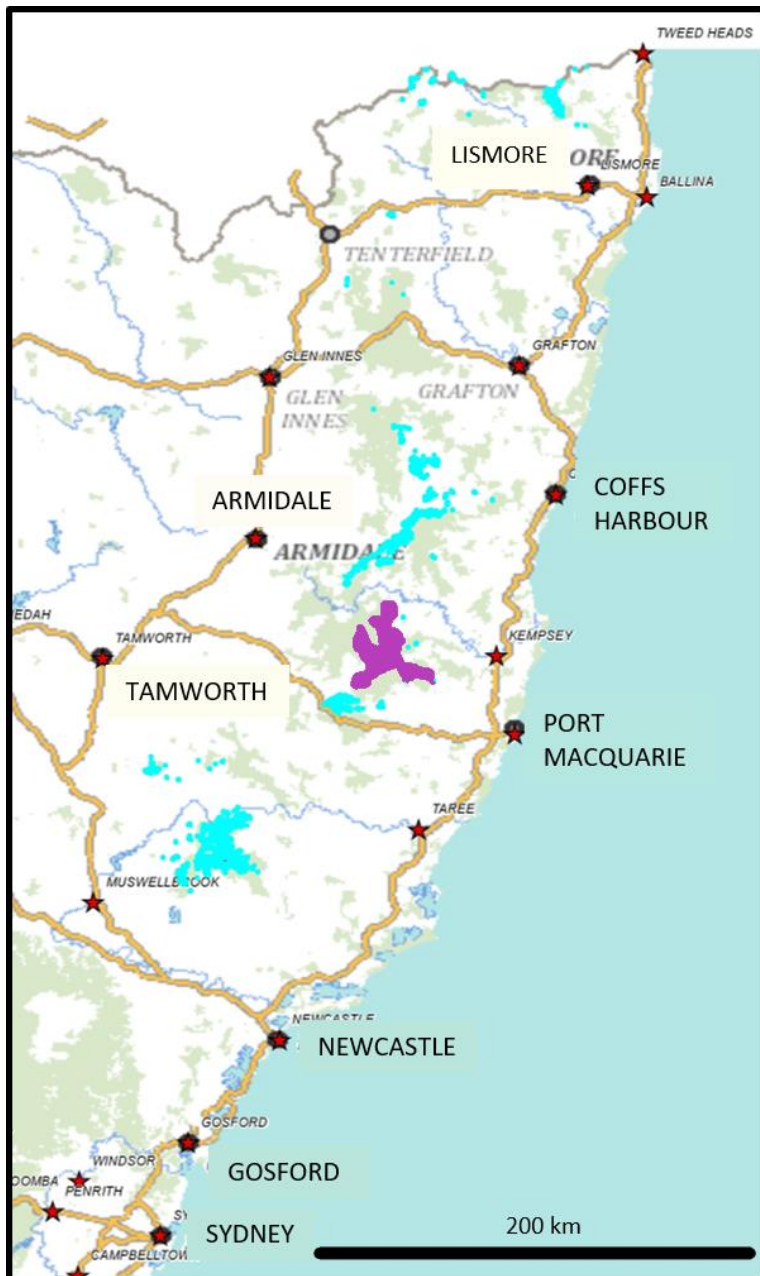
Figure 1. Geographic distribution of Nothofagus moorei. The disjunct locations of *N. moorei* are shown in blue. The location of Werrikimbe and Willi Willi National Parks is shown in purple.

Northern NSW site - 'Werrikimbe' and 'Willi Willi' National Parks

Among the alliances with *N. moorei, Nothofagus-Ceratopetalum* is the focal alliance of this thesis. The largest area of this alliance occurs in the Upper Hastings area, including Werrikimbe National Park and Willi Willi National Park (formerly Mt Boss), approximately 60 km west from Port Macquarie. This is within the upper reaches of the Forbes and Wilson River catchments. This *Nothofagus-Ceratopetalum* pairing occurs at altitudes of 800 m – 1240 m (Downing et al., 2014,

Floyd, 1990). While *N. moorei* is the dominant species, *Ceratopetalum apetalum* forms a dense lower canopy layer (Floyd, 1990). The area was chosen for the present study for its lack of human disturbance and because it contains some of the largest contiguous sections of cool temperate rainforests dominated by *Nothofagus moorei* in Australia. The forests in this area are classified in the Hastings-Macleay Group of the Gondwana Rainforests of Australia World Heritage property (Floyd, 1990)

The study area is characterised by moderate to steep slopes (up to 30 degrees) dissected by small upper headwater streams which drain eastwards towards the coast. The soils are derived from acid volcanic parent material and are infertile, highly acidic, and high in soil exchangeable aluminium. The low soil exchangeable nutrient levels compared to the levels present in the litter layer highlight the importance of the litter layer in conserving essential plant growth nutrients (Porada, 1980).

Like most *Nothofagus* species*, N. moorei* is found only in particular climatic conditions. Since 2009, one of my supervisors, Dr. Ross Peacock (unpubl.), has been recording several climate variables within Werrikimbe National Park (S 31.19784167, E 152.40027778). These records show that there is high variability in air temperature, high yearly rainfall usually above 1000 mm, and high relative humidity never reaching below 50 % (Fig. 2). These data indicate that these climate conditions are preferred by *N. moorei.* Simultaneously, over the past 60 years, there has been a clear increase in the mean annual temperature and a slight decrease in annual rainfall (Fig. 3). With increasing temperatures and a drier environment, these forests are at an increased risk of fire. There are also distinct seasonal trends as shown in figure S-1 of Appendix 1.
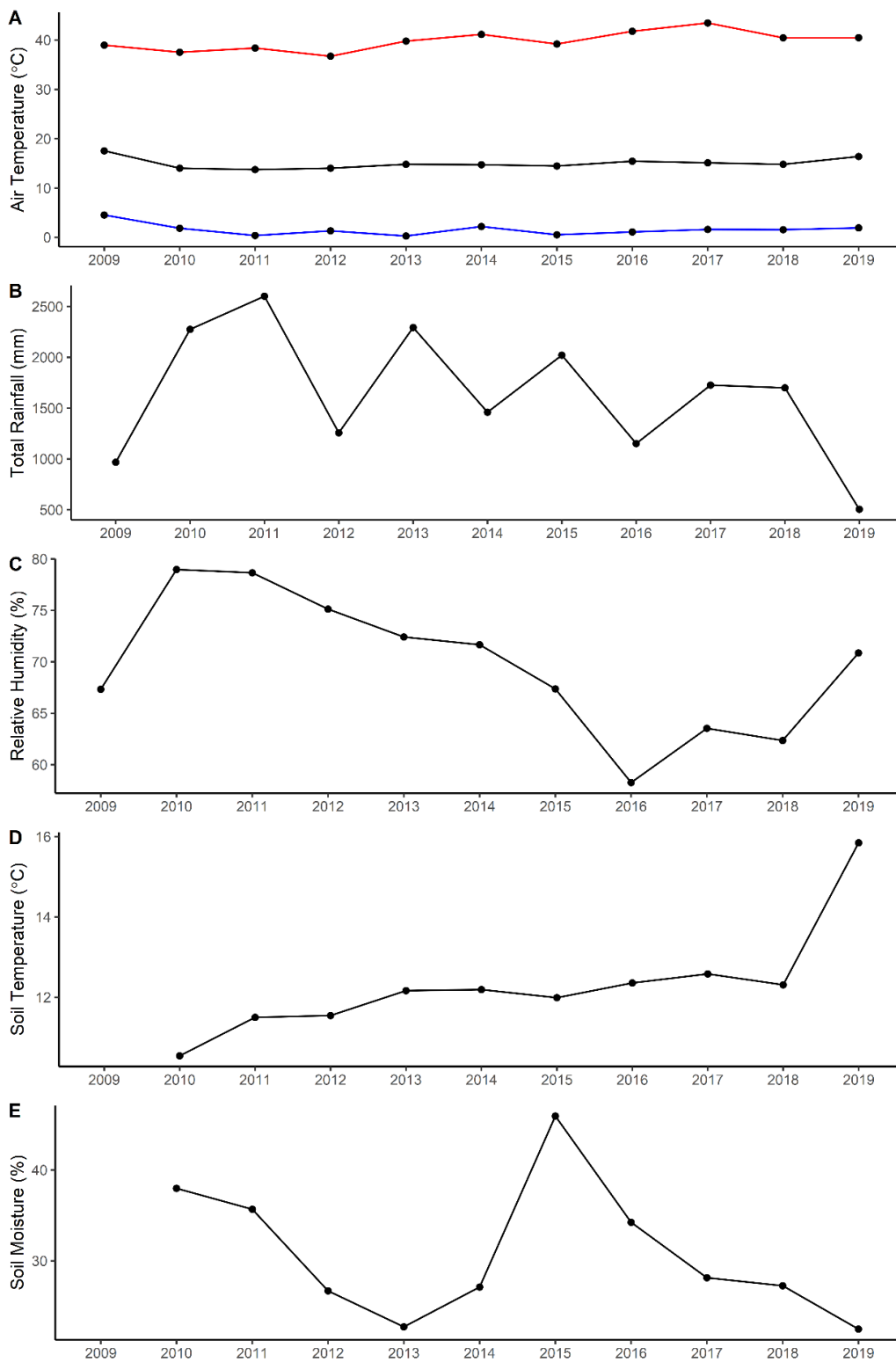
Figure 2. Annual climate averages in Werrikimbe National Park from late 2009 - early 2019.
(A) Air temperature (red line: maximum; blue line: minimum; black line: average); (B) Relative humidity; (C) Total precipitation; (D) Soil temperature; (E) Soil volumetric moisture. Climate monitoring stations were installed and maintained by Dr. Ross Peacock.
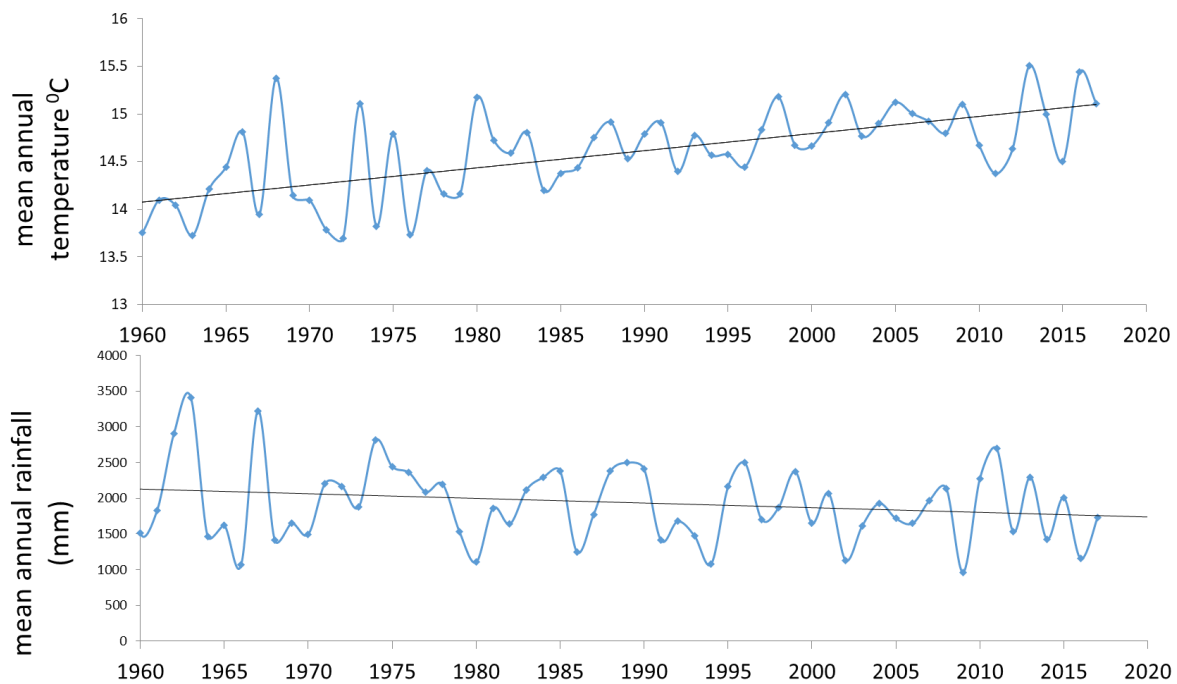
Figure 3. Long-term warming and drying trends at a location near the study sites. Data were sourced from the Bureau of Meteorology (www.bom.gov.au) for station number 060068 Yarras (Camerons Forestry Camp), S 31.19784167, E 152.40027778, elevation 862 m and climate monitoring stations were installed and maintained by Dr. Ross Peacock. This site is approximately 4 - 6 km from the study sites.

To date there has been very little research regarding the regeneration strategies and interactions of *N. moorei,* with the exception of the observations of Karl Vogel (unpubl.). Vogel's notes from the 1957-1959 describe the masting, reproductive structures, and seedlings of *N. moorei* at Werrikimbe National Park, as well as observations of Crimson Rosellas (*Platycercus elegans)* foraging in the tree. Much could be explored for this species in terms of biotic interactions, reproductive strategies, and seedling recruitment.

Questions and hypotheses

This Masters Research project consisted of three individual studies focusing on different aspects of the biology of these forests, and on *N. moorei* in particular (Fig. 4). The first two sections of this project utilise observational data, to discover more about the natural history of *N. moorei* and associated species in this forest. The third section involves an experiment conducted in situ to assess the impact of vertebrate exclusion on juvenile rainforest trees.
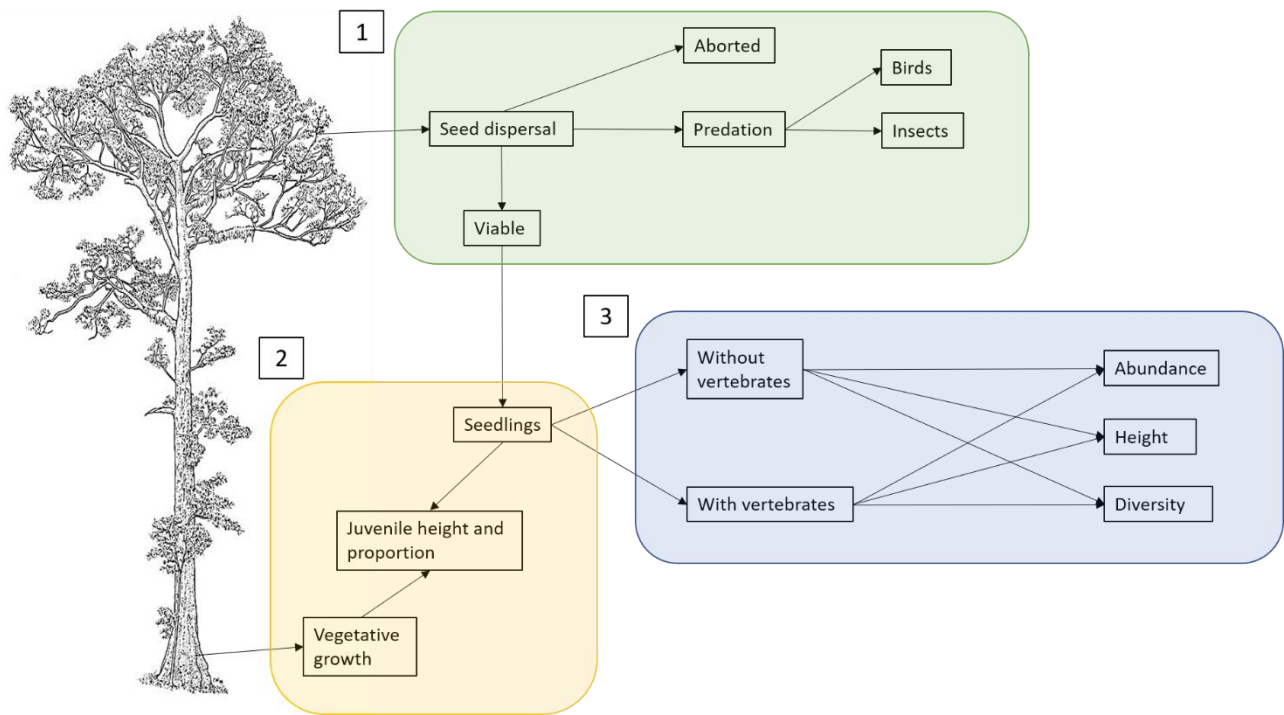
Figure 4. Structure and relationship of the components of this thesis. This thesis consists of three individual studies addressing different stages of the life cycle of *Nothofagus moorei*, its biotic interactions, and the plant community in which it is found. Box 1: Pre-dispersal seed predation. Box 2: Regeneration modes of rainforest trees. Box 3: Effects of excluding vertebrates on juvenile success. Image of *N. moorei* from Plant Net (http://plantnet.rbgsyd.nsw.gov.au).

Firstly, I examine pre-dispersal seed predation on *N. moorei* during a large masting season. I asked the following questions:

- What proportion of fruits and seeds are damaged by predators? (and of these, what proportion are damaged by insects *versus* by parrots?)

- Considering undamaged fruits, what proportion of seeds have developed to maturity once they have been released from the canopy?

- Do these proportions differ over the masting season?

Secondly, I explore the different regeneration modes occurring in these cool temperate forests to better understand the life history of the system. I addressed the following questions:

- Which species are using both vegetative and sexual modes of regeneration and what are the proportions of each mode?

- Which mode of reproduction results in taller juveniles? Does this differ between species?

Thirdly, I investigate the effects of vertebrate exclusion on *N. moorei* and other key species in the system. I addressed the following questions:

- What is the effect of vertebrate exclusion on the abundance, height, richness and diversity of woody tree juveniles? Does this differ between species?

In addition, I asked whether height influenced juvenile abundance and whether species diversity influenced growth rate, as these were potentially important ecological factors to consider when interpreting results from the vertebrate exclusion experiment.

These questions can be represented as a series of hypotheses (Fig. 5). In addition, I also explored the responses of juvenile rainforest trees to climate variables such as temperature, humidity and rainfall. This additional analysis was necessary to determine whether the plants were responding to vertebrate exclusion or solely to the environment.

Exclusion of vertebrates

H1: Lower seedling mortality (higher abundance)

There will be a higher abundance of seedlings in cages as they will be protected from disturbance (being uprooted and broken).

AH1: Less germination (lower abundance)

Vertebrates are needed to disturb the soil to create favourable conditions for germination and survival (soil turnover, litter removal to expose soil and seedlings).

NH1: There will be no differences in abundance between plots excluding vertebrates and those not.

H2: Increased height

Seedlings will be able to grow more in the absence of vertebrate disturbance.

AH2: Shorter seedlings

Seedlings will have more resource competition from inter/intra-specifics and grow less.

NH2: There will be no differences in height between plots excluding vertebrates and those not.

H3: Higher species diversity

More species will be able to grow in the absence of damage by vertebrates.

AH3: Lower species Diversity

Fast growing species will outcompete and dominate the plot.

NH3: There will be no differences in diversity between plots excluding vertebrates and those not.

H = hypothesis, AH = alternate hypothesis, NH = Null hypothesis

Figure 5. Hypotheses addressed in this thesis in relation to the vertebrate exclusion experiment.

2. PRE-DISPERSAL SEED PREDATION ON *NOTHOFAGUS MOOREI*

Methods

Background

Evidence of pre-dispersal predation on *N. moorei* by parrots and unidentified insect larvae was observed in August 2017 (pers. obs. by Homberger, Peacock and Smart). To quantify the extent of predation over the course of the masting season, litter traps were established beneath the canopies of *N. moorei* trees at Werrikimbe National Park by Dr. Ross Peacock and myself in late October 2017. No flowering or seed dispersal was observed from August 2018 to April 2019 (pers. obs. Peacock and Smart).

Experimental design

Litter traps were set up along Cants Trail (S 31.16796, E 152.36516) on 10 November 2017 (Fig. 6) in order to collect data for the duration of the 2017-2018 masting season. Cants Trail has an elevation of 1217 m (accuracy +/-5 m). Two types of litter trap were used impromptu as a response to the masting event. One of them consisted of two polyethylene cylindrical stand up bags (diameter 450 mm × height 600 mm) (Fig. 7a). The other litter traps were constructed from three pieces of polyester/cotton blend fabric (one measuring 200 × 245 cm, the second 165 × 220 cm, the last 150 × 120 cm) suspended approximately 50 cm from the forest floor using metal poles (Fig. 7b). Each trap was placed beneath the canopy of one or two mature *N. moorei* trees each, within 5 m of the trunk. The litter traps were on 11 December 2017 (open for 31 days), 10 January 2018 (open for 30 days) and 3 February 2018 (open for 24 days).

These months were selected because *N. moorei* fruits are being released in the largest quantities during this time. Litter was not collected during other months at this site as there was very little reproductive effort, as evidenced by annual litter collection traps collected by Dr. Ross Peacock (unpubl. data) along Hastings Forest Way (S 31.156430, E 152.369929) (Fig. 8) approximately 1.6 km north-east at a long term litterfall study site. Polyethylene cylindrical stand up bags were also used this site, with counts being calculated per metre square from 12 litter traps (Fig. 9).

Figure 6. Location of study sites. Map showing the location of (A) the Cants Trail site, just off road from Cockerawombeeba Trail; (B) the Hastings Forest Way site. They are approximately 1.6 km apart.

Figure 7. Litter traps used in the pre-dispersal seed predation study. Photographs show (A) the polyethylene litter trap (photo, R. Peacock, 2017); (B) the suspended fabric litter trap (photo, A. Smart, 2017).
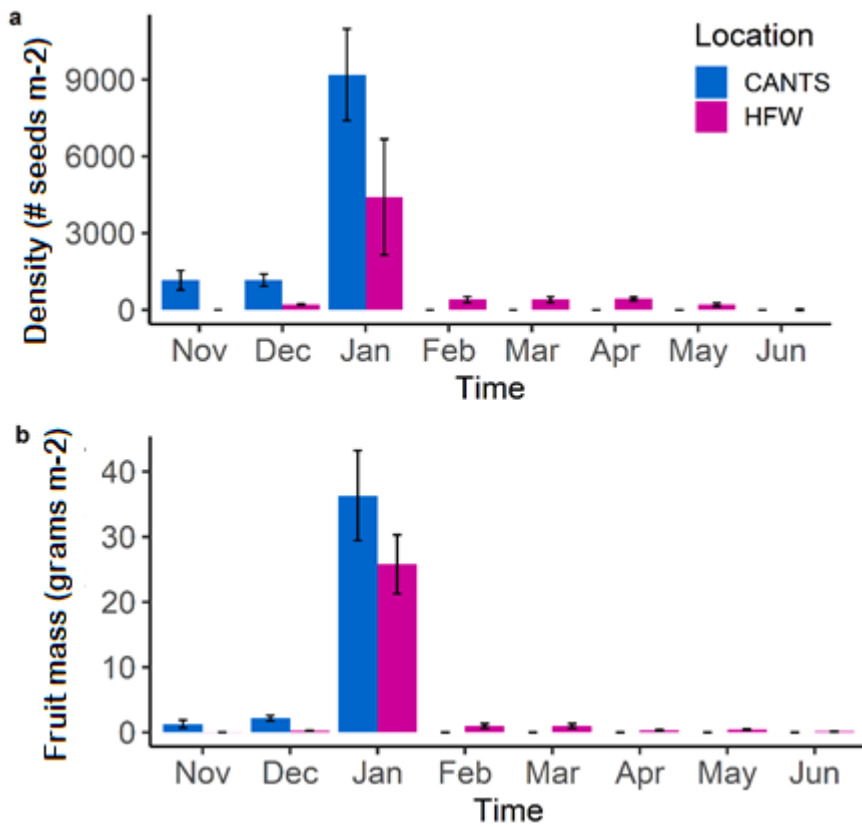
Figure 8. Count and mass of *Nothofagus moorei* fruits from two sites. Preliminary data from a companion study at a nearby study site (Hastings Forest Way, HFW - pink bars) and the current study (Werrikimbe National Park Cants Trail, CANTS – blue bars). (a) density, and (b) mass of *N. moorei* fruits collected in litter traps from November 2017 – January 2018.Means and standard errors are shown.

Figure 9. Location of the 12 litter traps included in the present study. This is also the site referred to in chapter 3 and part of chapter 4.

Bird observations

Parrots were observed foraging in *N. moorei* during both the flowering season (August 2017 – November 2017) and the associated masting season (December 2017 – February 2018) (pers. obs. by Homberger, Peacock and Smart). Subsequently, animal ethics was approved by Macquarie University for the period of December 2018 – December 2019 (reference: 2018/032) with the expectation of observing Crimson Rosellas (*Platycercus elegans*) and King Parrots (*Alisterus scapularis*). Observations occurred at Cants Trail and Hastings Forest Way. Scheduled observation times, 06:00, 09:00, 12:00, 15:00 and 18:00, were set to identify any parrot activity in *N. moorei*. Observation intervals were 20 minutes long and were conducted on 13th – 19th December, 10th – 14th January, 7th – 11th February, and 28th February – 4th March. Parrots were rarely seen, although heard from the base of *N. moorei* trees during the non-masting season December 2018-March 2019 (pers. obs. Smart). Due to the absence of parrot activity this part of the project was discontinued.

Analysis of litter

Litter was analysed to determine the extent of damage by birds versus insects. Litter mostly consisted of *N. moorei* leaves, twigs, buds, bracts, and other reproductive structures, such as cupules and male flowers, although litter from adjacent tree and tall shrub species was occasionally found. The fruits develop within the cupule. When the cupule matures it becomes a woody structure that opens to release the fruit; *N. moorei* cupules have four valves that spread apart to release two 3-winged fruits and one 2-winged fruit (Maiden, 1921) (Fig. 10). Litter from the non-target species was discarded along with leaves and twigs of *N. moorei.* The remaining litter was sorted into the reproductive structures of *N. moorei,* segregating the cupules, flowers, and fruits. Fruits remaining attached to cupules were removed to facilitate a full visual inspection for damage.

While much of the material collected was green – indicating it was from the current masting event – collections may have included a small number of fruits from the previous season. Fruits can remain on the tree for more than 12 months, as evidenced by the occasional dried cupule or fruits found in 2019, despite there being no evidence of reproductive behaviour by the trees (pers. obs. Smart). Due to the large quantity of material collected, a portion of the samples were oven-dried prior to sorting to reduce the rate of decay. Therefore, identification of fresh *versus* old fruits was not possible.
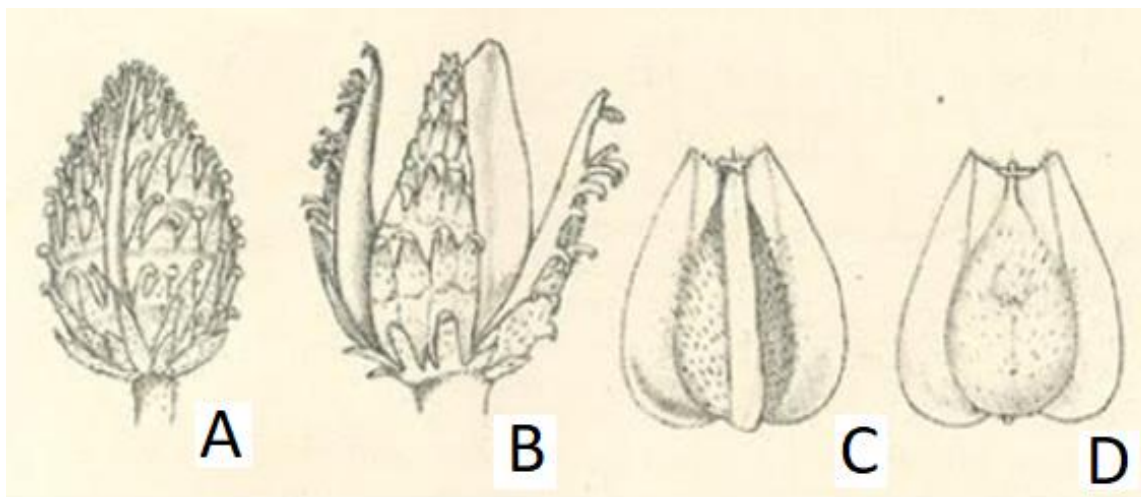
Figure 10. Fruit morphology in *Nothofagus moorei*. (A) A closed cupule; (B) an open cupule; (C) a 3-winged fruit; (D) a 2-winged fruit. Illustration reproduced from Maiden (1921).

To quantify extent of predation on of *N. moorei,* the fruits were sorted into two main groups, "damaged" and "undamaged". Damaged fruits were further sorted into subgroups, "predation by parrots", identified by either a transverse or a longitudinal cut along the side of the fruit, and "predation by insects", identified by the presence of a 1-3 mm escape bore hole in the fruit (Fig. 11). A third subgroup "broken" were those with unidentifiable damage. To quantify the amount of fruits in each subgroup, each sample was weighed, and 100 randomly selected fruits were used for each group and subgroup. I calculated the proportion damage in each category on the basis of these subsamples."
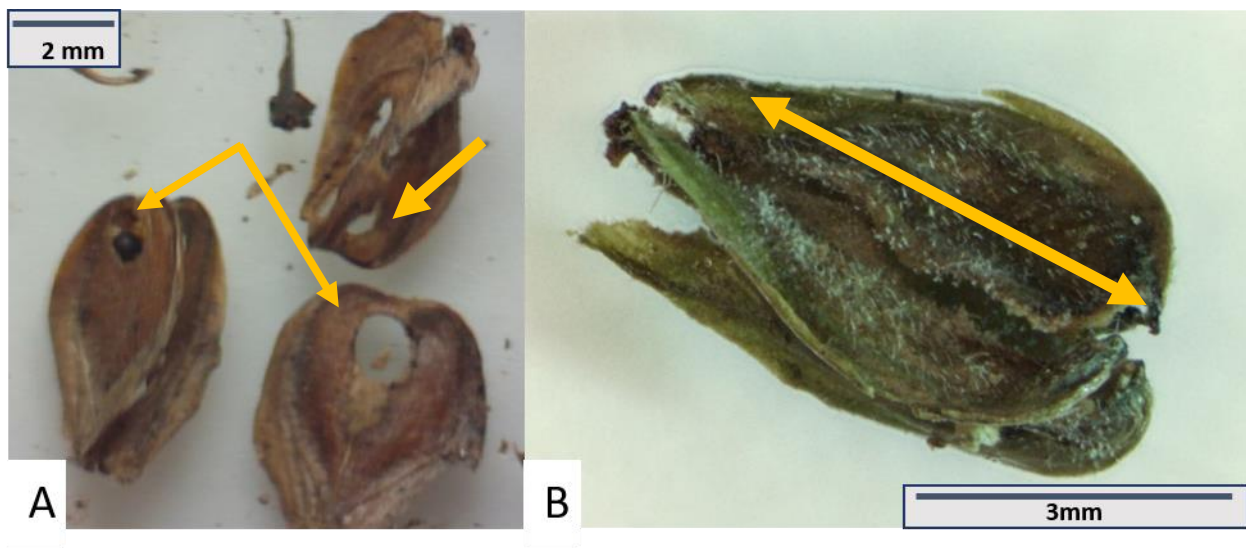
Figure 11. Predation on fruits of *N. moorei*. (A) Insect predation, as evidenced by holes; (B) Parrot predation, identified by the longitudinal tear down the side of the fruit.

Further examination of the randomly selected 100 undamaged fruits revealed whether the seeds had developed to maturity or had been aborted. These fruits were then dissected underneath a dissecting microscope, to assess the development of the seed inside. To quantify the amount of viable seeds per sample, each fruit was dissected using a razor blade to assess if there was an intact and fully developed seed inside (evidence of a firm seed with embryo). If a fruit was empty or contained only a spongy dehydrated endosperm it was considered unviable (Fig. 12).
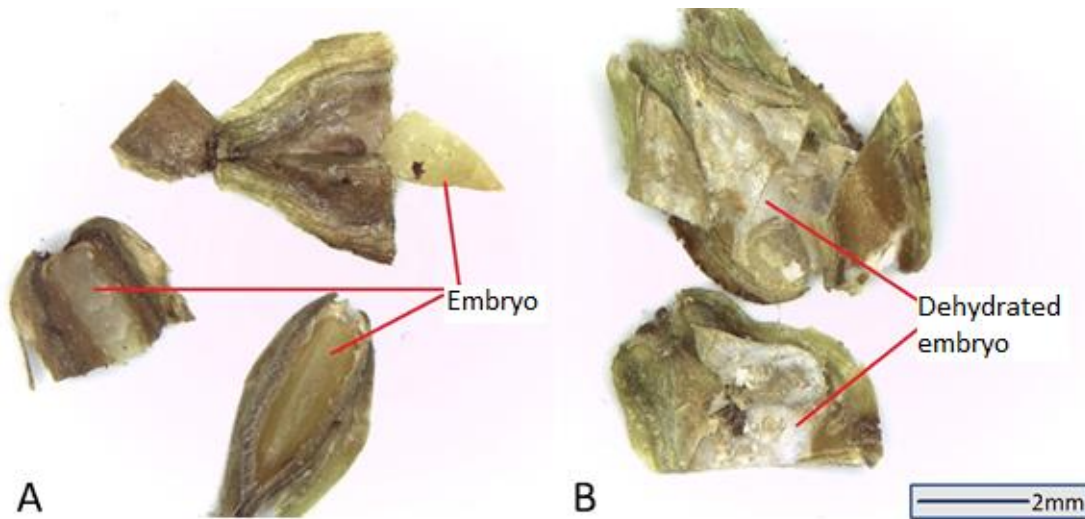
Figure 12. Dissected fruits of *N. moorei*. (A) A developed seed embryo as indicated; (B) an undeveloped seed consisting only of dehydrated endosperm as indicated (Images by G. Errington).

Statistical analysis

One-way Analysis of Variance (ANOVA) was used to test for differences in the proportions of damaged versus undamaged fruits over the masting season. Time (sampling period within the masting season) was treated as both a discrete variable and a continuous variable, and produced similar conclusions. A repeated measures analysis was not used because the goal was to test for differences across time rather than differences across non-independent groups. Thus, the model structure was: Damage ~ Time. Subsequently, I used an analysis of covariance (ANCOVA) to determine whether the damage type and not just the amount of damage, was consistent over time. The model structure was: Damage ~ Predator*Time, where predator was a discrete variable and time was treated as a continuous variable. Lastly, I tested whether the proportion of viable seeds changed over time, using one-way ANOVA with model structure: Proportion seeds viable ~ Time. In all cases, the proportion data were log-transformed to meet statistical assumptions of normality (determined via Shapiro-Wilks normality test on the model residuals). In cases where data transformations did not satisfy normality assumptions, we visually inspected the data using normal Q-Q plots to determine the appropriateness of the model. All statistical analyses were conducted in R studio 1.1.463 and R 3.5.1 (R-Core-Team, 2013). Linear regression models were conducted using base R. The ANOVA was conducted using the "anova" function in base R. Pairwise comparisons among groups were evaluated using a Tukeys HSD test with the 'lsmeans' and 'effects' packages. Figures were made using 'ggplot2', 'multcompView', 'multcomp' and 'cowplot'.

Results

Damaged fruits

The proportion of damaged versus undamaged fruits differed significantly between the three sampling times (ANOVA, $P = 0.002$, $F_{1,16} = 12.36$), seemingly decreasing across the masting season (Fig. 13a). Similarly, when time was treated as a continuous variable, the proportion of damaged fruits was significantly lower later in the season (Linear regression, $P = 0.019$, $F_{2,6} = 8.229$).

Of the proportion of fruits that were damaged, the proportion damaged by birds *versus* insects was consistent over time, and was dominated by insects (Linear regression, $P = 0.81$, $F_{2,6} = 0.224$; Fig. 13b). When we averaged across the masting season, there was significantly more predation by insects than birds (ANOVA, $P < 0.001$, $F_{1,16} = 32.44$).

Undamaged fruits

Within the total amount of undamaged fruits, 79% were undeveloped. However, the regression analysis revealed a significantly higher proportion of developed seeds in the later stages of the masting season, i.e., January (Linear regression, $P < 0.001$, $F_{2,6} = 115.94$) (Fig. 13c).
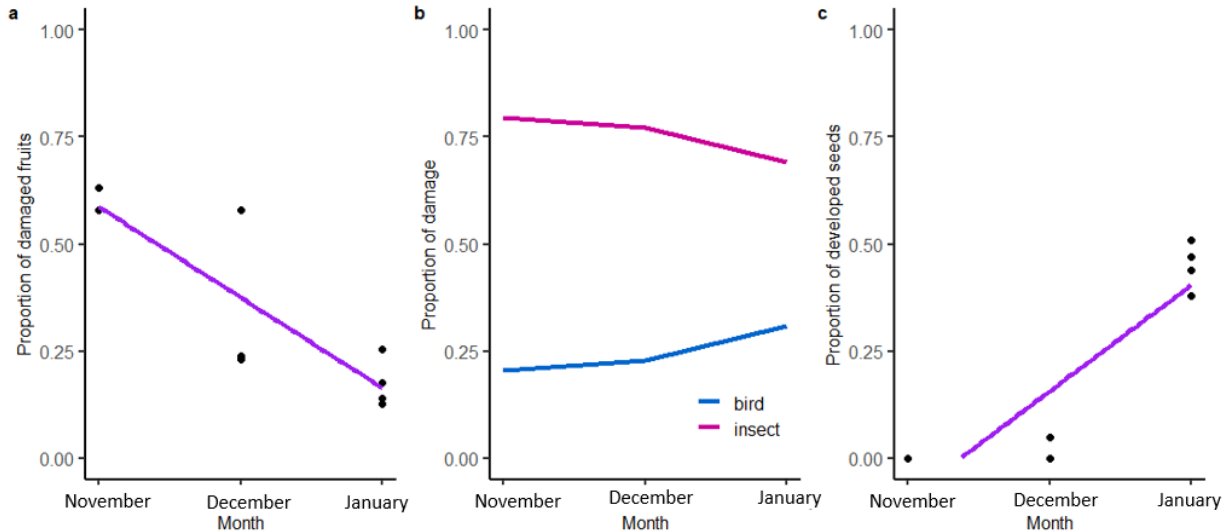
Figure 13. Damage to *N. moorei* fruits across the masting season. (a) Proportion of damaged fruits over the masting season, with fitted linear regression. (b) Mean proportions of fruits damaged by both birds and insects. (c) Scatter plot with fitted regression line displaying the higher proportions of developed seeds by the third month sampled, January. In panels (a) and (c) each data point represents litter bag replicates (n = 9).

3. REGENERATION MODES OF COOL TEMPERATE RAINFOREST TREES

Methods

Background

To determine the regeneration modes of *N. moorei* and co-occurring species, I utilised data from an existing long-term rainforest dynamics experiment established in 1961 by the Forestry Commission of New South Wales, which was designed to study the effects of silvicultural management on rainforest tree regeneration, growth and survival. The experiment has been managed since 1961 and includes a wealth of data on mature trees, saplings, seedlings, phenology, litterfall and climate. In this thesis I only utilised the seedling and sapling data component of this experiment including data from 1980, 1983, 1985, 2006, 2009 and 2019. I omitted data from1962, 1963 and 1975 because they were conducted using an incompatible protocol.

More information is needed about the study location and the general selection of species.

Experimental design

Four treatment plots (approximately 80×100 m) each contained a single quadrat (approx. 40 m $\times$ 40 m: 0.4 acre), and each quadrat contained two transects consisting of 20 subplots measuring 2 m $\times$ 2 m, arranged linearly (Fig. 14). The unit of replication was the transect (N=8), but the transects were nested within quadrat because they were non-independent (see Statistical Analysis). The data from the subplots were combined, rather than being treated as replicates. These plots were arranged in a 2 by 2 grid over the same area as the litter traps mentioned in the previous study (Fig. 9). All trees > 10 cm DBH in the 40×40m plot were permanently tagged and periodically measured, with the seedling and sapling cohort measured within two transect lines of twenty 2×2 m plots.

All vascular plant species in each quadrat were recorded, but only the juvenile woody species were counted. Only the tallest individual of each species had its height measured to the nearest cm using a 3 m measuring pole, while the individuals that remained were not measured. The mode of regeneration was recorded as "seedling" or "vegetative". Plants with a vegetative origin were identified as having sprouted off and attached to a larger parent trunk or surface root; plants designated as having a seed origin were clearly independent of one another based on the lack of surface level root connections and location of germination. Many seedlings < 10 cm were established on decaying logs, ferns and nested between the roots of competing tree species. Plants with a stem diameter more than 10 cm at breast height were considered as adults and not recorded.

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We considered any plants up to 3 m in height as juveniles, and those above 3 m were excluded from analyses (including plants once they reached 3m or over). In addition, all records of non-woody species were excluded from analysis as their abundance and height was not recorded. Lastly the 20 subplots in each transect were disregarded from the final analyses because the subplot boundaries shifted over the decades, perhaps due to the changes in personnel monitoring them. That is, this study considers each transect as a replicate nested within each quadrat.
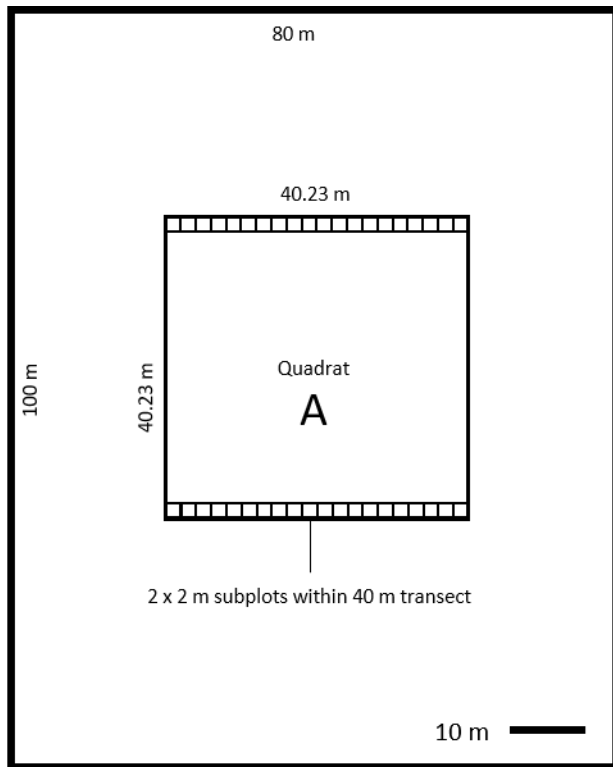
Figure 14. Quadrat layout used in the survey of juvenile regeneration strategies. In 1961, two transects, each with 20 sub-plots arrayed along them, were placed along the edges of a 0.4 acre (ca. 40 × 40 metre) quadrat. Four such quadrats were arrayed within a larger plot (100 m × 80 m).

Focal species

Four woody species in addition to *N. moorei* were selected as the five focal species for this chapter and the next (*Ceratopetalum apetalum, Cryptocarya meisneriana, Orites excelsus* and *Tasmannia insipida).* This choice was based on which species were the most abundant in the plots used in the vertebrate exclusion experiment (Chapter 4). These species were also among some of the most abundant observed in the juvenile regeneration survey (this chapter; Table 2).

Statistical analysis

I first calculated the proportions of individuals in each species utilizing each regeneration mode. I further calculated the proportion of seed-derived juveniles within each of seven size classes (ranging from 0 to 3 m in height). Linear mixed models (LMM) were used to test whether the proportion of seed-derived juveniles varied across plant size, where size was a fixed factor, transect was nested within the quadrat as a random effect, and year was included as an additional random effect. The model structure was Proportion Seed Derived ~ Plant Size + (1|Year) + (1|Quadrat/Transect). LMM were also used to determine whether height varied significantly among the regeneration modes and the model structure was: Height ~ Regeneration Mode + (1|Year) + (1|Quadrat/Transect). The species were analysed separately and data from all years was combined. Height was transformed using the Tukey's ladder of powers to meet statistical assumptions of normality (determined via Shapiro-Wilks test on the model residuals). In cases where data transformations did not satisfy normality assumptions, we visually inspected the data using Q-Q plots to determine whether the model was appropriate. All statistical analysis was conducted in R studio 1.1.463 and R 3.5.1 (R-Core-Team, 2013). LMM were conducted using the packages 'lme4'. We evaluated the significance of the fixed effects in all mixed models using a Wald test, and this was done using the function "Anova", from the 'car' package. Figures were created using 'ggplot2', and 'cowplot'.

Results

Species using both modes of regeneration

In total, 26 woody species were present in the transects. 11 out of 26 woody species showed evidence of using both vegetative and seed regeneration strategies (Table 2). Pooling the data from all years revealed that among five focal species, all showed a lower proportion of juveniles with vegetative origin except for *Cryptocarya meisneriana* (0.60 veg *versus* 0.40 seed).

Considering all woody species together, juveniles of vegetative origin were on average significantly taller than those derived from seed (LMM; $P < 0.0001$, $F_{1, 1946} = 251.08$). Among the five focal species, this trend was also evident in *N. moorei* ($P < 0.0001$, $F_{1, 297} = 23.94$), *C. apetalum* ($P < 0.0001$, $F_{1, 482} = 174.66$) and *C. meisneriana* ($P < 0.0001$, $F_{1, 273} = 31.417$; Fig. 15), but not in *O. excelsus* ($P = 0.767$, $F_{1, 176} = 0.088$) or *T. insipida* ($P = 0.184$, $F_{1, 83} = 1.768$).

Table 2. Regeneration strategies of species co-occurring with *N. moorei* in Werrikimbe National Park. List of all woody species censused showing the proportion of those originating from seed and the total number (N) of both seedling and vegetative juveniles across all plots and years. The five ("focal") species are highlighted in bold.

Species	Seed	N	Species	Seed	N
Alyxia ruscifolia	0.87	107	***Orites excelsus***	**0.99**	303
Anopterus macleayanus	1	73	*Persoonia media*	1	38
Ceratopetalum apetalum	**0.85**	6147	*Pittosporum revolutum*	1	31
Citriobatus pauciflorus	1	2	*Quintinia sieberi*	1	7
Cryptocarya foveolata	1	132	*Quintinia verdonii*	0.98	622
Cryptocarya meisneriana	**0.4**	1456	*Rapanea howittiana*	1	7
Cryptocarya nova-anglica	1	1	*Schizomeria ovata*	1	3
Doryphora sassafras	0.64	655	*Sloanea woollsii*	1	1
Elaeocarpus reticulatus	0.95	56	*Synoum glandulosum*	1	1
Endiandra sieberi	1	6	***Tasmannia insipida***	**0.9**	246
Helichrysum rufescens	1	2	*Tristaniopsis collina*	0.7	323
Notelaea venosa	0.57	14	*Trochocarpa laurina*	1	3
Nothofagus moorei	**0.77**	2143	*Wilkiea huegeliana*	1	3
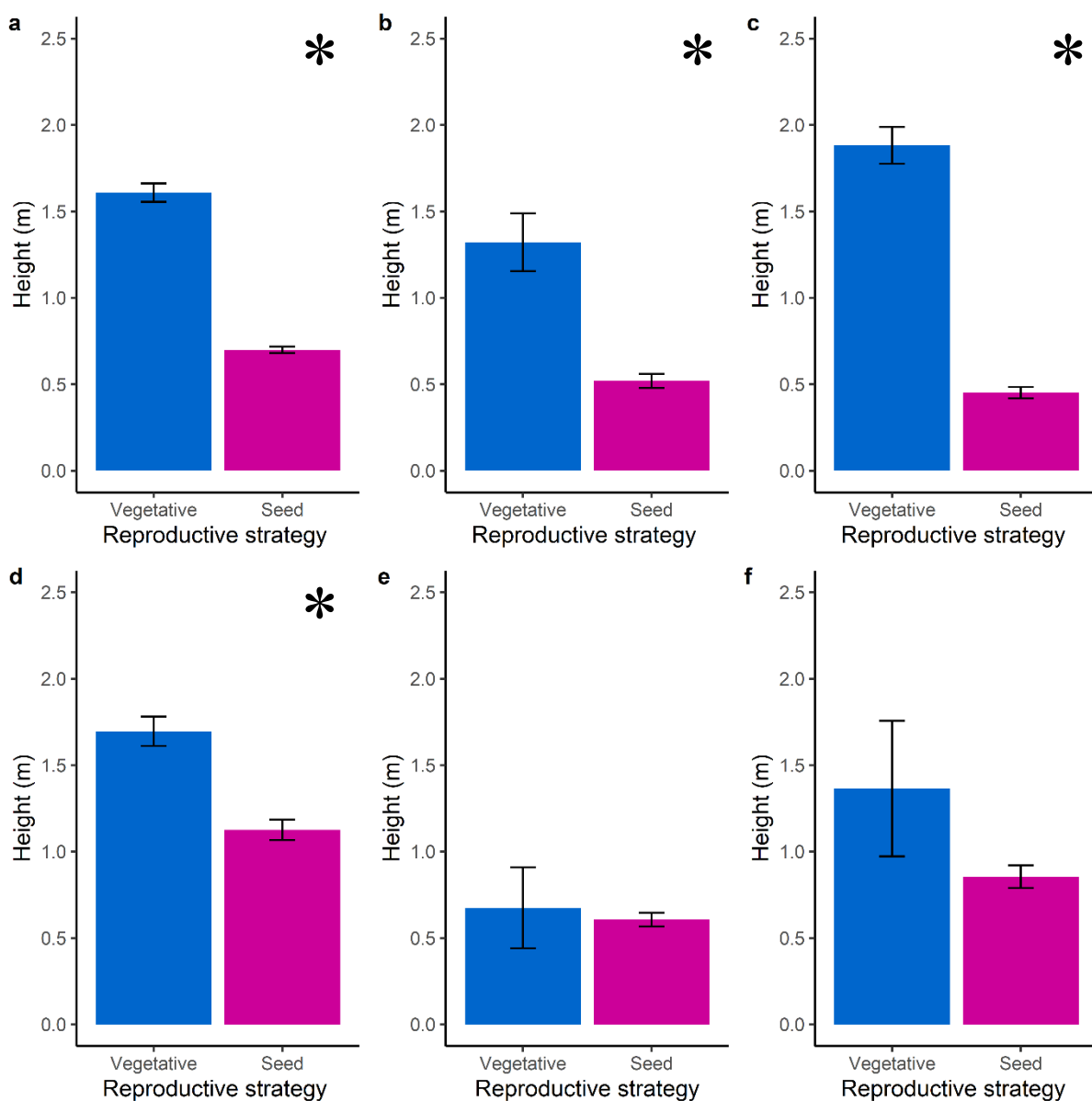
Figure 15. Comparison of heights of seed-derived and vegetative-derived juveniles for common species at Werrikimbe and Willi Willi National Park. The maximum height of: (a) all woody species; (b) *N. moorei;* (c) *C. apetalum;* (d) *C. meisneriana*; (e) *O. excelsus*; and (f) *T. insipida*. Means ± SE bars are shown. * indicates statistical significance.

Height and proportions of vegetative- and seedling-derived juveniles

Although seed-derived individuals were more abundant than those of vegetative origin, seed-derived plants were shorter statured. Therefore, I investigated the extent to which plant origin varied across size class. In the smaller height classes (0 – 0.3 cm) most plants were seed-derived, and the proportion of seed-derived juveniles dropped markedly with increasing plant height (Fig. 16a).

When pooling individuals smaller than 0.3 cm in height, there was a clear reduction in the proportion of seed-derived individuals (ANOVA, $P <0.001$, $F_{1,46}= 33.99$). I detected the same trend in *N. moorei* ($P = 0.004$, $F_{1,6} = 20.599$), *C. apetalum* ($P = 0.012$, $F_{1,6} = 12.757$ and *C. meisneriana* ($P = 0.003$, $F_{1,6} = 22.401$), but not in *O. excelsus* ($P = 0.846$, $F_{1,6} = 0.041$) or *T. insipida* ($P = 0.149$, $F_{1,6} =2.741$; Fig. 16b).
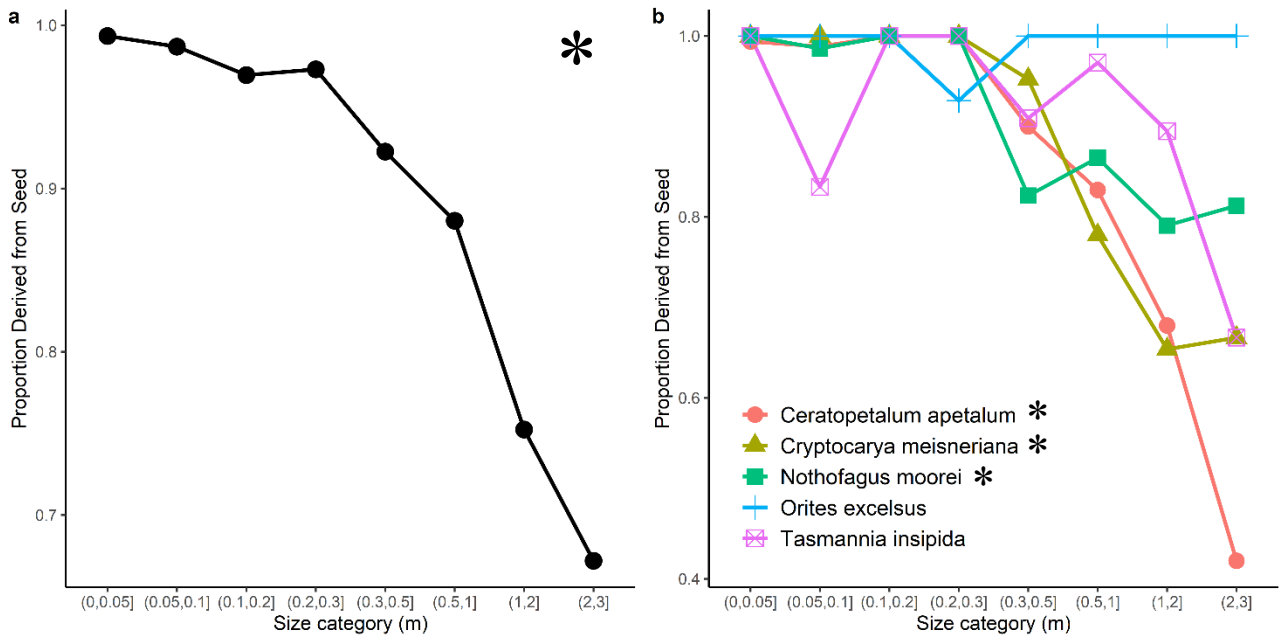
Figure 16. Proportions of juveniles originating from seed, for species divided into height classes. (a) all species combined; (b) the five focal species. Error bars represent standard error. * indicates statistical significance.

4. THE EFFECT OF VERTEBRATE EXCLUSION ON RAINFOREST JUVENILES

Methods

Background

To quantify the effect of large vertebrates on recruitment, growth and survivorship among juveniles of dominant rainforest canopy species. The largest ground-dwelling vertebrates observed in the cool temperate rainforest at Werrikimbe and Willi Willi National Park are the Australian Brush Turkey *(Alectura lathami)* and the Superb Lyre Bird *(Menura novaehollandiae)* (Peacock, unpubl.; Fig. 17). However, other vertebrates from adjacent woodland and sclerophyll forests are not limited to their core habitats and may enter the cool temperate rainforest, such as the spotted-tailed quoll *(Dasyurus maculatus)*, Parma wallaby *(Macropus parma)* and Red-legged pademelon *(Thylogale stigmatica)* (NPWS, 2005).

Experimental design

The vertebrate exclusion experiment was set up in 2009 and consisted of 70 "open cages" (dimensions: h, w, l = 900 mm) each paired within 5 m of a mesh cage. Open cages consisted of four corner pegs (marking out an area of 900 mm × 900 mm). "Mesh cages" had a 100 × 100 mm grid steel mesh on the top with a 40 mm × 40 mm grid on the sides. The mesh was designed to prevent large vertebrates from entering the plots and disturbing the seedlings. The mesh also decreased the number of twigs and branches from crushing the seedlings whilst allowing small to medium-sized twigs and leaves to fall through, simulating normal litterfall. The tops of the cages were cleared of twig material annually in January to prevent a build-up of litter that would decrease light availability for the seedlings below. The cage pairs were randomly placed within 6 sites within Werrikimbe National Park and Willi Willi NP. Five cage pairs were within existing rainforest growth experiment plots measuring 40 by 30 m while 10 cage pairs were located within another existing rainforest growth experiment (previously mentioned in chapter 3), measuring 40 by 40 m.

All vascular plant species rooted within the plot were recorded, but only woody species were counted, and the tallest individual of each woody species was measured; again, the remaining individuals were not measured, therefore there was only one measurement per census for each species. Censuses of all plant species were conducted in 2009, 2011, 2013, 2015, and 2019 to assess abundance of all species. An additional two censuses in 2014 and 2018 were conducted, focusing only on the abundance of *N. moorei* seedlings during a masting season.

Figure 17. Superb lyre bird adjacent to a 'Mesh' cage (right) and an 'Open' cage (left). (Photo, R. Peacock).

Climate data

Light environment

In 2019, photographs of the canopy directly above each cage were taken and were analysed using the software ImageJ (Rasband, 1997-2018). Canopy photographs were captured at a 35mm format equivalent focal length of 15mm. The images were converted into 8-bit binary to measure the percentage of light.

Temperature, rainfall, relative humidity, soil temperature and soil moisture

Temperature, rainfall, and relative humidity have been recorded on site since September 2009 to 2019. Rainfall (mm) and the intensity of solar radiation (W/m^2) were measured with a RIMCO 8020 series tipping bucket rain gauge and an SP440 silicon pyranometer respectively (McVan Instruments Pty Ltd Mulgrave Victoria Australia http://www.mcvan.com). Temperature and humidity were measured within an aspirated shield. Data was stored on a CR200 Campbell Scientific Datalogger.

Soil temperature and soil moisture have been recorded continuously on site since July 2010. A standard temperature probe (model PB-4724, Gemini Data Loggers (UK) Ltd) measured soil

temperature at a depth of 150mm and logged the data every 30 minutes with a TGP-4020 data logger (Gemini Data Loggers (UK) Ltd). Volumetric soil moisture was similarly measured every 30 minutes with a TGP-0911 soil moisture logger (Gemini Data Loggers (UK) Ltd) at a depth 150 mm.

The mean for each climate variable (except rainfall, this was summed) was calculated for three time periods (inclusive of the census month); (1) The three spring months prior to the census date; as spring is when the most growth occurs (2) Six months prior to the census date; to get a sense of the climate recently prior to the census and (3) 12 months prior to the census date; to get a sense of the climate of the previous year to census. For each day, we extracted 9 AM relative humidity and maximum and minimum temperatures. The daily average was taken for soil moisture and the total precipitation was summed. From these we calculated monthly mean values and annual means.

Height change

To calculate the average change in height for each species, I first calculated the average height of all species in a given census year (time t). Only one individual per species was measured during each census, therefore the change in height is calculated at the species level and not the level of individual plants. I subtracted the height at census t+1 from the height of the same species in the previous census t. Subsequently, I averaged these values across all census years to produce the average change in height for each species.   Hereafter I refer to the change in height as "growth", although change in height can also take on negative values in this framework. There was insufficient replication to determine whether species diversity influenced height change in the five focal species individually.

Statistical analysis

A series of linear mixed models were used to analyse the effect of cage type (i.e. the presence or absence of vertebrates) on juvenile plant abundance, maximum height, growth, species richness and diversity. Species diversity was calculated in addition to species richness, because species diversity accounts for evenness among species. Thus, species diversity may be low even when species richness is high, if there are a few dominant species and many rare species. I calculated species diversity using the Shannon Weiner diversity Index, $H = \sum_{i=1}^{s} p_i \, ln p_i$, where s is the number of species per cage and p_i is the proportion of species *i* relative to the total number of species. The

mean for each response variable was calculated for each cage and for each census period (i.e., 2009-2011, 2011-2013, 2015-2015, 2015-2019). The model structure used to evaluate the effect was cage type was: Response variable ~ Cage Type + (1|Site/Cage pair) + (1|Year). Year and cage pair nested within site were included as random effect terms.

The effects of climate on these response variables were also analysed. For each response variable, linear mixed   models were used to determine the effect of the climate variable (the fixed factor) with cage pair nested within site as random effect terms. The model structure was: Response variable ~ Climate + (1|Site/Cage pair) + (1|Year). Models were compared using year as both a random and a fixed factor, but we present results from analyses with year as a random factor alone. Lastly, I tested whether the change in height was influenced by species richness or diversity, to test the hypothesis that in more diverse plots, the height of the individual species would be reduced (possibly due to competition for resources). The model structure for this analysis was Change in height ~ Species Diversity (or Richness) + (1|Site/Cage pair) + (1|Year).

Response variables were transformed as appropriate to meet statistical assumptions of normality (determined via Shapiro-Wilks normality test on the model residuals) (Table 3). A generalized linear model with a negative binomial distribution was specified for response variables with a high abundance of zeros (Bolker, 2007), i.e. species abundance, because some species were not found in every cage. A Poisson distribution was specified for count data, in this case, species richness (Bolker, 2007). A Gamma distribution was specified for the diversity index, as it is always positive and has a skewed distribution (Bolker, 2007). In cases where data transformations did not satisfy normality assumptions, we visually inspected the data using normal Q-Q plots to determine the appropriateness of the model.

Given that mixed models were often used to account for variation among sites and years, and that response variables were transformed as necessary to meet normality assumptions (Table 3), a subset of the figures below were generated using predictions from the statistical models, rather than raw data, when the two were not equivalent. These include figures 17d, 18e, 18f and 19b. In these cases, the mixed models detected significant effects of the predictor variables that were not apparent when raw data were shown. For mixed models, we also report effect sizes from the model output, which accounts for effects of random factors. Similarly, for all other models, reported effect sizes are based on model output.

All statistical analyses were carried out using the statistical software program R studio 1.1.463 and R 3.5. (R-Core-Team, 2013). LMM were conducted using the package 'lme4'. We evaluated the

significance of the fixed effects in all mixed models using a Wald test, and this was done using the function "Anova", from the 'car' package. To evaluate whether the means of the response variables were significantly influenced by the treatment effect we conducted an Analysis of Variance (ANOVA). The ANOVA was conducted using the "anova" function from the R. All figures were made using 'ggplot2' and 'cowplot'.

Table 3. Models and transformations applied to data. All models presented are mixed models with cage number nested within site, and year as random factors.

Model (response ~ predictor)	Data transformation or Error distribution
Abundance ~ Cage type Abundance ~ Climate	Negative binomial model
Height ~ Cage type Height ~ Climate	Transformed using Tukey's ladder of Powers
Richness ~ Cage type Richness ~ Climate	Model using a Poisson distribution
Diversity ~ Cage type Diversity ~ Climate	Model using a Gamma distribution
Height growth ~ Cage type Height growth ~ Climate	Transformed using Tukey's ladder of Powers
Height ~ Richness	Transformed using Tukey's ladder of Powers
Height growth ~ Diversity	Log 10 transformation

Results

Total plot abundance and species abundance

Considering the entire dataset, the total abundance of juvenile plants in plots was on average 8.5 %
higher in the presence of vertebrates, i.e., in the "open cages" ($P= 0.039$, $F_{1, 2031} = 4.244$; Fig. 18a).
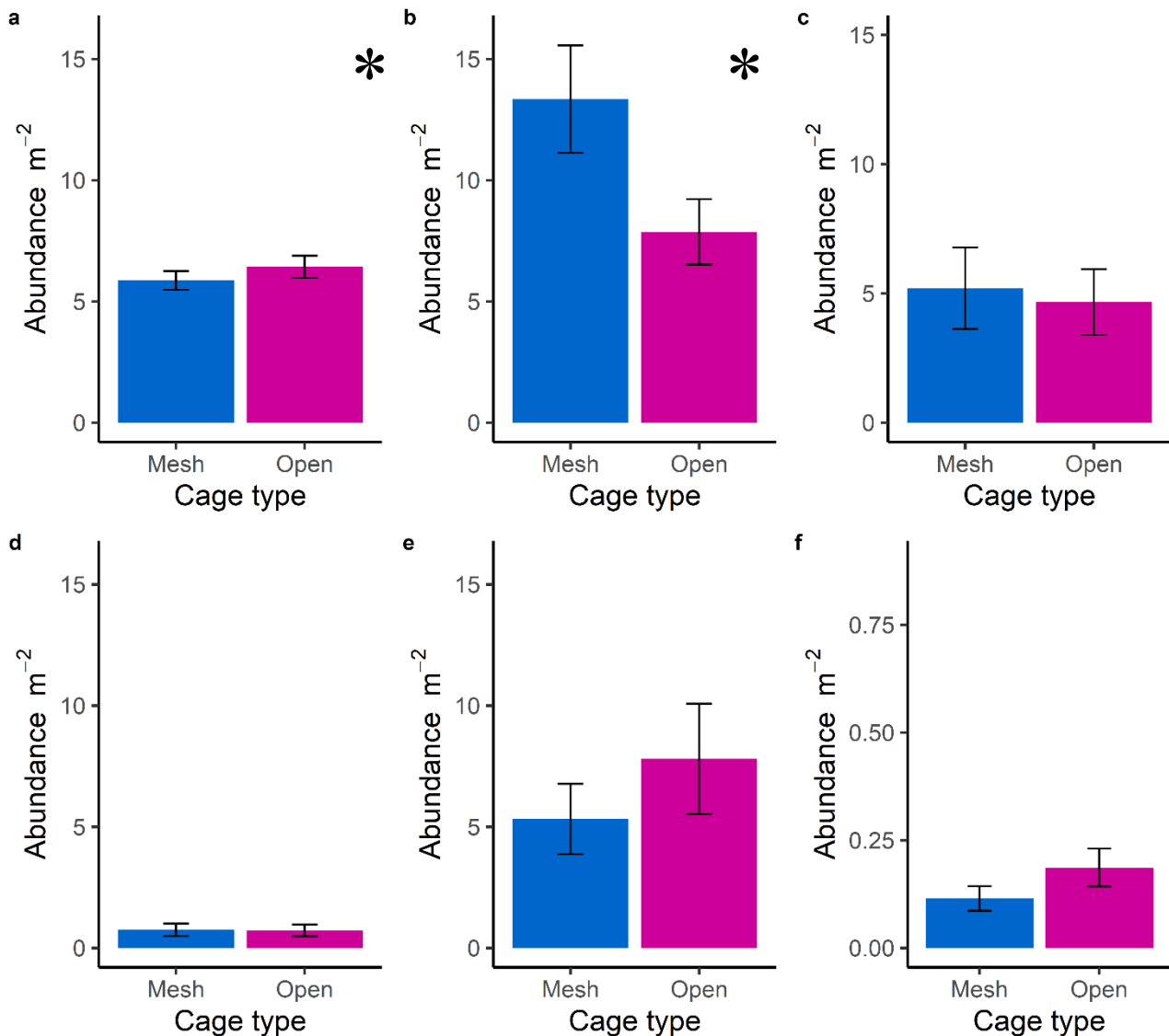
**Figure 18. Effect of vertebrate exclusion on juvenile abundance of species at Werrikimbe and
Willi Willi National Park.** Mean: (a) total plot abundance including all species; (b) Abundance of
N. moorei; (c) Abundance of *Ceratopetalum apetalum;* (d) Abundance of *Cyrptocarya
meisneriana*; (e) Abundance of *O. excelsus*; (f) Abundance of *T. insipida.* Note these graphs
encompass all years censused. Means ± SE bars are shown. Note graph (f) has a different scale on
the Y axis, considering a smaller range in abundance. * indicates statistical significance.

The focal species varied in their responses to the treatment. *Nothofagus moorei* was on average 17.9 % more abundant when protected from vertebrates, i.e., in the mesh cages than in open cages ($P = 0.0009$, $F_{1, 734} = 10.866$; Fig.18b). No effect of vertebrate exclusion was observed for *Ceratopetalum apetalum* ($P = 0.758$, $F_{1, 93} = 0.095$; Fig. 18c) or *C. meisneriana* ($P = 0.918$, $F_{1, 95} = 0.011$; Fig, 18d). Both *Orites excelsus* (Fig. 18e) and *Tasmannia insipida* (Fig. 18f) were marginally more abundant in the open cages (*O. excelsus*: $P = 0.095$, $F_{1, 164} = 2.789$; *T. insipida*: $P = 0.073$, $F_{1, 503} = 3.219$).

Height

Maximum height was on average 10.7 % lower within mesh cages than within open cages ($P < 0.0001$, $F_{1, 587} = 24.143$; Fig.19a). Within individual species, this trend was also evident in *C. apetalum,* which had a 5.9 % decrease in height ($P = 0.026$, $F_{1, 69} = 4.9288$; Fig. 19c). By contrast, the opposite effect was found for *T. insipida*, with seedlings on average 33.6 % taller within the mesh cages ($P = 0.008$, $F_{1, 40} = 7.058$; Fig 19f). Height was not influenced by the treatment for *N. moorei* ($P = 0.961$, $F_{1, 252} = 0.002$; Fig, 19b), *C. meisneriana* ($P = 0.691$, $F_{1, 68} = 0.158$; Fig. 19d), and *O. excelsus* ($P = 0.317$, $F_{1, 140} = 1.000$; Fig. 19e).
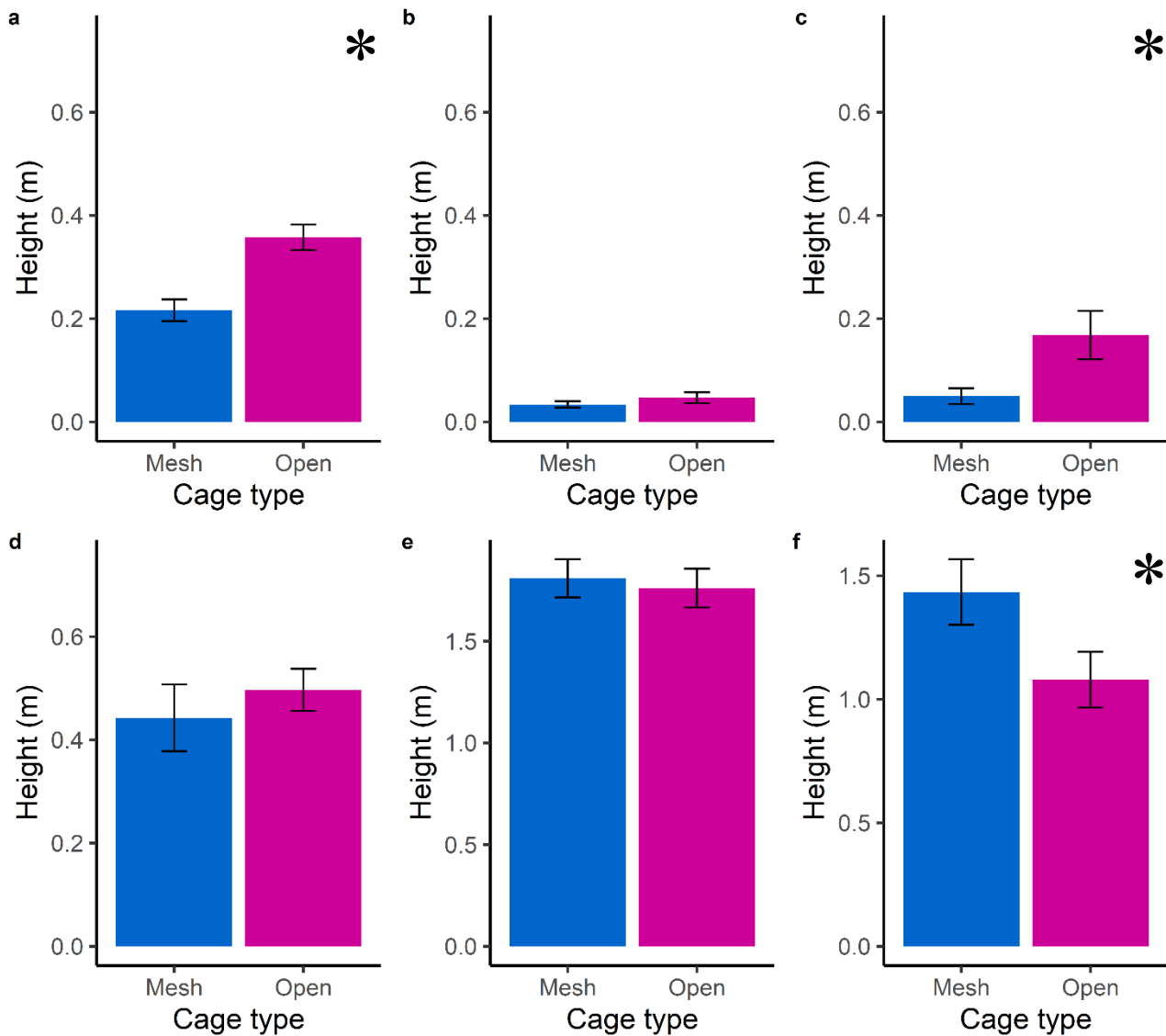
Figure 19. Effect of vertebrate exclusion on juvenile height of species at Werrikimbe and Willi Willi National Park. Maximum height for: (a) all species; (b) *N. moorei;* (c) *C. apetalum;* (d) *C. meisneriana;* (e) *O. excelsus;* (f) *T. insipida.* Means ± SE bars are shown. Note graph (e) and (f) have a different scale on the Y axis, considering a larger range in abundance. * indicates statistical significance.

Richness and diversity

Species richness was on average 28 % higher in the presence of vertebrates, i.e. in the open cages (LMM, $P < 0.0001$, $F_{1, 2032} = 31.006$; Fig.20a). Species diversity showed the opposite trend, being 8.3 % lower in open cages (LMM, $P < 0.0001$, $F_{1, 886} = 17.317$; Fig. 20b). This difference between the two metrics indicates greater dominance by key species in the absence of vertebrates.
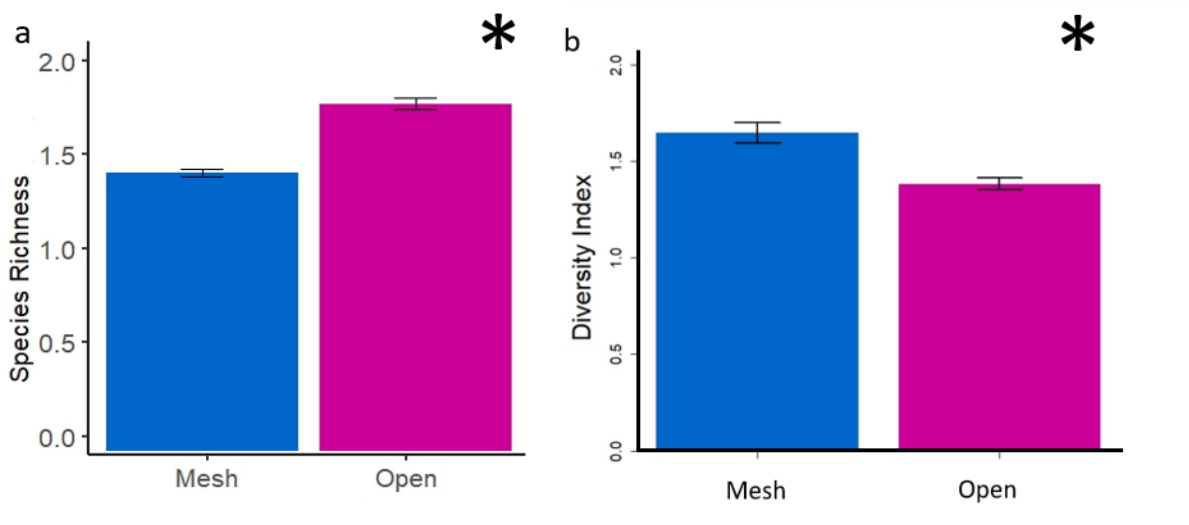
Figure 20. Effect of vertebrate exclusion on juvenile species richness at Werrikimbe and Willi Willi National Park. Effects of cages on a) woody species richness; and b) woody species diversity. Means ± SE bars are shown. * indicates statistical significance.

Relationship between juvenile tree height and abundance

Woody plant abundance had no effect on the maximum height of individuals (LMM, $P = 0.430$, $F_{1, 587} = 0.624$). Likewise, no trend was detected for any of the five focal species (all species, $P > 0.1$).

Relationship between height change and diversity

The pace of height change was positively associated with higher species richness ($P = 0.018$, $F_{1, 154} = 5.587$), for example resulting in a 6.8 % increase in height change when richness increases from 1 to 5. Likewise, height change was positively associated with diversity, ($P = 0.022$, $F_{1, 154} = 5.228$; Fig. 21), resulting in 4.1% increase in height change when diversity increased from 0 to 1.4.
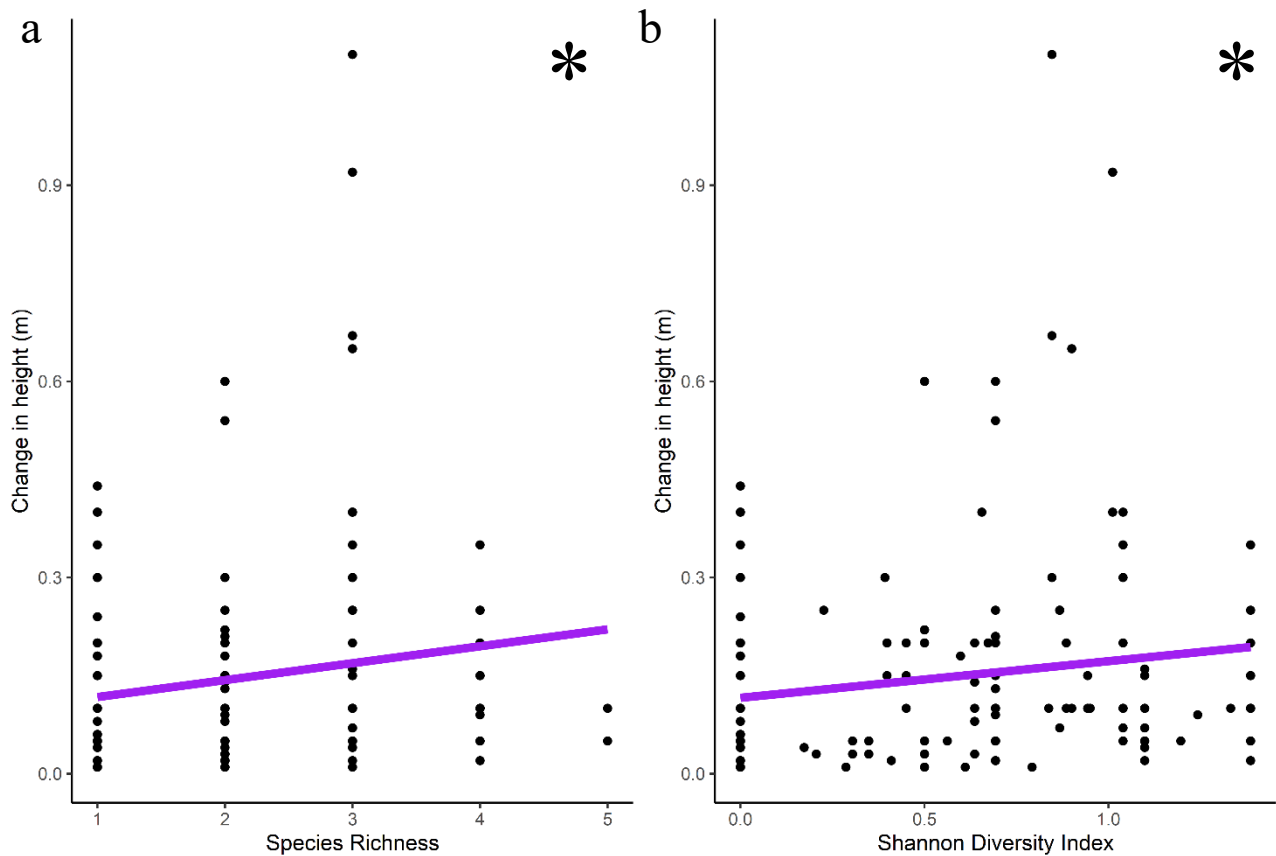
Figure 21. Relationship between richness / diversity and the change in height. Change in height versus (a) species richness, and (b) species diversity within the cage experiment. Raw data are shown but see Appendix 1 (S-2) for figures based on the model prediction.

Climatic variables and plant variables

Linear mixed models were used to determine whether climate influenced plant height, abundance, richness and diversity. The focal climate variables were mean air and soil temperature, mean humidity, mean soil volumetric moisture and total precipitation. Three time periods were considered in this analysis (spring prior to the census, six months prior to census, 12 months prior to census). Light availability was considered for 2019 only. Results for all climate analyses are presented in Tables S-1, S-2, S-3 and S-4 of Appendix 1. For temporal analysis see Figure S-3 of Appendix 1. In summary:

Juvenile plant height was negatively influenced be mean soil temperature from the 12 months prior to the census (LMM, $P < 0.0001$, $F_{1, 587} = 14.059$). For *N. moorei*, there was a slight reduction in height with increasing mean soil temperature in spring ($P = 0.0583$, $F_{1, 252} = 3.5844$).

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Likewise, using the climate data from the 6 months prior to census there was also a positive effect of soil temperature, air temperature, total precipitation, and relative humidity (all $= P < 0.05$).

Considering all species, several effects were detected when using the climate data 12 months prior to the census. Total plot abundance positively correlated with mean air temperature and mean soil temperature (both, $P < 0.01$). While total plot abundance negatively correlated with total precipitation ($P = 0.009$, $F_{1, 2031} = 6.856$), for *N. moorei*, a positive effect was detected between Spring soil temperature and abundance (LMM, $P = 0.035$, $F_{1, 734} = 4.431$) and a negative between the six month relative humidity and abundance (LMM, $P = 0.030$, $F_{1, 734} = 4.685$).

There was a positive effect of mean soil temperature in the 12 months preceding the census and species richness ($P = 0.001$, $F_{1, 2032} = 11.43$). There was a positive effect of mean air temperature, mean soil, mean relative humidity, and total precipitation (all, $P < 0.01$) for the six months prior to census on species diversity. Diversity also increased with mean air temperature and total precipitation from the 12 months preceding the census (both, $P < 0.05$).

Overall, mean height change decreased with mean air temperature ($P = 0.0001$, $F_{1, 153} = 14.343$). While a positive association was detected with the ten year mean relative humidity ($P = 0.0001$, $F_{1, 153} = 14.056$) and height change.

There was a negative correlation between total plot abundance and available light ($P < 0.0001$, $F_{1, 620} = 17.898$). Considering *N. moorei* abundance there was no correlation detected with the percentage of light available ($P > 0.05$).

5. DISCUSSION

Summary of study

The goal of this study was to investigate the key factors limiting the reproductive output and success of a long-lived rainforest tree species *Nothofagus moorei*. The first section examined the consequences of pre-dispersal seed predation that occurs within the canopy during seed embryo development. The second section examined the survival and growth of juvenile rainforest trees post-germination. Here I investigated the consequences of two modes of regeneration, those originating from seed and those from vegetative growth. The third and final section investigated the responses of juvenile rainforest trees to the exclusion of vertebrates, with a brief examination of the effects of climate variation on seedlings following ten years of observations. A summary of results showing how each section is connected is shown in Fig. 22.
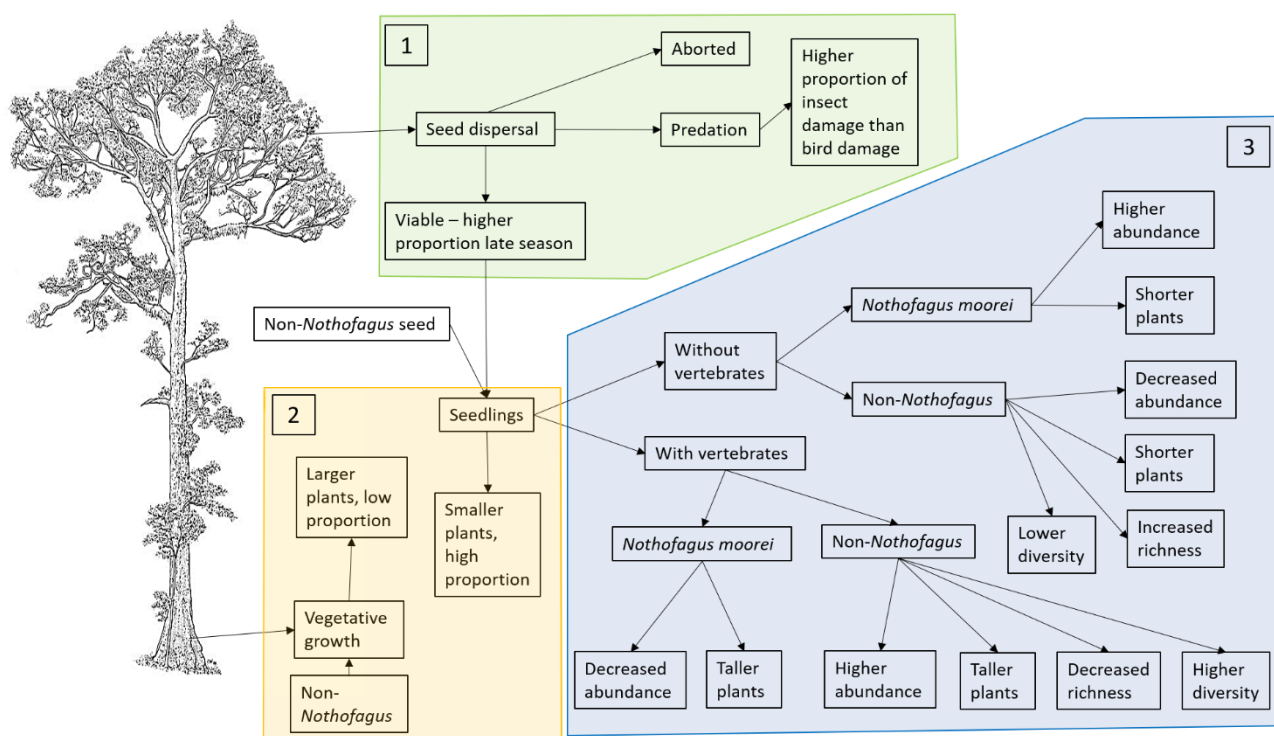
Figure 22. Summary of chief findings from the entire project. Box 1 refers to the study of pre-dispersal seed predation; Box 2 refers to the study of regeneration modes of rainforest trees; Box 3 refers to the vertebrate exclusion experiment. Image from http://plantnet.rbgsyd.nsw.gov.au .

The reproductive output and success of *N. moorei* is constrained by multiple factors including, but not limited to, seed predation, seed abortion, the origin of the seedling, and physical disturbances by ecosystem engineers. The results of this thesis cover the methods of regeneration while also revealing that some biotic interactions with animals can have both a positive and negative influence the success on *N. moorei* and co-occurring rainforest species.

While I have addressed the factors influencing the abundance, maximum height and height change of juveniles, I cannot statistically account for variation in emergence time as there is no estimate of age. It is possible, considering the slow growth in this system, that the seedlings measured have been around longer than our records and may thus be influenced by factors not considered in the present study. Additional studies would be necessary to clarify the extent to which climate patterns on longer time scales correlate with the observed changes in height and abundance.

Pre-dispersal seed predation of *N. moorei*

Considered as a proportion of seeds/fruits affected, insect predation was at its highest earliest in the season. This is in accordance with the "starvation-satiation hypothesis" proposed by Janzen (1971) in his review of seed predation. The lack of mature seeds in November and December could result from predation by birds and insects. Any mature seeds that developed in this period would be quickly consumed by predators. Another possible cause is a high abortion rate in the beginning of the season, which could be linked to climatic factors or a lack of fertilisation caused by self-incompatibility (Stephenson, 1981, Wiens, 1984, Buechline et al., 2016, Akhalkatsi and Losch, 2005, Richardson et al., 2005). For example, *Nothofagus solandri* seed production was correlated with cool but moist summers (Richardson et al., 2005). However, to date there has been no published research clarifying the extent and importance of seed abortion or self-incompatibility of Australian *Nothofagus* species.

The type of insect or insects feeding upon *N. moorei* seeds and fruits is yet to be determined, but observations of other plants suggest it is likely to be one or both of the following: (1) seed borers (Price, 2011), or (2) species with parasitic larvae (Schoonhoven et al., 2005). Seed borers are more likely to be affected by the starvation and satiation proposed in the hypothesis. By contrast, parasitic larvae feeding behaviour is likely more influenced by the current population of breeding adults during the flowering season when oviposition occurs. The limitation of the insect's dispersal range may explain why there is more insect predation than parrot predation.

Regeneration modes of cool temperate rainforest trees

For tree species in this vegetation type, two different modes of regeneration are both common: sexual reproduction via seed, and asexual reproduction through vegetative regeneration. *Nothofagus moorei* is known to reproduce (or regenerate) through both modes (Johnston and Lacey, 1983, Read and Hill, 1985a, Read and Hope, 1996, Read and Brown, 1996). However, although this is well-

known qualitatively, few if any quantitative surveys have been made. *N. moorei* is a masting species, which makes it especially interesting in this regard. Even less is known about many of the tree species that co-occur with *N. moorei* at Werrikimbe and Willi Willi National Park, in regard to their relative reliance on seed and vegetative regeneration. The purpose of this juvenile regeneration study was thus to help close this knowledge gap, at the same time providing important information regarding the life history of this historically important keystone species.

We were fortunate to be able to make use of an unpublished long-term dataset concerning this question, run for many years by staff at the Forestry Commission of New South Wales. In general, regeneration by seed was clearly dominant for most species in this ecosystem. For *N. moorei* we found 77% of juveniles had a seedling origin, and 23% a vegetative origin. However, in *Cryptocarya meisneriana* and *Doryphora sassafras*, the proportions were closer to half/half, indicating that vegetative reproduction is especially important for these species. Both species have been described to be found commonly with multi-stemmed trunks, with little seedling regeneration observed in undisturbed closed canopies (Harden, 1990, Floyd, 2008, Johnston and Lacey, 1983). A greater proportion of vegetatively derived seeds may be adaptive, as clonal sprouts may benefit from resources provided by the parent tree, which would enhance their survival.

On the face of it, we would expect the abundance of seedlings (and therefore the proportion of juveniles recorded as being from seed) to drop sharply as one considers ever-taller size classes – as a result of both interspecific competition and intraspecific competition or "self-thinning" (Westoby, 1984). Indeed, this was observed in this study. What was especially interesting, however, was that the proportions of seed- versus vegetatively-derived juveniles remained largely stable up until plants reached ca. 30 cm height and, only after that, did the proportion of seedling juveniles markedly drop (in species showing vegetative regeneration; not *Orites excelsa*, for example: see Figure 16). Considering the generally assumed slow growth rates of the tree species in this ecosystem, seedlings that are 30 cm in height may potentially be many decades old.

A resource allocation trade-off between sexual reproduction and vegetative regeneration is evident in many species of plants (Chu et al., 2011, Ceplitis, 2001, Sutherland and Vickery, 1988), but clearly, each mode has its advantages under particular situations. For example, studies of herbaceous plants found that vegetative sprouts had access to stored nutrient reserves of the parent plant, enabling them to grow during difficult periods and in patchy environments (Stuefer et al., 1996, Stuefer et al., 1994, Klimes et al., 1993) In contrast, seeds (and therefore young seedlings) are only supplied with limited resources from the parent ("limited" relative to vegetative sprouts), but

may be produced in great numbers and – depending on their dispersal mode – may have potential for being dispersed to unoccupied locations considerable distances from parent trees (Westoby et al., 1997). In line with the idea of these general trade-offs, here we found a generally higher abundance of seedling-derived juveniles, whereas vegetative juveniles were less abundant but significantly taller, even when the data were divided into height classes.

We know rather little about seed size variation among the species in this system, but it is possible that seed size is patterned with respect to regeneration mode. For example, seeds produced by *O. excelsus* are produced more regularly and are larger than those of *N. moorei*; as such, they offer a greater initial investment for early seedlings, effectively reducing mortality (Floyd, 2008). As found here, *O. excelsus* juveniles sampled at Barrington Tops were largely found to be of seed origin (Turner, 1976). We also know relatively little about seed viability. Work by Forestry Commission of NSW staff (Burgess, 1956) suggested that seed viability of *N. moorei* is high but probably limited to just a few weeks after maturity. Consistent with that suggestion, laboratory germination of one-year-old seeds yielded < 1 % germination (Peacock unpubl). In the related species, *N. cunninghamii*, seed viability is thought to be generally low, especially in in non-mast years (Hickey et al 1983). For these reasons, factors that reduce juvenile survival post germination are of particular concern.

Long term research studies in these cool temperate rainforests are rare, and rarer still are studies that clarify regeneration strategies, phenological patterns, and variation in life history. While the tree species in this ecosystem may seem ecologically similar, they are taxonomically diverse and, as shown here, their relative reliance on seedling versus vegetative regeneration may also vary consistently. Variation in life history and preference for vegetative regeneration strategies allow species to coexist and communities to remain stable, especially when species may be shade-intolerant, subject to physical disturbance and subject to sporadic masting events.

Vertebrate exclusion experiment

The cage experiment revealed that the exclusion of vertebrates – arguably ecosystem engineers – resulted in mixed responses among juveniles of co-occurring woody tree species. While many juvenile plants may be uprooted or damaged by these animals, the results of this study show that many species seem to benefit from the vertebrate's disruptive behaviour. Indeed, for two of the five focal species (*O. excelsus* and *T. insipida*), seedling abundances were higher in open plots, where vertebrates such as the Australian brush turkey and superb lyre bird are likely to disturb the litter

and soil on a frequent basis. By contrast, the central species of this thesis, *Nothofagus moorei*, was found at higher abundances in caged plots (17.9% higher, on average). Responses considered in terms of maximum juvenile height also varied among species: both for all species combined and in *C. apetalum*, maximum heights were lower within cages, whereas the opposite was true for *T. insipida*. Species richness was on average lower within the cages; however, when evenness was taken into account using Shannon Weiner's diversity index, the opposite trend was observed: diversity was higher in the presence of vertebrates.

Vertebrate effects on soil and litter

Australian brush turkeys use their large feet to scratch up the soil and litter layer while foraging for invertebrates and when building mounds used to incubate their eggs. The physical disturbance resulting from these activities is easy to observe, with mounds sometimes several metres in diameter and over a metre high, and a paucity of leaf litter in surrounding areas. Another potential ecosystem engineer in this system is the superb lyre bird. This species scratches up the soil-litter layer while foraging for invertebrates, and as part of male courtship displays.

These activities may affect not just the litter layer but also the physical and chemical properties of the soil. For example, Ashton and Bassett's (1997) showed that surface soil in a *Eucalyptus* forest affected by superb lyre birds had higher percentages of carbon, nitrogen and phosphorus than surface soil in surrounding areas without lyre birds, with potential flow-on effects to the rate of nutrient cycling within the forest. From their review of the effects of soil-disturbing animals across a range of Australian ecosystems, Elridge and James (2009) concluded that these types of effects may be quite general. That is, litter disturbance commonly results in significant redistribution of organic matter and nutrients, qualifying the animals responsible to be termed "ecosystem engineers". Of course, disturbances do not just occur above ground. Underground disturbance by earthworms is known to enhance soil aggregates that allow improved air and water infiltration into the soil (Zhang and Schrader, 1993, Edwards and Shipitalo, 1998). Indeed, very large earthworms can be found at Werrikimbe and Willi Willi National Park (up to 1 m; pers. obs. Peacock; Fig. 23a), and these leave very noticeable large casts where they have surfaced (approximately 15 cm diameter; pers. obs. Smart; Fig.23b). Soil redistribution by both vertebrates and invertebrates may also reduce runoff, in turn increasing soil moisture (Mallen-Cooper et al., 2018). In this system, I would argue that all of Brush Turkeys, Lyre Birds and giant earthworms might qualify as "ecosystem engineers".

Figure 23. Earthworm (A) and cast (B) at Werrikimbe National Park. (Photos, A. Smart).

Effects on plants

In the *Eucalyptus* forest studied by Ashton and Bassett (1997), soil disturbance by Lyre Birds was associated with higher rates of seed germination, seedling establishment, plant growth and survival. Evidence from other systems suggests a degree of generality to these positive effects on plant success. For example, disturbances that aerate the soil are seemingly required by many trees for the development of their root systems (Taylor and Ashcroft 1972 in Heth, 1991). In a global meta-analysis of the effects of soil-disturbing vertebrates, Mallen-Cooper et al. (2018) concluded that disturbance promotes the recruitment of many species. That said, the same analysis suggested that plant abundances may at the same time decrease. The results from my study suggested that the effects of vertebrates are not straightforward and not consistent across all species, which increases the difficulty in generating predictions regarding future shifts in community composition.

Vertebrate exclusion effects on abundance

Overall, the lower abundance of juvenile trees with the exclusion of vertebrates suggested a general picture of plants benefiting from the disturbance of the soil-litter layer where they germinate. However, the five focal species varied in their responses. Notably, the exclusion of vertebrates on the abundance *N. moorei* had the opposite effect to the overall trend: on average there were more *N. moorei* individuals in caged plots. These results support observations that have noted that *N. moorei* occurs in high densities when there is less soil disturbance, such as on fallen logs and in between tree roots (pers. obs. Peacock). This outcome could be connected to the traits of *N. moorei* itself.

Whilst *N. moorei* is the dominant species of the system, its seeds are small, resulting in relatively weak seedlings. The shallow roots of *N. moorei* allow it to be uprooted easily, while at the same time the disturbance by vertebrates also reduces the stability of the soil (Read and Brown, 1996). In contrast, species, such as *T. insipida* and *O. excelsus* produce more robust seedlings that can withstand disturbance better than *N. moorei*.

Vertebrate effects on height

The absence of vertebrates had a negative effect on the height of juvenile trees for all species combined, indicating that seedlings benefitted in terms of height from soil disturbance. However, this finding was not strongly supported by the individual analysis of the five focal species, which may be an artefact of the limited sampling sizes of the individual species. The only species that was similarly affected was *C. apetalum,* while the opposite was found for *T. insipida*.

Vertebrate effects on richness and diversity

Species richness was also higher in the presence of vertebrates, supporting the suggestion that disturbances create new microhabitats which can be taken advantage of by juvenile trees (Runkle, 1985). A positive effect of ecosystem engineers on species richness appears to be a general phenomenon, and has been detected across various ecosystems and taxa (Romero et al., 2015). Interestingly, here we found the opposite trend when Shannon-Weiner diversity was used as the metric rather than species richness (diversity was lower in the presence of vertebrates). This diversity index incorporates information regarding the evenness among species' abundances. In a system such as this, with some species highly abundant and many others relatively rare, there is considerable potential for richness and diversity (incorporating evenness) to show different trends. Consider the 26 species recorded over almost 40 years in chapter 3; while some species were recorded more than 1000 times, such as *N. moorei* and *C. apetalum*, many were observed less than ten times.

Additional plant responses

Unrelated to the presence/absence of vertebrates, I explored whether abundance and diversity influenced plant height, as this might suggest intense competition among juveniles. I found that the abundance of woody species in a plot did not influence the height of any given species. This was contrary to my expectation; I expected that higher juvenile abundance would indicate higher

competition for light, and lead to reduced growth. There was, however, a positive relationship between height change rate and diversity. These additional results imply that resource competition between individuals (regardless of species) was not especially strong, at least among juvenile plants most typically observed as part of the vertebrate exclusion experiment. (By contrast, we assume that competition for light would be intense immediately following mass germination events). Juvenile growth rates were on average higher in more diverse plots, perhaps suggesting that at least some species may benefit from conditions that promote greater species evenness. If a single species was dominant, and diversity was lower, then this would presumably indicate a clear competitive hierarchy, with one or a few species clearly outcompeting their neighbours for resources. However, at least for this stage of the life cycle, we detected the opposite trend.

Responses to climate variables

As the distribution of *N. moorei* is limited to high altitude, high humidity climates, several climate variables were assessed to determine their effect on juvenile rainforest trees in general and specifically on *N. moorei*. I hypothesized that drier years, for example, would be associated with reductions in abundance of *N. moorei*, and I considered climate patterns at three different time scales (three months of Spring, six months prior to census date, and 12 months prior to census date). Few if any generalities emerged. The only consistent climate predictor was soil temperature. Increased soil temperature had a positive effect on the height of *N. moorei* juveniles, on the abundance of all species, and on richness and diversity. This concurs with research of temperate tree species of Switzerland, where low temperatures were found to limit root growth (Alvarez-Uria and Korner, 2007). Contrary to this, when we consider the height of all species combined in this study, soil temperature had a negative effect. This suggests that as climates become warmer, *N. moorei* may benefit while its' co-occurring species may be disadvantaged. However, for other climate variables such as air temperature, total precipitation, soil moisture, and humidity, few effects were detected and no generalities emerged.

Despite literature suggesting that *N. moorei* is more shade intolerant than other species in this system (Read and Hill, 1985b), the abundance of *N. moorei* was not influenced by light availability. When species were combined, a negative effect of light was detected, suggesting a reduced ability to tolerate high light among juvenile trees of cool temperate rainforests. However, we caution that these findings are based on results from one time-point in 2019, ten years after the cages were installed.

Future directions and conclusions

Nothofagus moorei is an iconic species that dominates the canopy of cool temperate rainforests of northern New South Wales and southern Queensland. These forests are limited to areas of high humidity at high altitudes and are often surrounded by sclerophyll forests. With such a confined distribution, these forests may be at risk from the rising temperatures and long-term reductions in precipitation. These changes in climate suggest that decreasing soil moisture content and humidity over time may place pressure upon these communities, increasing the risk of the surrounding sclerophyll forests catching fire. The results of the present study, while not directly determining how *N. moorei* or cool temperate rainforests will fair under future climates, provide crucial knowledge of its regeneration strategies and the biotic interactions and abiotic that affect it. These could be a foundation on which to base future predictions regarding its tolerance to shifting climates.

Future research is needed to investigate the mechanisms that promote self-thinning at different life stages, by tracking the fates of seedlings and vegetative sprouts. It would also be valuable to determine more quantitatively the extent to which *N. moorei* and co-occurring species in *Nothofagus* forests vary in their degrees of shade tolerance at different sizes. This could be investigated measuring plant traits that correlate with shade tolerance as well as whole plant performance, such as photosynthetic capacity, leaf mass per unit area and leaf longevity (Kitajima, 1994, Valladares and Niinemets, 2008).

The long-term data sets used in this thesis are unique and are of high importance to understanding the natural history of these forests. While there is room for future research, this thesis addresses several key aspects of the life history of *N. moorei* and some of its' co-occurring species. Nonetheless, this thesis clarifies life history traits from long-term surveys and uses an experimental framework to provide valuable insight regarding understudied regenerative processes driven by ecosystem engineers. By combining these modes of study we hope to address a crucial gap in our understanding of the long-term stand dynamics of Australia's ancient tree species.

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APPENDICES

Appendix 1
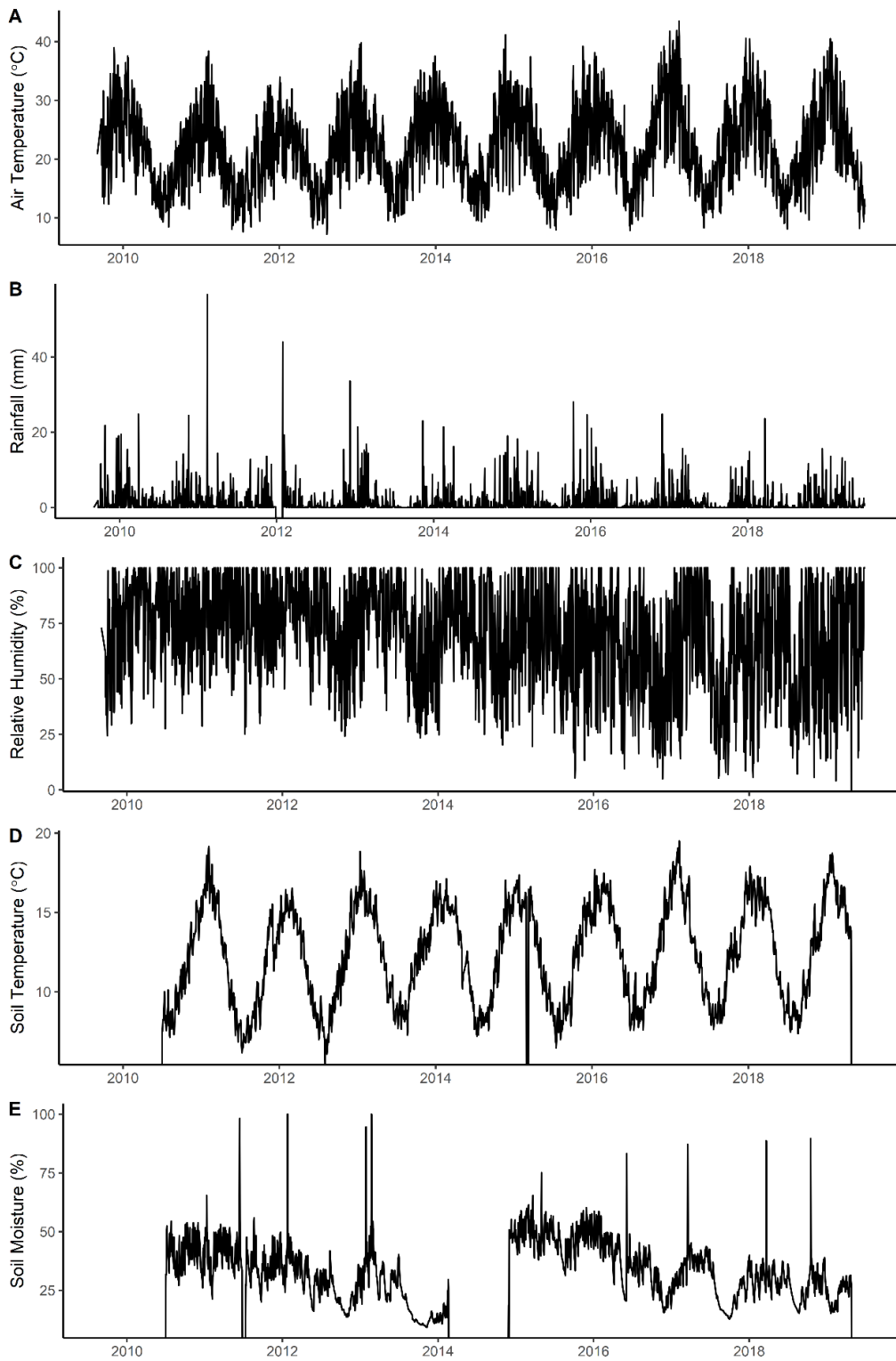
Figure S-1. Maximum monthly climate data.

Reflects the seasonality in climate factors from late 2009 to early 2019.
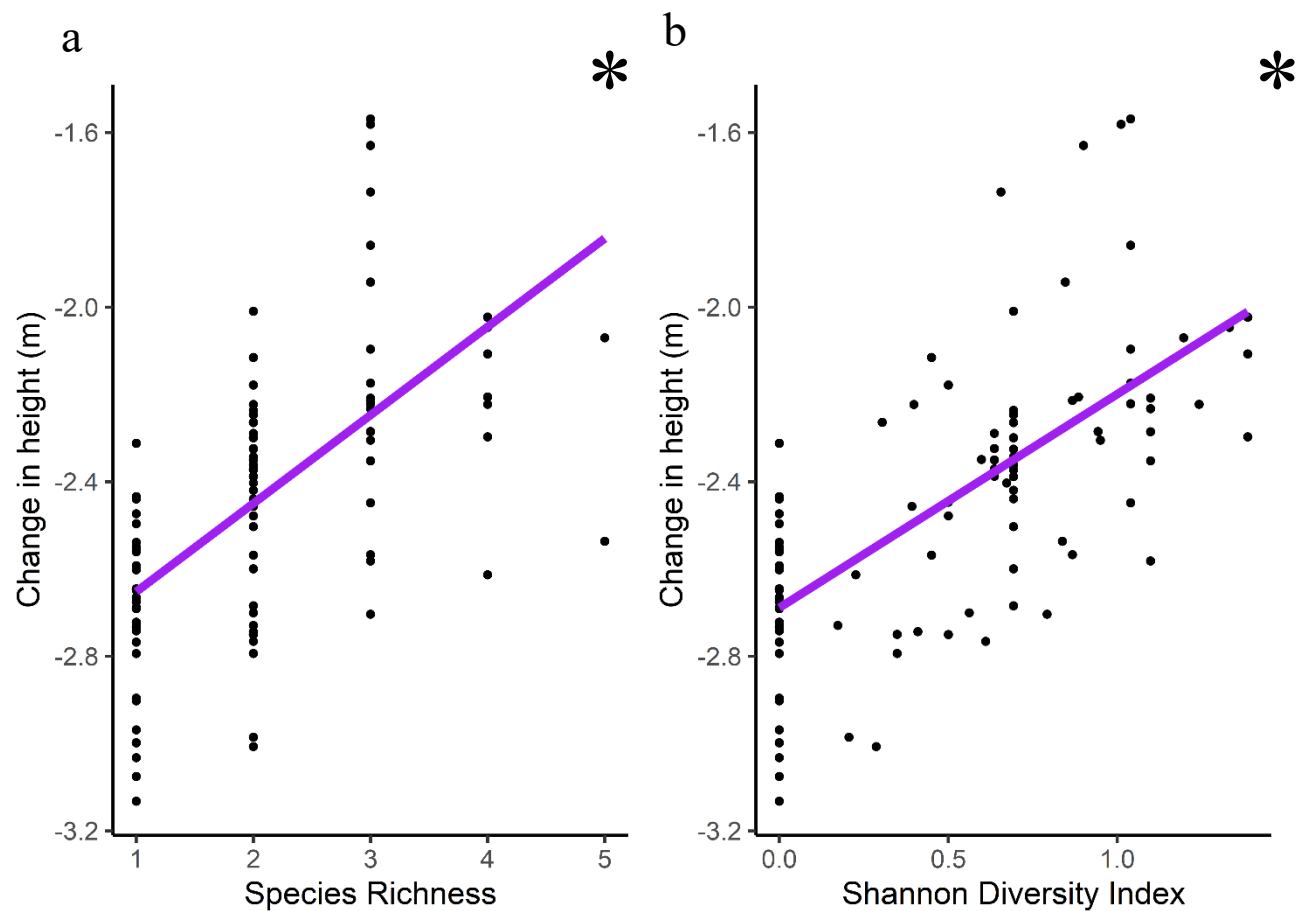
Figure S-2. The relationship between height change and richness / diversity using the model prediction. These graphs represent the predictions from the mixed model, where the change in height is log transformed.
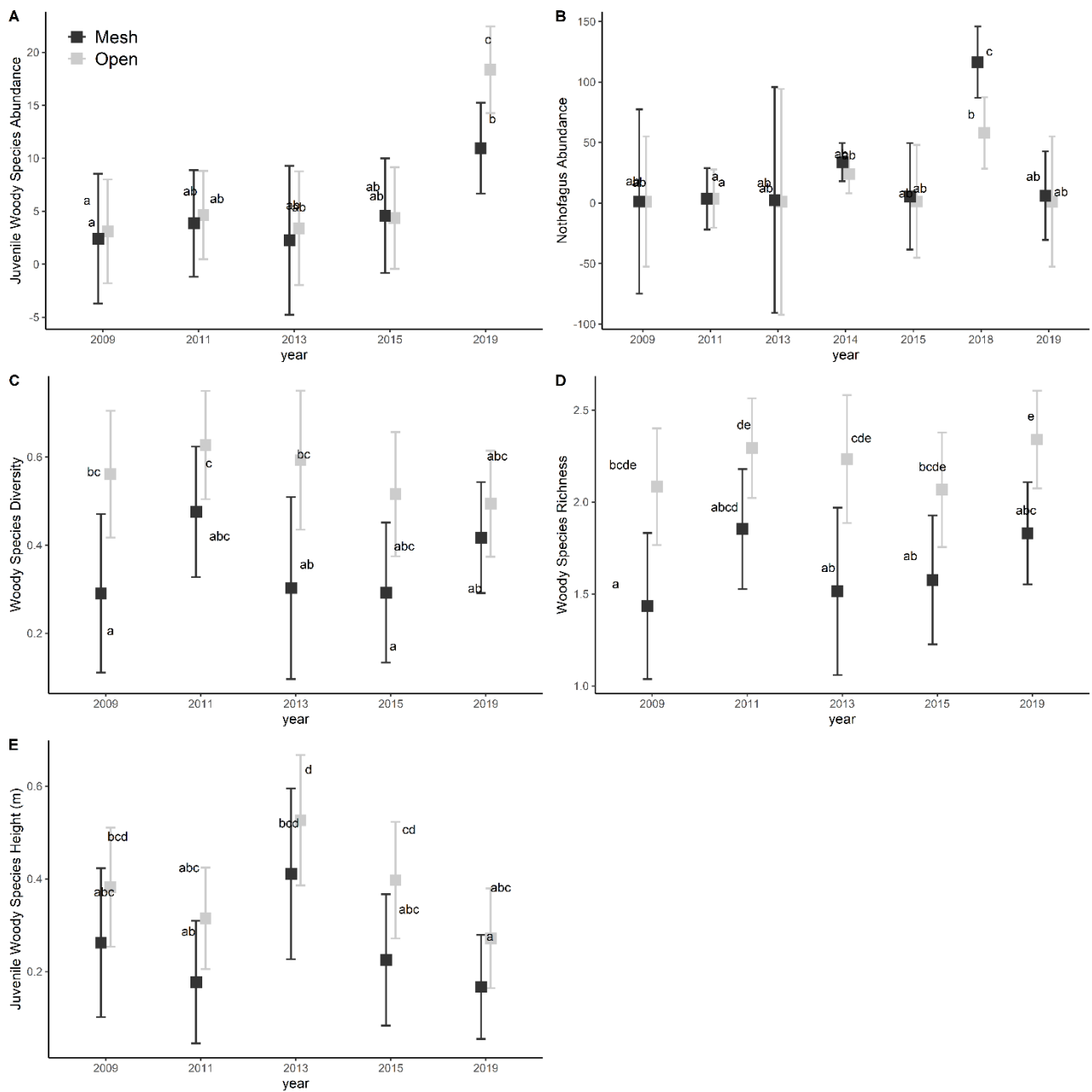
Figure S-3. Temporal patterns of juvenile woody species in open and mesh cages. A) abundance of all species; B) abundance of *N. moorei*; C) species diversity; D) species richness; E) mean height of all species

Table S-1. Results from the analysis of climate variables. Results of the linear mixed models for the response all species of juvenile plants to climatic variables. Significant results are presented in bold text.

Climate variable	Time (prior census date, inclusive)	Response variable	P - value	*F*-value	Df	Direction of effect
Mean air temperature (c°)	Spring	height	0.727	0.122	1, 587	na
Total precipitation (mm)	Spring	height	0.314	1.012	1, 587	na
Mean relative humidity (%)	Spring	height	0.889	0.019	1, 587	na
Mean soil temperature (c°)	Spring	height	0.097	2.763	1, 587	negative
Mean soil volumetric moisture (%)	Spring	height	0.520	0.413	1, 587	na
Mean air temperature (c°)	6 months	height	0.973	0.001	1, 587	na
Total precipitation (mm)	6 months	height	0.263	1.252	1, 587	na
Mean relative humidity (%)	6 months	height	0.365	0.819	1, 587	na
Mean soil temperature (c°)	6 months	height	0.991	0.001	1, 587	na
Mean soil volumetric moisture (%)	6 months	height	0.717	0.132	1, 587	na
Mean air temperature (c°)	12 months	height	0.365	0.821	1, 587	na
Total precipitation (mm)	12 months	height	0.208	1.587	1, 587	na

Mean relative humidity (%)	12 months	height	0.424	0.641	1, 587	na
Mean soil temperature (c∘)	**12 months**	**height**	**0.0002**	**14.059**	**1, 587**	**negative**
Mean soil volumetric moisture (%)	12 months	height	0.621	0.244	1, 587	na
Mean air temperature (c∘)	Spring	total abundance	0.527	0.399	1, 2031	na
Total precipitation (mm)	Spring	total abundance	0.251	1.318	1, 2031	na
Mean relative humidity (%)	Spring	total abundance	0.888	0.019	1, 2031	na
Mean soil temperature (c∘)	Spring	total abundance	0.205	1.608	1, 2031	na
Mean soil volumetric moisture (%)	Spring	total abundance	0.506	0.443	1, 2031	na
Mean air temperature (c∘)	6 months	total abundance	0.718	0.130	1, 2031	na
Total precipitation (mm)	6 months	total abundance	0.825	0.049	1, 2031	na
Mean relative humidity (%)	6 months	total abundance	0.615	0.252	1, 2031	na
Mean soil temperature (c∘)	6 months	total abundance	0.783	0.076	1, 2031	na
Mean soil volumetric moisture (%)	6 months	total abundance	0.661	0.193	1, 2031	na
Mean air temperature (c∘)	**12 months**	**total abundance**	**0.018**	**5.555**	**1, 2031**	**positive**
Total precipitation (mm)	**12 months**	**total abundance**	**0.009**	**6.856**	**1, 2031**	**negative**
Mean relative humidity (%)	12 months	total abundance	0.105	2.634	1, 2031	na

Mean soil temperature (c◦)	**12 months**	**total abundance**	**0.0006**	**11.903**	**1, 2031**	**positive**
Mean soil volumetric moisture (%)	12 months	total abundance	0.626	0.237	1, 2031	na
Mean air temperature (c◦)	Spring	Richness	0.297	1.858	1, 2032	na
Total precipitation (mm)	Spring	Richness	0.378	0.776	1, 2032	na
Mean relative humidity (%)	Spring	Richness	0.177	1.821	1, 2032	na
Mean soil temperature (c◦)	Spring	Richness	0.288	1.128	1, 2032	na
Mean soil volumetric moisture (%)	Spring	Richness	0.271	1.211	1, 2032	na
Mean air temperature (c◦)	6 months	Richness	0.558	0.343	1, 2032	na
Total precipitation (mm)	6 months	Richness	0.587	0.295	1, 2032	na
Mean relative humidity (%)	6 months	Richness	0.622	0.243	1, 2032	na
Mean soil temperature (c◦)	6 months	Richness	0.829	0.046	1, 2032	na
Mean soil volumetric moisture (%)	6 months	Richness	0.418	0.657	1, 2032	na
Mean air temperature (c◦)	12 months	Richness	0.659	0.194	1, 2032	na
Total precipitation (mm)	12 months	Richness	0.273	1.203	1, 2032	na
Mean relative humidity (%)	12 months	Richness	0.74	0.109	1, 2032	na
Mean soil temperature (c◦)	**12 months**	**Richness**	**0.0007**	**11.43**	**1, 2032**	**positive**

Mean soil volumetric moisture (%)	12 months	Richness	0.636	0.224	1, 2032	na
Mean air temperature (c∘)	Spring	Diversity	0.543	0.393	1, 886	na
Total precipitation (mm)	Spring	Diversity	0.863	0.029	1, 886	na
Mean relative humidity (%)	Spring	Diversity	0.129	2.303	1, 886	na
Mean soil temperature (c∘)	Spring	Diversity	0.077	3.132	1, 886	positive
Mean soil volumetric moisture (%)	Spring	Diversity	0.589	0.291	1, 886	na
Mean air temperature (c∘)	**6 months**	**Diversity**	**0.002**	**9.667**	**1, 886**	**positive**
Total precipitation (mm)	**6 months**	**Diversity**	**0.003**	**8.681**	**1, 886**	**positive**
Mean relative humidity (%)	**6 months**	**Diversity**	**0.007**	**7.392**	**1, 886**	**positive**
Mean soil temperature (c∘)	**6 months**	**Diversity**	**0.001**	**10.833**	**1, 886**	**positive**
Mean soil volumetric moisture (%)	6 months	Diversity	0.12	2.4172	1, 886	na
Mean air temperature (c∘)	**12 months**	**Diversity**	**<0.0001**	**45.809**	1, 886	**positive**
Total precipitation (mm)	**12 months**	**Diversity**	**0.027**	**4.886**	**1, 886**	**positive**
Mean relative humidity (%)	12 months	Diversity	0.368	0.812	1, 886	na
Mean soil temperature (c∘)	12 months	Diversity	0.389	0.742	1, 886	na
Mean soil volumetric moisture (%)	12 months	Diversity	0.999	0	1, 886	na

Table S-2. Climate results for N. moorei. Results of the linear mixed models for the response of juvenile *N. moorei* plants to climatic variables.

Climate variable	Time (prior census date, inclusive)	Response variable	P - value	*F*- value	Df	Direction of effect
Mean air temperature (c∘)	Spring	height	0.876	0.025	1, 252	na
Total precipitation (mm)	Spring	height	0.486	0.485	1, 252	na
Mean relative humidity (%)	Spring	height	0.859	0.032	1, 252	na
Mean soil temperature (c∘)	Spring	height	0.058	3.584	1, 252	negative
Mean soil volumetric moisture (%)	Spring	height	0.901	0.016	1, 252	na
Mean air temperature (c∘)	**6 months**	**height**	**0.026**	**4.961**	**1, 252**	**positive**
Total precipitation (mm)	**6 months**	**height**	**0.005**	**7.905**	**1, 252**	**positive**
Mean relative humidity (%)	**6 months**	**height**	**0.040**	**4.204**	**1, 252**	**positive**
Mean soil temperature (c∘)	**6 months**	**height**	**0.009**	**6.710**	**1, 252**	**positive**
Mean soil volumetric moisture (%)	6 months	height	0.581	0.304	1, 252	na
Mean air temperature (c∘)	12 months	height	0.705	0.144	1, 252	na
Total precipitation (mm)	12 months	height	0.122	2.387	1, 252	na
Mean relative humidity (%)	12 months	height	0.436	0.607	1, 252	na
Mean soil temperature (c∘)	12 months	height	0.076	3.157	1, 252	negative

Mean soil volumetric moisture (%)	12 months	height	0.695	0.154	1, 252	na
Mean air temperature (c∘)	Spring	total abundance	0.583	0.301	1, 734	na
Total precipitation (mm)	Spring	total abundance	0.992	0.001	1, 734	na
Mean relative humidity (%)	Spring	total abundance	0.204	1.612	1, 734	na
Mean soil temperature (c∘)	**Spring**	**total abundance**	**0.035**	**4.431**	**1, 734**	**positive**
Mean soil volumetric moisture (%)	Spring	total abundance	0.532	0.390	1, 734	na
Mean air temperature (c∘)	6 months	total abundance	0.438	0.602	1, 734	na
Total precipitation (mm)	6 months	total abundance	0.089	2.893	1, 734	negative
Mean relative humidity (%)	**6 months**	**total abundance**	**0.030**	**4.685**	**1, 734**	**negative**
Mean soil temperature (c∘)	6 months	total abundance	0.342	0.903	1, 734	na
Mean soil volumetric moisture (%)	6 months	total abundance	0.072	3.235	1, 734	negative
Mean air temperature (c∘)	12 months	total abundance	0.449	0.572	1, 734	na
Total precipitation (mm)	12 months	total abundance	0.177	1.827	1, 734	na

Mean relative humidity (%)	12 months	total abundance	0.295	1.098	1, 734	na
Mean soil temperature (c∘)	12 months	total abundance	0.220	1.502	1, 734	na
Mean soil volumetric moisture (%)	12 months	total abundance	0.393	0.731	1, 734	na

Table S-3. The response of height change to climate variables. Results of the linear mixed models used for the response of height change in plant juveniles and climate variables.

Climate variable	P - value	*F*- value	Df	Direction of effect
Mean air temperature (c∘)	**0.0001**	**14.343**	**1, 153**	negative
Total precipitation (mm)	0.454	0.561	1, 153	na
Mean relative humidity (%)	**0.0001**	**14.056**	**1, 153**	positive
Mean soil temperature (c∘)	0.083	3.002	1, 153	negative
Mean soil volumetric moisture (%)	0.786	0.074	1, 153	na

Table S-4. Results for the light analysis on plant abundance. Results of the linear mixed models for the response of abundance and height of plants to the percentage of light gaps in the canopy above the plot.

	Response variable	P - value	*F*- value	Df	Correlation
All species	abundance	0.177	1.827	1, 113	na
All species	height	0.128	2.316	1, 192	na
N. moorei	abundance	0.169	1.890	1, 134	na
N. moorei	height	0.063	3.452	1, 14	negative