Post-dispersal seed predation in a conifer-broadleaf forest remnant: the importance of exotic mammals

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Abstract of a thesis submitted in partial fulfilment of the requirements for the Degree of Ph.D.

Post-dispersal seed predation in a conifer-broadleaf forest remnant: the importance of exotic mammals

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Despite extensive international acceptance of the critical role of mammalian post-dispersal seed predation in many plant communities, in New Zealand we have limited knowledge of these predators' influence on plant recruitment in our forests. The principle objective of my thesis was to determine the importance of exotic mammals as post-dispersal seed predators in a New Zealand conifer-broadleaf forest remnant. To address this goal, I used a series of field-based experiments where the actions of different post-dispersal seed predators were separated by wire-mesh exclosures.

My study was conducted at Mount Peel Forest Park Scenic Reserve, South Canterbury, New Zealand. Being a human modified conifer forest currently dominated by broadleaf species, it is typical of forest remnants in New Zealand. This presented an opportunity to study a wide range of both potential post-dispersal seed predators and broadleaf tree species.

My findings indicate that exotic mammals are not only post-dispersal seed predators at Peel Forest, but are responsible for the majority of post-dispersal predation events observed. Ship rats (*Rattus rattus*) were the dominant post-dispersal seed predators, while brushtail possums (*Trichosurus vulpecula*), house mice (*Mus musculus*) and native invertebrates were also important post-dispersal seed predators for several tree species. Through use of time-lapse video and cafeteria experiments I found that exotic mammalian seed predators, when compared to native invertebrate seed predators, preyed upon larger-seeded plant species and were responsible for considerable seed losses of several tree species. However, exotic mammalian seed predators do share several foraging characteristics with native invertebrate seed predators, as predators foraged in similar habitats and responded in a similar way to changes in seed density.

In investigating if post-dispersal seed predation by mammals had a flow-on effect to plant recruitment, I observed natural seedling densities at Peel Forest were significantly higher in the absence of mammalian seed predators, but I found no evidence that the presence of mammals significantly altered the overall species richness. At the community level, I did not find an interaction between habitat and exotic mammals, however I present evidence that for individual plant species a significant mammal : habitat interaction occurred. Consequently, even though my cafeteria experiment implied there was no

significant difference in the overall amount of seed preyed upon within different habitats, the less favourable microsite conditions for germination under an intact continuous canopy allows mammals to exacerbate habitat-related patterns of seed mortality and have a noticeable effect on seedling establishment.

In an effort to validate the use of manipulative experiments to predict the long-term effect of post-dispersal seed predation on plant dynamics, I attempted to link results of my cafeteria experiment with observed seedling abundance at Peel Forest. Seven tree species were used in this comparison and a strong correlation was observed. This result shows that the level of post-dispersal seed predation determined in the cafeteria experiment provided a good predictor of the effect of mammalian post-dispersal seed predation on seedling establishment.

To fully gauge the impact of mammalian post-dispersal seed predators on seedling establishment, the relationship between these seed predators and the type of recruitment limitation experienced by a plant species was also investigated. By using a combination of seed addition, plot manipulations and seed predator exclusion I was able to investigate this relationship. I found evidence that seed limitation at Peel Forest is positively correlated with seed size, and that while mammalian post-dispersal seed predators can further reduce plant recruitment of plant species experiencing seed limitation, the influence of mammals in determining plant recruitment was limited for plant species experiencing microsite limitation.

My study has proven that exotic mammals are now the dominant post-dispersal seed predators at Peel Forest, the amount of seed preyed upon varies among plant species, and post-dispersal seed predation by mammalian species can lead to differences in seedling richness and abundance. I proved that the influence of exotic mammals on seedling establishment is also linked to habitat structure and recruitment limitations. When combined these observations suggest that exotic mammalian post-dispersal seed predators may play an important role in determining landscape abundance and distribution of plants at Peel Forest.

Keywords: post-dispersal seed predation, seedling establishment, recruitment limitation, cafeteria experiment, seed addition, time-lapse video analysis, exotic mammals, seed traits, conifer-broadleaf forest, *Rattus rattus, Mus musculus, Trichosurus vulpecula.*

Table of Contents

List of Figures

List of Tables

Acknowledgements

Chapter One: General introduction

Despite being the focus of intense theoretical and empirical research (Harper 1977; Halloy 1995; Silvertown 2004), there is no consensus regarding the mechanisms involved in controlling plant recruitment (Begon et al. 1990; Hambäck and Beckerman 2003); but it is clear that animals can play critical roles in the shaping of plant communities. Herbivory encompasses many different types of interactions, and differs in duration and consequence to the plant (Strauss and Zangerl 2002). Although large bodied animals are known to have significant effects on plant communities through selective removal of biomass and death of established individuals (see Augustine and McNaughton 1998 for a review), it is principally at the seed and seedling stages that animals influence plant mortality (Harper 1977; Clark et al. 1998; Zobel et al. 2000) and consequently have the greatest impact on plant communities (Crawley 2000).

1.1 Seed predation

The enormous amount of seed produced by plants, coupled with the general rareness of seedlings and saplings, is vivid testimony to the intensity of seed mortality (Bazzaz 1991; Crawley 1992). Previous literature reviews have found that it is not uncommon for plants to lose 90-100% of a seed crop to seed predators (Crawley 1992; Hulme 2002), which may result in significant impacts on plant population dynamics (Inouye et al. 1980; Heske et al. 1993; Asquith et al. 1997). These high levels of seed lost are not unexpected, as seeds are potentially a valuable food resource. In addition to the chemical compounds found in all plant tissue, seeds contain storage reserves made up of carbohydrates, lipids, and proteins (Marquis and Batzli 1989), but contain relatively little water, resulting in seeds being relatively nutrient-rich compared to other plant tissues (Crawley 2000).

Seed predation is a comparatively well defined event. The definition of predation used in my thesis is the "consumption of one organism (the prey) by another organism (the predator), in which the prey is alive when the predator first attacks it" (Begon et al. 1990). While this includes grazers, parasitoids and parasites, to be a true predator an organism needs kill their prey more or less immediately and they kill several prey during their lifetime (Begon et al. 1990). Seed predation is therefore an event where a predator specifically targets and kills seeds throughout their lifetime and although initially they seem similar, seed predators are

also different from frugivores (Hulme 2002). Rather than focusing on the seed themselves, a frugivore is interested in the fruit flesh (mesocarp) that surrounds the seeds. Frugivory is often mutualistic as the frugivore acts as a dispersing agent for the plant (Herrera et al. 1994; Jordano and Godoy 2002) or in some cases the seeds are required to pass through the digestion system of the frugivore to enable germination to occur (Temple 1977; Stiles 2000).

Seed predation can occur either pre- or post-dispersal. Pre-dispersal seed predators are typically specialists as fruiting of plants are generally clumped and predictably distribution both in space and time. The majority of pre-dispersal seed predators are insects, especially from the orders of Coleoptera, Hemiptera and Lepidoptera (Crawley 1992). Most pre-dispersal predators time their life-cycle to coincide with seed production of one or a few plant species, and many pre-dispersal predators mature within a single seed or seed head (Janzen 1971).

In contrast, post-dispersal seed predators are typically mobile, less specialised organisms as dispersed seeds are often widely scattered (Hulme and Benkman 2002). Small mammals are major post-dispersal seed predators and are known to have significant impacts on plant population dynamics, especially in temperate ecosystems (Hulme 1998; Blaney and Kotanen 2001). Ants have been shown to be important post-dispersal seed predators in arid and semi-arid ecosystems but ants act mainly as seed dispersers rather than as predators in temperate ecosystems (Mittelbach and Gross 1984; Blaney and Kotanen 2001). Birds, Lygaeid bugs, carabid beetles, crabs, and even fish have also been shown to be post-dispersal seed predators in many communities (Crawley 2000; Hulme and Benkman 2002; Meeson et al. 2002; Lindquist and Carroll 2004).

1.2 Factors influencing post-dispersal seed predation

Plants often produce many more flowers than they could ever turn into ripened fruits packed with proteins and carbohydrates. This allows the parent plant the opportunity to compensate for pre-dispersal seed predation through differential abortion of damaged fruit prior to the completion of seed development (Sallabanks and Courtney 1992). However, once the seed has left the plant, the parent has very few options to limit seed losses to predation (Blaney and Kotanen 2001).

1.2.1 Seed characteristics

Changes in seed characteristics are the most common way plants attempt to influence the survival of seeds after dispersal. Post-dispersal seed predators, in both forests and other plant communities, have been shown to be highly selective of the seeds they eat with seed resource characteristics influencing preferences (Willson and Whelan 1990; Osunkoya 1994). Due to their high nutritional value, seeds often receive a greater investment in defences than vegetative tissue (Janzen 1971). First, seeds may be poisonous or have a large amount of secondary compounds that either impair digestibility or make them unpalatable (Campbell 1978; Kollmann et al. 1998). Common chemical defences include non-protein amino acids, cyanogenic glycosides and protease inhibitors (Thompson and Hagen 1999; Hulme and Benkman 2002). Second, the physical attributes of seeds can affect the risk of predation; these seeds often have low levels of toxins (Crawley 2000). Seed size is a common attribute affecting levels of seed predation. Optimal foraging theory predicts that predators should prefer seeds with the greatest reward (Mitchell 1989). Theoretically, gross returns to predators should increase with increasing seed size (Celis-Diez et al. 2004), however, the net gain may differ depending on the specific predator involved. A seed too large for one predator species to effectively handle, may also be too small to locate on the forest floor by another predator resulting in no net gain to either predator (Blate et al. 1998; Fenner and Kitajima 1999). Seed colour is another attribute that influences post-dispersal seed predation rates. Seeds that are cryptic and blend in with their surroundings may avoid being detected by visual searching seed predators. Most seeds have a dull colour and this is thought to be in response to seed predation (Nystrand and Granstrom 1997). Seed size also impacts the time it takes for the seed to be encapulated into the forest floor substrate. Hulme (1994) found that buried seeds experienced substantially lower rates of seed predation compared to seeds exposed on the surface. Once buried, small seeds are relatively safe from small mammals but rodents will dig up larger seeds from considerable depths (Bekker et al. 1998). The thickness of the seed coat (Moles and Drake 1999) and surface structure of the seed (Nystrand and Granstrom 1997; Saracino et al. 2004) may also influence rates of post-dispersal seed predation.

1.2.2 Seed density

The density of seeds on the forest floor also plays an important role in regulating post-dispersal seed predation losses. Though at certain times seeds are plentiful, generally seed

abundance is less predictable than the abundance of other plant resources such as leaves. While some plants protect their seeds with physical or chemical defences other plant species protect their seeds by manipulating the quantity of seeds produced, a concept known as 'mast-seeding'. In this defence, plant species have a bimodal distribution of seed outputs, (i.e. years of either large or small seed outputs) rather than a continuous variation around a mean (Kelly 1994). If mast years are synchronised within the population then this strategy may considerably reduce the effect of seed predation at the population level (McKone et al. 1998; Kelly and Sork 2002) by saturating any individual seed predators present allowing some seed to survive.

1.2.3 External factors

Not only can seed characteristics and seed density be influential, but the external environment can also be a powerful factor in determining the amount of seed lost to post-dispersal predators. Following seed dispersal, variation in weather (Edwards and Crawley 1999), altitude (Rey et al. 2002), season (Lu and Zhang 2004) and temperature (Hobbs 1985) have all been shown to influence levels of post-dispersal seed predation. However, the most commonly reported external factor influencing post-dispersal seed predation is the surrounding vegetation structure. It has been suggested that the failure of seeds to establish in dense vegetation is largely due to post-dispersal seed predation rather than interference from established plants (e.g. Reader 1993; Holl 2002). Mammalian post-dispersal seed predation is often reported to be greatest in vegetation of higher structural complexity than nearby open habitats (Gross 1984; Myster and Pickett 1993; Manson and Stiles 1998). This may relate to vegetation cover contributing to anti-predator strategies of the seed predators (Dickman 1992; Cox et al. 2000), or the use of cover may be a result of competition with other animals (Falkenberg and Clarke 1998).

1.3 Importance of post-dispersal seed predation to plant communities

Post-dispersal seed predation is only one of numerous factors underlying plant demography and evolution, nevertheless the generalist feeding habits of many post-dispersal seed predators and the limited ability of plants to compensate for post-dispersal seed losses suggest this type of predation may have a considerable impact on plant populations (Hulme 1998; Blaney and Kotanen 2001).

The influence of post-dispersal seed predation on plant recruitment and demography can be two-fold. First, at a population and community level, post-dispersal seed predation is thought to play an important role in recruitment of existing populations (Schupp 1988; Hulme 1996; Blate et al. 1998), colonisation ability into new areas (Schupp et al. 1989; Myster and Pickett 1993) and spatial distribution (Hulme 1997; Clark et al. 1998; Forget et al. 1999) of plant species. Second, predators may be important at an individual plant level, regardless of whether post-dispersal seed predation has an effect on the overall population of the plant species. At this level, seed predators may influence the relative representation of different genotypes in future generations (Janzen 1971; Howe and Smallwood 1982).

However, the effects of post-dispersal seed predation on plant recruitment will vary depending on the species and community involved (Hulme 1996) and is a function of both seed density and environmental conditions necessary for successful germination (Grubb 1977). Seed predators will only play a role in controlling recruitment for plant species which depend solely on seed rather than vegetative spread for regeneration (Inouye et al. 1980; Brown and Heske 1990) and even then, post-dispersal seed predators may only be influential under certain conditions. When conditions are favourable for germination and the seed density is low, post-dispersal seed predation can have a significant impact on recruitment (Anderson 1989; Louda and Potvin 1995). This is because at low seed densities there is no opportunity for compensatory reductions in other mortality factors (Crawley 1992). If plant recruitment is limited by factors other than seed availability (e.g. competition, seedbank or lack of suitable germination sites), then while seed predation may be the proximate cause of death for that individual, there may be no detectable impact on the population as the individual may never have contributed to the population (Anderson 1989; Hulme 1996; Edwards and Crawley 1999).

1.4 The New Zealand situation

While the majority of New Zealand's plants and vertebrates have been described taxonomically, the factors influential in the dynamics of the structurally complex, species-rich conifer-broadleaf forests of New Zealand are not fully understood (Lusk and Smith 1998). The majority of research into plant community dynamics in New Zealand forests has focused on the availability of suitable microsites for establishment (e.g. Stewart 1986), the role of the canopy openings formed by disturbance (e.g. Duncan 1991; Rogers 1999), and level of shade

tolerance (e.g. McAlpine and Drake 2002; Smale and Smale 2003). Previous studies on the effects of grazing by ungulates (Forsyth et al. 2002), brushtail possums (*Trichosurus vulpecula*) (Nugent et al. 2000) and some invertebrates (Hodge et al. 1998) has been conducted, our understanding of seed predation in New Zealand ecosystems is limited (Sullivan et al. 1995). While no comprehensive study of the post-dispersal seed predators in New Zealand conifer- broadleaf forests has been conducted, what is certain is that the species composition of these predators has changed since human arrival to New Zealand.

1.4.1 Pre-human New Zealand

Prior to human arrival, New Zealand's post-dispersal seed predator guilds potentially comprised largely of avian and invertebrate species. While the taxonomy of this pre-human fauna is well understood, our understanding of the ecosystem functioning of this unique fauna is less complete. Most species of forest birds are known to include fruit in their diet (Clout and Hay 1989) but few are believed to have been specialised post-dispersal seed predators. Species known to have foraged on the forest floor and whose diet contained seeds include red-crown parakeet (*Cyanoramphus novaezelandiae novaezelandiae*), weka (*Gallirallus australis*) and various species of kiwi (*Apteryx* spp.) (Reid et al. 1982; Clout and Hay 1989; Heather and Robertson 1996). Both brown teal (*Anas chlorotis*), and the New Zealand quail (*Coturnix novaezelandiae*) had a high percentage of vegetation in their diets (Worthy and Holdaway 2002), but as these avian species are believed to have eaten complete fruit rather than dispersed seeds, the role they played as post-dispersal seed predators or secondary dispersal agents is unknown. The extinct species, Finsch's duck (*Euroyanas finschi*) was an important ground foraging bird in pre-human New Zealand. Finsch's duck was very common throughout inland regions but not in closed-canopy conifer forests and is considered to have been a consumer of low vegetation and fallen fruit (Worthy and Holdaway 2002). Several species of moa are also believed to targeted fallen fruit on the forest floor (Duncan and Holdaway 1989; Burrows 1994) but it is unknown if they played a role as post-dispersal seed predators. See Chapter Two for further discussion on avian post-dispersal seed predators.

The majority of post-dispersal seed predators in pre-human New Zealand were expected to have been invertebrates. Though studies of Orthoptera have shown that these invertebrates are important seed predators (Mirams 1957; Duthie et al. 2006), and invertebrate seed predators of grassland and alpine ecosystems have been studied (Ledgard 1979; Bremner

1991; Kelly et al. 1992; Lord and Kelly 1999), in general very little is known about the diet and behaviour of ground dwelling invertebrates in New Zealand conifer-broadleaf forests (Howarth and Ramsay 1991).

Though the diet of many of New Zealand's native fauna suggests that post-dispersal seed predation occurred, there is speculation that this type of seed predation was not an influential component of New Zealand's pre human forest ecosystems. The main arguments put forward for this viewpoint are: 1) many important post-dispersal seed predators of forest plants,(e.g. ants and rodents) were either not originally present in numbers comparable to overseas ecosystems (Howarth and Ramsay 1991), or never part of the New Zealand fauna, and 2) the high frequency of mast-seeding plants in New Zealand is a evolutional response to both the presence of specialist invertebrate pre-dispersal predators and the absence of generalist post-dispersal predators (Kelly 1994). However, these statements may simply reflect our limited knowledge of the pre-human fauna as globally post-dispersal seed predators exist in most community types (Crawley 2000; Danell and Bergstrom 2002) so it is unlikely that a valuable food resource such as seeds would not have been utilised in pre-human New Zealand forests.

1.4.2 Post-human New Zealand

Human introduction of mammalian post-dispersal seed predators occurred in two waves. First, Polynesian settlers introduced kiore (Polynesian rat, *Rattus exulans*) approximately 800 years ago (although a date of 2000 years ago has been suggested by Holdaway (1996)). Second, European settlers introduced a wide suite of mammalian seed predators beginning with the arrival of Captain Cook in 1769. These included three species of rodent (Norway rat (*R. norvegicus*), ship rat (*R. rattus*) and the house mouse (*Mus musculus*)) and the brushtail possum (Campbell 1978; Nugent et al. 2000; Innes 2001).

Currently in New Zealand the dominant mammalian post-dispersal seed predators is probably a rodent species. Rodents are major post-dispersal seed predators overseas, especially in temperate ecosystems (Hulme 1998; Blaney and Kotanen 2001). On the New Zealand mainland, the most widespread rodent in low and mid altitude native forests is the ship rat (Innes 1990). Ship rats eat both plant and animal foods, with seeds and fruit forming an important dietary component when available (Beveridge 1964; Best 1969; Campbell 1978; Innes 1990). The house mouse is also widespread, especially in disturbed habitats (Murphy

and Pickard 1990) and is known to be a seed predator (Murphy and Pickard 1990; Fitzgerald et al. 1996). Also common throughout most of the New Zealand mainland is the brushtail possum (Cowan 1990). Brushtail possums are known to feed extensively on the forest floor (Cowan and Clout 2000), usually feeding on low growing herbs, grasses, fallen leaves and invertebrates (Cowan and Moeed 1987; Nugent et al. 2000). Seeds are regularly observed in possum diets but have been traditionally used as an indicator of pre-dispersal fruit consumption (e.g. Coleman et al. 1985; Nugent et al. 2000; Dungan et al. 2002) rather than evidence of post-dispersal seed predation. In a controlled environment, Williams et al. (2000) found that seeds of various plant species survived ingestion by brushtail possums, and suggested that these mammals are potentially an important seed disperser in many forest ecosystems, rather than a key seed predator. Previous studies have also recorded exotic bird species foraging seeds on the forest floor but these events are considered to be rare (see Beveridge 1964; Burrows 1994).

At the conception of this thesis, no clear agreement to the importance of exotic mammals as post-dispersal seed predators in New Zealand existed. While there is evidence of seed in the diets of mammals, and studies have attributed recruitment depressions of several coastal tree species to rodent seed predation (e.g. Allen et al. 1994; Campbell and Atkinson 2002), there has also been speculation that the role played by exotic mammals as post-dispersal seed predators in New Zealand may have been overestimated (Moles and Drake 1999) or that these mammals have simply replaced pre-existing native seed predators such as weta (e.g. Campbell 1978; Ramsay 1978). While the role of mammalian species as post-dispersal seed predators remains unclear, the introduction of these species to New Zealand has markedly altered the pre-human post-dispersal seed predator community. Seeds form only a component of these exotic mammals' diets; the majority being invertebrates, vertebrates or other plant matter. Exotic mammals in New Zealand are known to have a negative effect on the populations of native birds (Best 1969; McLennan et al. 1996), skinks and geckos (Towns et al. 1997) and molluscs and invertebrates (Ramsay 1978; Gales 1982; Cowan and Moeed 1987). Many native post-dispersal seed predators are now extinct as a direct result of mammalian predation (e.g. Finsch's duck; see Chapter Two for a full summary). Often where native and exotic species currently co-exist, the native species have had their distribution and population density heavily reduced due to competition with or direct predation by exotic mammals (e.g. weka). Other species (especially invertebrates) have undergone behavioural changes to survive in the presence of mammals. Weta have been shown to reduce the

distance travelled per night while foraging in areas with mammals present (Bremner et al. 1989; Rufaut and Gibbs 2003). These changes to the seed predator fauna has the potential to strongly impact plant recruitment and lead to shifts in the composition of forest plant communities since the arrival of mammals to New Zealand.

1.5 Thesis objectives

Previous New Zealand based research examining the role of exotic mammals in forest plant mortality has focused on herbivory by ungulates and brushtail possum, while the effects of small mammals on early plant establishment has in the past been overlooked. Despite this, we need to incorporate the consequences of multiple mammals as they impact on different phases of the plant lifecycle. Overseas studies have shown considerable seed losses to seed predators (Holl 2002; Hulme 2002) resulting in significant reductions in seedling establishment (Inouye et al. 1980; Heske et al. 1993; Asquith et al. 1997). But apart from a preliminary study by Moles and Drake (1999), at the conception of my thesis there had been limited experimental research into the role of small exotic mammals as post-dispersal seed predators and their influence on early seedling establishment on mainland New Zealand. However, in recent years, several studies have been published and have begun to fill some gaps in our knowledge. Wilson et al. (2003) and Wilson et al. (2006) have investigated the effect of rodents, brushtail possums and deer on seed and seedling survival in South Island forests, while Ruscoe et al. (2004) and Ruscoe et al. (2005) have studied the population dynamics of the house mouse with respect to seedfall in beech forests. However, more research is required before a full understanding of the importance of small mammals to forest ecosystems will be obtained. Though my thesis adds to our understanding of this potentially important component of ecosystem dynamics, it also compliments these recent studies.

The principle objective of my thesis is to determine the relative importance of exotic mammals as post-dispersal seed predators in New Zealand conifer-broadleaf forests. To address this goal, I have four specific objectives:

1. to determine the overall level of post-dispersal seed predation in a conifer-broadleaf forest and determine the relative proportion of seed lost to exotic mammalian predators;

2. to investigate how habitat variation affects the level of post-dispersal seed predation by exotic mammals;

3. to investigate how variation in seed morphological traits and seed density affect the amount of seed lost to mammalian post-dispersal seed predators; and

4. to determine the flow-on effects of post-dispersal seed predation by exotic mammals on early seedling establishment.

1.6 Study area

Fieldwork for my thesis was conducted at Mount Peel Forest Park Scenic Reserve (Peel Forest) which lies along the southern edge of the Rangitata River in South Canterbury, New Zealand (43°54'S, 171°15E), and is the largest (400ha) remnant of conifer-broadleaf forest along the edge of the Canterbury plains (Kelly 1972). Peel Forest has a mild, moist temperate climate (Molloy 1983) with an annual precipitation of 1160 mm (Massam 1986). My experiments were conducted in a 60-hectare section of flat river floodplain spanning an altitudinal range of 300 to 360 metres located within conifer-hardwood secondary growth forest (Figure 1.1).

I chose Peel Forest as it is typical of forest remnants in New Zealand, and allowed a range of broadleaf plant species, each with different seed characteristics, to be studied. Until approximately 100 years ago, the majority of the study area experienced 40 years of light milling for totara (*Podocarpus totara*), kahikatea (*Dacrycarpus dacrydioides*) and rata (*Metrosideros* spp.) (Kerr 1972; Massam 1986). This resulted in a modified regenerating conifer forest dominated by broadleaf species. Currently, the dominant canopy trees are wineberry (*Aristotelia serrata*), five finger (*Pseudopanax arboreus*) and lacebark (*Hoheria sexstylosa*), with a few emergent totara, kahikatea and matai (*Prumnopitys taxifolia*). Lianes (*Clematis* spp, *Muehlenbeckia* spp. and *Parsonia* spp) are common in the canopy especially after 2002 when a snow disturbance event damaged a considerable proportion of the canopy trees at Peel Forest. The dense shrub tier contains mahoe (*Melicytus ramiflorus*)*,* pate (*Schefflera digitata*), *Coprosma rotundifolia*, and tree ferns (*Cyathea* spp., *Dicksonia* spp.). Depending on the canopy cover, the composition of the ground layer varies. In areas of semi-open canopy, ferns such as *Blechnum* spp, *Polystichum* spp, and *Asplenium* spp dominate the ground layer; graminoids such as *Microlaena avenacea* and *Uncinia uncinata* are also present. Under an intact continuous canopy, the ground layer is sparser, consisting of scattered ferns and seedlings. Although the study area follows a uniform topography, the
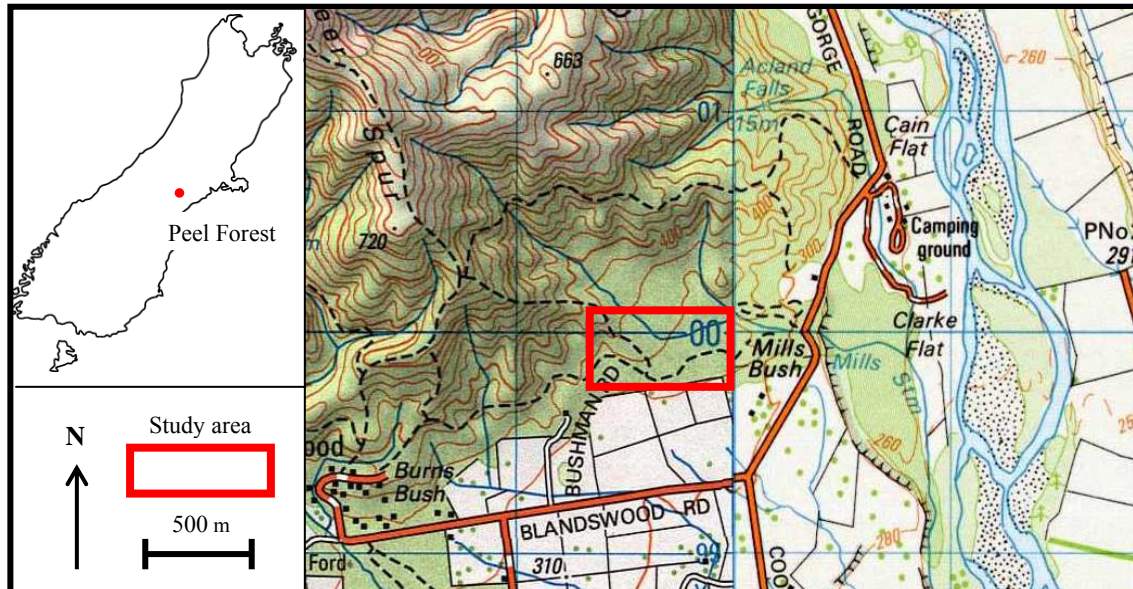
Figure 1.1: *Location of Peel Forest Park Scenic Reserve and specific study area*

distribution and density of plant species is highly heterogeneous. Allan (1925) provides a detail description of the flora at Peel Forest.

Peel Forest also contains a wide range of potential post-dispersal seed predators. The native fauna of Peel Forest has been heavily reduced since the arrival of humans. Five-minute bird counts (see Dawson et al. 1978) performed monthly throughout my thesis indicated that though bird diversity was relatively high at Peel Forest, no native avian post-dispersal seed predators were recorded. The remnant native seed predators at Peel Forest are assumed to be limited to invertebrates. The forests in New Zealand have been shown to be highly resistant to invasion by adventive invertebrate species (Harris and Burns 2000) so it is assumed that any invertebrate post-dispersal seed predators observed in the study will be a native species. Molluscs, weta (*Hemiandrus* sp), beetle families and ant species recorded in pitfall traps from the study area are likely to be representative of post-dispersal seed predators present.

Tracking tunnels baited with peanut butter revealed that the following small mammals were present in Peel Forest: house mouse, hedgehog (*Erinaceus europaeus*) and at least one species of mustelid (*Mustela* spp.). Though tracking tunnels cannot be used to distinguish among rat species, the tunnels also indicated that at least one species was present. Both Norway rat, and ship rat have previously been recorded in Peel Forest (Kelly 1972) and are expected to be currently present. Brushtail possums were also common throughout the study area. Other exotic mammals present at Peel Forest included feral pigs (*Sus scrofa*), feral cats (*Felis catus*), and at least one species of deer (*Cervus* spp.). Five-minute bird counts indicated that the exotic ground feeding birds; blackbirds (*Turdus merula*), greenfinch (*Carduelis chloris*) and chaffinch (*Fringilla coelebs*) were present at low densities throughout the study area.

1.7 Experimental design

To fully understand the relative importance of exotic mammals as post-dispersal seed predators at Peel Forest I conducted five main experiments, each designed to complement one another. I focused on fleshy-fruited, avian-dispersed broadleaf tree species, as these dominate New Zealand's conifer-broadleaf temperate forests. All experiments separated the actions of different seed predators by wire-mesh exclosures. This was important as different predators are likely to differ in the temporal and spatial scales of their effects, their preference for plant

species and the consequences of their foraging (Hulme and Borelli 1999). The five main experiments are as follows:

1.7.1 Time-lapse video of post-dispersal seed predation events

To determine which species of animal were responsible for specific post-dispersal seed predation events, I monitored seeds of four of the study species using two time-lapse video set-ups. Each video set-up consisted of a 'Panasonic' Hi-resolution, monochrome, infra-red camera attached to a 'JVC SR-L900E' time-lapse video recorder. To investigate 'large-bodied' predators (i.e. mammalian and avian predators), a camera was set up approximately two metres from a seed depot (Figure 1.2), while to identify invertebrate predators a camera was focused 10 cm above a seed depot (Figure 1.2). Seed remains were examined in conjunction with the video footage to allow predator identification from seed remains in the other experiments. This experiment is detailed in Chapter Two.

1.7.2 Cafeteria experiment

To address the first two objectives of my thesis, I undertook a cafeteria experiment. The use of cafeteria experiments is relatively common overseas (see Crawley 1992 for a review). The cafeteria experiment was the principal experiment performed as part of my thesis and ran for three field seasons (April and August) from 2000 to 2002. I chose nine plant species for this study representing ranges of seed size, mass, and plant abundance at Peel Forest (Figure 1.3). A range of habitats that differed in canopy cover was included to investigate the influence of habitat variation on predation rates. At each experimental site, within a 2m radius, I established four seed depots within wire exclosures to determine which animals were acting as a seed predator (Figure 1.4). The details and outcomes of this experiment are presented in Chapter Two.

1.7.3 Seed density experiment

I designed an experiment that focused on the importance of seed density in the ability of seed predators to both locate and prey upon seeds while foraging on the forest floor (Objective Three). Understanding the effect of seed density on seed predation is complex, as it may interact with habitat, season, plant species and types of predators. I focused on two components of seed density previously shown overseas to influence rates of seed predation.

Figure 1.2a: *The 'large-bodied' predator (i.e. mammal and avian) setup for the time-lapse video experiment. Camera was positioned approximately 2 metres away from the seed depot. The marker post was removed once the camera was correctly focused.*

Figure 1.2b: *The invertebrate predator setup for the time-lapse video experiment. The camera was placed 10 cm above the seed depot.*

Figure 1.3: *Seed size of the nine plant species used in the cafeteria experiment. Species are (from left):* Melicytus ramiflorus, Schefflera digitata, Coprosma robusta, Pseudopanax arboreus, Coprosma rotundiflora, Coprosma lucida, Pennantia corymbosa, Griselinia littoralis *and* Hedycarya arborea. *Scale bar = 3cm.*

Figure 1.4: *Examples of two of the mammal exclosure treatments used in the cafeteria and seed density experiments (on left); an "invertebrates only" treatment and a "rodents and invertebrates only" treatment. Each exclosure is 0.3 $\times$ 0.3 $\times$ 0.3m.*

In 2000, I investigated the influence of initial seed density of a single plant species on post-dispersal seed predation, while in 2001 I focused on the influence of relative seed density where seeds of two species were present in depots together. These experiments used a simplified layout of the design used in the cafeteria experiment and are present in Chapter Two.

1.7.4 Natural seed germination experiment

To investigate the flow-on effects of post-dispersal seed predation by exotic mammals within Peel Forest (Objective Four), I monitored natural seed germination for three years within 14 experimental units located under one of two canopy conditions. Each experimental unit contained four predator exclusion plots. Each exclosure was 1.2×0.9m consisting of 0.6m high wire walls, with a roof (Figure 1.5). Within each exclosure treatment, a seedling plot (1.0×0.75m) was permanently marked. I used germination as a measure of realised seed survival from seed predation. I present the details and outcomes of this experiment in Chapter Three.

1.7.5 Recruitment limitations at Peel Forest

To further investigate the influence of mammalian post-dispersal seed predators on early seedling establishment (Objective Four), I conducted a preliminary seed addition experiment designed to highlight interactions between the reproductive strategies of the study plant species, the importance of the available seed and the role of mammalian seed predators. I based the experimental design on the recommendations made by Turnbull et al. (2000) in their review of seed limitation experiments. This experiment ran between May 2002 and May 2003. The experimental plots were a factorial combination of two mammalian post-dispersal predator exclosure treatments × two soil-litter disturbance treatments × three seed densities, giving a total of 12 seedling plots per block (Figure 1.6). In Chapter Four I discuss the outcomes of this experiment.

1.8 Thesis layout

Chapter Two uses results from the time-lapse video, cafeteria and seed density experiments to discuss the relative importance of remnant native and exotic fauna as post-dispersal seed predators, how habitat and seed characteristics influence these observed predation levels and

Figure 1.5: *Example of long-term natural seedling plots. In foreground is a "Mice and invertebrates only" exclosure. Each exclosure was 1.0 × 1.2 × 0.6m.*

Figure 1.6: *Set up for the seed limitation experiment. Each experimental unit had 12 experimental plots; mammals were excluded from half of the plots.*

the importance of seed density in the foraging behaviour post-dispersal seed predators. Chapter Three presents results of the natural seed germination experiment to assess the influence of mammalian post-dispersal seed predators on early seedling establishment. While Chapter Four reports on the preliminary seed addition experiment performed to further investigate the influence of mammalian post-dispersal seed predators on early seedling establishment. The concluding chapter provides a synthesis of all experiments, discusses the limitations and possible improvements to this research as well as discussing additional questions that have arisen from this research. Appendixes are provided with summaries of the raw data from all major experiments conducted at Peel Forest.

As the majority of chapters are written in a "manuscript" format, there is a level of repetition in parts of the introduction and methodology sections. These have been kept to a minimum, but have been retained to allow each chapter to stand-alone as a complete manuscript.

Chapter Two: Post-dispersal seed predation in a conifer-broadleaf forest remnant, Canterbury, New Zealand: how similar are exotic mammals to remnant native invertebrate predators?

2.1 Introduction

Globally post-dispersal seed predators exist in most community types (Crawley 2000; Hulme 2002) and post-dispersal seed predation is thought to play an important role in the regeneration (Schupp 1988; Hulme 1996; Blate et al. 1998), colonisation ability (Schupp et al. 1989; Myster and Pickett 1993) and spatial distribution (Hulme 1997; Forget et al. 1999) of many plant species. However, the nature of these effects depends chiefly on the seed predator assemblage present (Danell and Bergstrom 2002). Despite this international acknowledgement of the importance of post-dispersal seed predators to plant population dynamics, in New Zealand conifer-broadleaf forests the role of post-dispersal seed predators remains largely unknown.

2.1.1 Seed predators in New Zealand

No comprehensive study focusing on post-dispersal seed predation in New Zealand has yet to be completed. Nevertheless, what is certain is that the species composition of these predators has changed since human arrival to New Zealand. Specifically, the arrival of large numbers of mammalian species in the last 200 years has had a traumatic effect on the native flora and fauna (King 1984; Wodzicki and Wright 1984). As a part of these introductions, several potential mammalian post-dispersal seed predators have become established in New Zealand. These include three species of rodent (Norway rat (*Rattus norvegicus*), ship rat (*R. rattus*) and the house mouse (*Mus musculus*)) and the brushtail possum (*Trichosurus vulpecula*) (Campbell 1978; Nugent et al. 2000; Innes 2001). Although overseas studies potentially underestimate the importance of other animals as post-dispersal seed predators, small mammals appear to have the greatest potential to influence seed mortality (Blaney and Kotanen 2001; Hulme and Benkman 2002). It has been shown that small mammals have a deleterious effect on New Zealand's inshore island ecosystems. Both Campbell (2002), and Campbell & Atkinson (2002) looked at forest regeneration after the eradication of rodents on inshore islands and though they concluded that rodents were impacting on early plant establishment, these studies fail to identify the exact mechanisms by which regeneration was affected. Allen et al. (1994) however, suggested that once Norway rats were eradicated from

Breaksea Island, seedling densities of several species increased initially having been release from direct predation, and then decrease as they experience competition from other plant species. On the mainland, the influence of small mammals on plant population dynamics remains even less clear.

On the New Zealand mainland, the most widespread rodent in low and mid altitude forests is the ship rat (Innes 1990). Ship rats are omnivores, with seeds and fruit forming an important dietary component when available (Beveridge 1964; Best 1969; Campbell 1978; Innes 1990). Also widespread are the house mouse and brushtail possum (Cowan 1990; Murphy and Pickard 1990). Diet analysis of all these mammalian species in New Zealand forests has revealed some seed predation (Beveridge 1964; Campbell 1978; Miller and Miller 1995; Fitzgerald et al. 1996; Nugent et al. 2000). Over the years, most research focusing on exotic mammals acting as a post-dispersal seed predator as occurred in beech forest ecosystems (see Murphy and Pickard 1990 for a summary). But more recently, Choquenot and Ruscoe (2000), and Ruscoe et al. (2005) have focused on the responses of rodents to changes in densities of beech seed. In conifer-broadleaf forests however, our understandings is still limited. In 1999, after a preliminary investigation, Moles and Drake deduced that mammals play a limited role as post-dispersal seed predators. While more recently, Wilson et al. (2003) and Wilson et al. (2006) have investigated the effect of rodents, brushtail possums and deer on seed and seedling survival in South Island forests.

With only two groups of native terrestrial mammals (bats and seals) prior to the arrival of humans, birds and invertebrates originally dominated the New Zealand fauna. Even though many post-dispersal seed predator species, such as ants and rodents, were not originally present in numbers comparable to overseas ecosystems, or were never part of the New Zealand fauna (Howarth and Ramsay 1991), it is unlikely that a valuable food resource such as seeds would have been under utilised. Based on the diet of extant species, their close relatives or sub fossils, several avian species are predicted to have been post-dispersal seed predators in pre-human New Zealand, especially in the eastern South Island's conifer-broadleaf forests (Table 2.1). However, given their dominance in New Zealand fauna in terms of number of species and biomass, the majority of post-dispersal seed predators would have been invertebrates (Booth et al. 1990). Though studies on weta have shown that these invertebrates are important seed predators (Mirams 1957; Duthie et al. 2006), and invertebrate seed predators of grassland and alpine ecosystems have been studied (Ledgard 1979; Bremner

1991; Kelly et al. 1992; Lord and Kelly 1999), in general, very little is known about the diet
and behaviour of ground dwelling invertebrates in New Zealand conifer-broadleaf forests
(Howarth and Ramsay 1991).

Table 2.1: *Potential post-dispersal seed predators in New Zealand's eastern South Island conifer-broadleaf forests.
Species are known to have foraged on the forest floor and contained seeds in their diet.* **Bolded** *are exotic species.
Based on diet analysis of extant species, sub fossils or close relatives. Sources: King (1990), Burrows (1994)
Heather & Robertson (1996) and Worthy & Holdaway, (2002)*

Guild	Pre-human		Post-human	
Avian (> 500g)	Finsch's duck	*Euryanas finschi*	—	
	kiwi (several species)	*Apteryx* spp.	—	
	small forest moa	*Anomalopteryx* and *Megalapteryx* spp.	—	
	South Island coot	*Fulica prisca*	—	
	South Island takahe	*Porphyrio hochstetteri*	—	
	weka	*Gallirallus australis*	—	
Avian (< 500g)	bush wren	*Xenicus longipes*	—	
	New Zealand quail	*Coturnix novaezelandiae*	—	
	red-crown parakeet	*Cyanoramphus novaezelandiae*	—	
	saddleback	*Phileshurnals coruncalatus*	—	
	piopio	*Turngra capensis*	—	
			blackbird	***Turdus merula***
			California quail	***Callipepla californicus***
			chaffinch	***Fringilla coelebs***
			dunnock	***Prunella modularis***
			greenfinch	***Carduelis chloris***
			goldfinch	***Carduelis carduelis***
Mammal	—		**brushtail possum**	***Trichosurus vulpecula***
	—		**Norway rat**	***Rattus norvegicus***
	—		**ship rat**	***R. rattus***
	—		**house mouse**	***Mus musculus***
Invertebrate	weta	Orthoptera	} Present but heavily reduced in abundance; larger bodied species may be locally extinct	
	beetles	Coleoptera		
	molluscs	Gastropoda		
			some additional exotic species	

The second impact of the arrival of mammals to New Zealand has been a reduction of these
native seed predators in New Zealand's forests. Seeds form only a component of these
mammals' diets, the majority being invertebrates, vertebrates or other plant matter. The
majority of native seed predators are now either locally or nationally extinct as a result of
direct mammalian predation (Table 2.1). Currently, many large bodied native seed predators
only survive on mammal-free islands (Ramsay 1978; Moeed and Meads 1987; Heather and
Robertson 1996). Often where native and exotic species co-exist, the native species usually

have their distribution and population density heavily reduced due to competition with or direct predation by exotic mammals (e.g. weka). Other native species (especially invertebrates) have undergone behavioural changes to survive in the presence of mammals; weta have been shown to reduce the distance travelled per night while foraging in areas with mammals (Bremner et al. 1989; Rufaut and Gibbs 2003). Although the relative contributions of remnant native and exotic species to seed predation events are unknown, I hypothesised that currently, exotic mammals are the main post-dispersal seed predators in New Zealand's eastern South Island conifer-broadleaf forests (Table 2.1).

No agreement as to the importance of mammals as post-dispersal seed predators in New Zealand exists. While there is evidence of seed in the diets of mammals, and studies have attributed recruitment depressions of several tree species to rodent seed predation (e.g. Allen et al. 1994; Wilson et al. 2006), there has also been speculation that the role played by exotic mammals as post-dispersal seed predators in New Zealand may have been overestimated (Moles and Drake 1999) or that these mammals have simply replaced pre-existing native seed predators (e.g. Campbell 1978; Ramsay 1978). However, the arrival of mammals undoubtedly altered the nature of post-dispersal seed predation with New Zealand conifer-broadleaf forests, but we don't know 1) how exotic seed predators differ from the remnant natives and 2) how important are these differences in regulating plant recruitment.

2.1.2 Factors influencing seed predator behaviour

Post-dispersal seed predators, in both forests and other communities, have been shown to be highly selective of the seeds they prey upon (Abramsky 1983; Kelrick et al. 1986). Morphological traits of the seed or the seed density may directly affect the amount of seed taken by predators, while the habitat in which the seed is deposited may affect the foraging behaviour of a predator and therefore its probability of encountering the seed. With potentially several different seed predators in New Zealand forests, I expect that these predators will respond differently to seed and habitat factors.

Morphological and nutrient resource characteristics of seeds have been shown to influence predators' preferences (Waldbauer and Friedman 1991; Osunkoya 1994; Celis-Diez et al. 2004). Theoretically, predators should favour larger seeds over smaller seeds (Thompson 1987; Hulme 1998; Celis-Diez et al. 2004), as these would provide the greatest net reward

(Waldbauer and Friedman 1991; Blate et al. 1998). However, seeds from different plant species are not equally attractive to different seed predators (Whelan et al. 1991; Hulme and Borelli 1999). While a seed may be too large for one predator species to effectively handle, the same seed may also be so small that handling them requires so much time and energy that there is no net gain in eating them (Blate et al. 1998; Fenner and Kitajima 1999). Due to exotic mammal's larger body sizes, I predict that these predators will target larger seeds than the smaller bodied remnant native invertebrate seed predators.

Seed density on the forest floor may also influence level of post-dispersal seed predation. As generalist post-dispersal seed predators forage over large areas, larger deposits of seeds should be easier to locate by the predator and density-dependent seed predation has been observed in several studies (Webb and Willson 1985; Casper 1988; Willson and Whelan 1990; Hulme 1994). But other researchers have found that seed density has little or no effect on post-dispersal seed predation (Mittelbach and Gross 1984; Hulme and Hunt 1999). Based on the body size of each predator, I predict that mammals and birds will fully utilise these larger depots by preying upon all seeds available (i.e. density dependent) while invertebrates (due to their limited body size) are predicted to be unable to effectively process large seed depots resulting in them displaying a density-independent response to seed density.

Elsewhere, research has shown that the densities of the mammalian species present in New Zealand conifer-broadleaf forests are positively correlated to the degree of vegetation cover and structural complexity (Gross 1984; Mittelbach and Gross 1984; Falkenberg and Clarke 1998; Cox et al. 2000). Invertebrate abundance and diversity have also been shown to increase with habitat complexity (Hansen 2000; Lassau et al. 2005), Therefore I predict that seed predation by all seed predators will be greatest in areas of high structural complexity.

In this chapter, I determine the roles played by, and how similar exotic mammals and remnant native invertebrate post-dispersal seed predators are in a conifer-broadleaf forest remnant. Based on evidence from overseas I test the following hypotheses regarding the relationship between and functioning of exotic and native post-dispersal seed predators:

1.   Exotic mammals have replaced native species as the dominant seed predators in remnant conifer-broadleaf forests.

2.   Both native invertebrates and exotic mammals forage in similar habitats leading to higher rates of seed predation in more structurally complex, closed forest habitats relative to open habitats.

3.   Native invertebrates and exotic mammals select seeds with different morphological traits; specifically because of their larger body sizes, exotic mammalian predators will target larger seeded species than smaller native invertebrate predators.

4.   Native invertebrates and exotic mammals will respond differently to increases in seed density; exotic mammalian predators will show a density-dependent response while native invertebrate predators will have a density-independent response to changes to seed density, due to differences in body size.

To test these hypotheses I performed three experiments. First, time-lapse video was used to identify the predator species involved in post-dispersal seed predation events. Second, a cafeteria experiment presented seeds of a range of native broadleaf tree species to native and exotic post-dispersal seed predators in the field. And third, a simplified version of the cafeteria experiment using seed depots of various seed densities was performed to investigate the interaction between seed density and post-dispersal seed predation events. In all experiments the actions of different predators were separated by using seed depots placed within exclosures utilising wire-mesh that excluded predator species of different sizes.

2.2 Materials and Methods

2.2.1 Study area

This study was conducted at Mount Peel Forest Park Scenic Reserve (770 hectare) which lies along the southern edge of the Rangitata River in South Canterbury, New Zealand (43°54'S, 171°15E). Peel Forest has a mild, moist temperate climate (Molloy 1983), with an annual precipitation of 1160 mm (Massam 1986). All my experiments were carried out in a 60 hectare section of river floodplain spanning an altitudinal range of 300 to 360 metres located within conifer-broadleaf secondary growth forest.

The majority of the study area was selectively logged for conifer species between 1860 and 1900 (Kerr 1972; Massam 1986). This resulted in a regenerating secondary forest dominated by broadleaf species. Currently, the dominant canopy species are wineberry (*Aristotelia serrata*), five finger (*Pseudopanax arboreus*) and lacebark (*Hoheria sexstylosa*), with a few emergent totara (*Podocarpus totara*), kahikatea (*Dacrycarpus dacrydioides*) and matai

(*Prumnopitys taxifolia*). The dense shrub tier contains mahoe (*Melicytus ramiflorus*)*,* pate (*Schefflera digitata*), *Coprosma rotundifolia*, and tree ferns (*Cyathea* sp., *Dicksonia* sp.). Ferns such as *Blechnum* sp., *Polystichum* sp., and *Asplenium* sp. dominate the ground layer; graminoids such as *Microlaena avenacea* and *Uncinia uncinata* are also present. See Chapter One for a full description of the study area.

2.2.2 Native fauna present

The native fauna of Peel Forest has been heavily reduced since the arrival of humans. Five-minute bird counts (see Dawson et al. 1978) performed monthly throughout my study indicated that although bird diversity was relatively high at Peel Forest, no known native avian post-dispersal seed predators were recorded. As conifer-broadleaf forests in New Zealand have been shown to be highly resistant to invasion by exotic invertebrate species (Harris and Burns 2000) I have assumed that any invertebrate post-dispersal seed predators observed in my experiments are native species. Molluscs, weta (*Hemiandrus* sp), numerous beetle and ant species were recorded in pitfall traps from within the study area and many of these species are likely to be post-dispersal seed predators.

2.2.3 Exotic fauna present

Tracking tunnels baited with peanut butter identified the following small mammals in Peel Forest: house mouse, hedgehog (*Erinaceus europaeus*)*,* at least one species of mustelid (*Mustela* sp.) and at least one species of rat. Both Norway and ship rats have previously been recorded in Peel Forest (Kelly 1972) and are expected to be present during my study. Brushtail possums were also common throughout the study area and were regularly seen and heard at night. Other exotic mammals present at Peel Forest include feral pigs (*Sus scrofa*), feral cats (*Felis catus*), and at least one species of deer (*Cervus* spp.). Five-minute bird counts revealed that the exotic ground feeding species; blackbird (*Turdus merula*), greenfinch (*Carduelis chloris*) and chaffinch (*Fringilla coelebs*) were present at low densities throughout the study area.

2.2.4 Study plant species

Nine plant species were chosen for my study (Table 2.2). The criteria used to select these species were that they had to: 1) be representative of the ranges of seed size, mass, and plant

abundance at Peel Forest, and 2) have sufficient viable seed available for the experiments. All seed was collected from several individuals either at Peel Forest or from lowland forests around Banks Peninsula, northeast of Peel Forest. All studied species are broadleaf tree or large shrub species known to grow up to 12 metres in height and have avian-dispersed fruits. All are common species within forests throughout New Zealand below 900 metres in altitude, although their abundance within the study area differed (Table 2.2). All fruit pulp was removed from the seed so as to resemble 'avian-dispersed' seeds.

Table 2.2: *Plant species, their seed characteristics and the years they were used in the cafeteria experiment. Mean seed mass and seed length of cleaned seeds were obtained from a random sample of 20 seeds per species. Abundance at Peel Forest: Rare – few adult trees within study area; Com – common, V.C. – very common; a dominant species in study area.*

Plant species	Family	Mean seed mass (mg)	Mean seed length (mm)	Abundance at Peel Forest	Used for experiment 2000	2001	2002
Coprosma lucida	Rubiaceae	17.0	6.50	Rare	Yes	Yes	Yes
Coprosma robusta	Rubiaceae	5.6	5.35	Rare	Yes	Yes	Yes
Coprosma rotundifolia	Rubiaceae	8.0	3.00	V.C.	Yes	Yes	Yes
Griselinia littoralis	Griseliniaceae	26.0	5.50	V.C.	Yes	Yes	No
Hedycarya arborea	Meliaceae	171.0	11.50	Rare	No	Yes	Yes
Melicytus ramiflorus	Violaceae	0.7	1.90	V.C.	No	Yes	Yes
Pennantia corymbosa	Hectorellaceae	17.0	7.60	Com	No	Yes	Yes
Pseudopanax arboreus	Araliaceae	9.0	4.10	V.C	Yes	No	Yes
Schefflera digitata	Araliaceae	0.6	2.50	Com	Yes	Yes	Yes

2.2.5 Identification of seed predators

To determine which animal species were responsible for specific post-dispersal predation events, I observed seed depots of four of the study plants (*C. rotundifolia, Hedycarya arborea, M. ramiflorus, S. digitata*), using two time-lapse camera set-ups. Each plant species was observed in each video set-up for three 48-hour periods between April and May 2001. Each video set-up consisted of a 'Panasonic' Hi-resolution, monochrome, infra-red camera attached to a 'JVC SR-L900E' time-lapse video recorder powered by an 'Exide Stowaway' 80-amp hour deep-cycling battery. Illumination for night time recording was provided by an infra-red light source attached to the camera. To investigate 'large-bodied' seed predators (i.e. mammalian and avian species), a camera was set up approximately 2 metres from a seed depot, while to identify invertebrate seed predators a camera was focused 10cm above a seed depot. For all observations, seed depots and cameras were placed under continuous forest canopies. Seed remains were examined in conjunction with the video footage to identify any

characteristic signs left by particular predators and these signs were used to identify predators from seed remains in the cafeteria experiment.

2.2.6 Determination of seed predation rates: a cafeteria experiment

To investigate differences between mammalian and invertebrate post-dispersal seed predators, in both the amount of seed preyed upon and the seed morphological traits they select, I conducted a cafeteria experiment where known seed depots of the nine study plant species were monitored in the field. The experiment ran for three field-seasons (April to August) from 2000 to 2002.

Not all of these nine study plant species were used each year as a suitable local seed source was not always available (Table 2.2). In 2000, six plant species were studied: *Coprosma lucida, C. robusta, C. rotundifolia, Griselinia littoralis, Pseudopanax arboreus* and *S. digitata*. In 2001, an additional three species were added to the experimental design: *H. arborea, M. ramiflorus* and *Pennantia corymbosa*. The natural seedfall of these species occurs between March and May and, apart from *C. robusta,* none of the plant species are known to form a persistent seed bank (Sem and Enright 1996; Moles and Drake 1999); rather these species form a transient seed bank before germinating the next spring, ensuring that seeds are naturally present on the forest floor throughout the study periods and are not foreign to the seed predators at Peel Forest.

To determine if native and exotic seed predators foraged in similar habitats and to investigate if higher rates of seed predation occurred in areas of higher structurally complexity, 24 experimental units were established. Each experimental unit was situated in one of three habitat types, based on canopy cover: (1) open canopy (middle of a single treefall gap), (2) partial canopy (within 5m of the edge of the gap), and (3) continuous canopy (at least 20m from the nearest treefall gap). To locate experimental units, all single treefall gaps within the study area were located, and then I randomly selected a subset of 16 for the cafeteria experiment (eight open canopy, eight partial canopy). With all single treefall gaps located, the eight continuous canopy experimental units were randomly allocated within areas of the study area known not to contain treefall gaps. To investigate habitat characteristics of the experimental unit that may influence predation levels, 18 habitat characteristics were measured at each experimental unit (Table 2.3).

Table 2.3: *The 18 habitat characteristics used to classify habitat structure of the 24 experimental units used in the cafeteria experiment. Measurement of habitat characteristics occurred in April 2001.*

Habitat characteristic	Characteristic description
Canopy height	Height of forest canopy measured in metres
Distance to nearest animal track	Distance to nearest 'recently used' animal track in metres; up to a maximum of 40m.
Distance to nearest canopy tree	Distance to nearest canopy tree from the middle of the experimental unit in metres.
Distance to nearest log	Distance to nearest log (min. 0.2m diameter) in metres.
Distance to nearest stream	Distance to the nearest permanent water course in metres; up to a maximum of 40m.
Distance to nearest treefall gap	Distance to nearest single treefall gap in metres; up to a maximum of 40m.
Litter depth	Average of 10 random samples; measured in cm.
Number of canopy trees	Number of canopy trees within a 5m radius of middle of experimental unit.
Number of logs	Number of logs within a 5m radius of middle of experimental unit.
Number of stems (>5cm dbh)	Number of stems (>5cm dbh) within a 5m radius of middle of experimental unit.
Percentage of bare ground	Percentage of bare ground within a 2.5m radius of middle of experimental unit.
Percentage of bare rock	Percentage of bare rock within a 2.5m radius of middle of experimental unit.
Percentage of canopy cover	Percentage canopy cover within a 5m radius of middle of experimental unit (determined using fisheye photography taken at 0.5m height).
Percentage of ground vegetation cover	Percentage cover of vegetation between 0-0.5m in height within a 2.5m radius of middle of experimental unit.
Percentage of litter cover	Percentage of litter cover within a 2.5m radius of middle of experimental unit.
Percentage of moss cover	Percentage of moss cover within a 2.5m radius of middle of experimental unit.
Percentage of understorey cover	Percentage of understorey cover within a 5m radius of middle of experimental unit.
Understorey vegetation height	Height of understorey vegetation measured in metres.

To examine which type of predator species were responsible for individual seed predation events within these experimental units, four seed depots were randomly placed within a 2m radius of the centre of each of the 24 experimental units. Each of these depots was assigned a different wire-mesh exclosure designed to limit the access of specific types of predators. As no avian post-dispersal seed predators were observed in the time-lapse video experiment, the exclosures were designed to limit mammalian and invertebrate seed predators. The four exclosure treatments within each experimental unit were:

(1) '*Possums, rodents and invertebrates access':* An open treatment, with no predator exclusion method used. Seeds were available to all mammalian and invertebrate predators.

(2) '*Rodents and invertebrates access only*': 50mm wire mesh cages (30 × 30 × 30cm) buried 10cm deep. Cages also had a mesh roof to prevent climbing predators entering and consuming the seeds. Seeds were available to rodents and invertebrates, but brushtail possums were excluded.

(3) '*Invertebrates access only*': Similar to the cage in (2) but consisting of 12mm wire mesh. All mammals were excluded; seeds were only available to invertebrates.

(4) '*Control*': A 12mm wire exclosure with the seeds elevated off the ground to exclude invertebrates; no predators could access the seeds.

The wire mesh diameters used to exclude mammalian predators were based on research at the Karori Wildlife Sanctuary, Wellington (Hitchmough 1994). All seeds could be removed from the small wire cage; thus not limiting seed removal from the depot.

Within each depot, ten seeds of a single plant species were presented on a petri dish (9cm diameter) buried flush with the ground and with a mesh 'drain' in the bottom to prevent water build-up within the dish. The use of ten seeds represented a trade-off between the seed available for the experiment, an attempt to provide a realistic number of seeds that occur naturally when dispersed by birds, and an adequate sample size.

At the beginning of each field-season, each plant species was randomly assigned to three experimental units (comprising one of each habitat type) and all seed depots within that assigned experimental unit. Seed removal was recorded over the following 15 days. The experiment was then repeated with the plant species being re-assigned to another three experimental units. This continued until all plant species had been placed once in all experimental units per field-season.

Seeds were classified as preyed upon if they were removed from the depot, or left within the depot and eaten to the point where germination was unlikely. Seed removed from the depots may have been dropped or cached by animals (Campbell 1978), thus escaping predation. Though assessment of this secondary dispersal was not possible in the context of this experiment, seed remains of the larger seeded species were frequently observed within one metre of the depot indicating that a predation event had occurred.

2.2.7 Predator response to seed density

Between April and June 2000, I investigated whether or not mammalian and invertebrate post-dispersal seed predators responded differently to increases in initial seed density. For this experiment, a variety of seed densities of three plant species (*C. robusta, G. littoralis,* and *S. digitata*) were observed in a simplified exclosure layout of the design used in the cafeteria experiment. Twenty-four experimental units (separate from the experimental units used in the cafeteria experiment) were established. Two habitats types based on canopy cover were included in the density experiment: 1) open canopy (middle of a single treefall gap) and 2) continuous canopy (at least 20m from the nearest treefall gap). As the treefall gaps has been previously mapped, the 12 open canopy experimental units were randomly allocated to single treefall gaps not already being used for the cafeteria experiment. The 12 continuous canopy experimental units were randomly placed within areas of the study area known not to contain treefall gaps. Within each of the 24 experimental units, three seed depots were randomly placed within a 2m radius. Each of these depots was assigned a different wire-mesh exclosure. The three exclosure treatments were: 1) 'Possums, rodents and invertebrates access', 2) 'Rodents and invertebrates access only' and 3) 'Invertebrates access only'. Full descriptions of these exclosure treatments are provided in the cafeteria experiment methods.

To determine if initial seed density influenced seed predation, I monitored four seed densities resulting in 12 plant species : seed density combinations. The seed densities were: 1, 5, 10 or 15 per depot. At any time only one plant species and one seed density were present in each depot within an experimental unit. At the beginning of the density experiment, each plant species : seed density combination was randomly assigned to one experimental unit within each habitat type. All plant species : seed density combinations were tested in the field at the same time. Seed removal was recorded over the following seven days. The experiment was then repeated with the plant species : seed density combinations re-assigned to other experimental units. No experimental unit had the same species or seed density present for two consecutive replicates. A total of 12 replications of each species : density combination were conducted to ensure each combination had been placed once in all experimental units under each canopy type.

2.2.8 Data analysis

All analyses were performed using the statistical analysis package R version 1.9.1 (R Development Core Team 2004).

To investigate whether exotic species have replaced native species as the dominant post-dispersal seed predators at Peel Forest, and whether native and exotic predators forage in similar habitats, I analysed the results of the cafeteria experiment in three ways. First, overall seed predation (the proportion of seed preyed upon over 15 days) was analysed, then to investigate differences in behaviour of predators in more depth, these results were divided into the two components of post-dispersal seed predation: 1) seed encounter (the probability of at least one seed being preyed upon in a depot) and 2) seed exploitation (the proportion of seeds preyed upon once a depot had been encountered by a predator) (see Willson and Whelan 1990; Hulme 1994).

For the overall seed predation and seed exploitation analyses, my response variable was the proportion of seeds preyed upon. To identify variables that might explain variation in the proportion of seed preyed upon, I included plant species (9 species), exclosure treatment ('Possums, rodents and invertebrates access', 'Rodents and invertebrates access only', 'Invertebrates access only' and 'control'), habitat type (open, partial, and continuous canopy) and all interactions (up to three-way) as explanatory variables. Field-season (3 seasons) was also included as an explanatory factor but due to the lack of replication it was not included in any interactions. I fitted a Generalised Linear Model (GLM) with a binomial error distribution and logit link function. As the models for the overall seed predation and seed exploitation were over-dispersed, significance testing was conducted using F–tests rather than χ^2 tests. To analyse variation in the levels of seed encounter, my response variable 'depot encountered within the 15 day period' was binary (i.e. depot encountered or not). A GLM with the same explanatory variables as for overall seed predation and seed exploitation models above was fitted. However, being a binary response variable χ^2 tests was used for significance testing.

To investigate differences in which seed morphological traits, exotic and native seed predators select during foraging, I focused on two components of seed predation (seed encounter and seed exploitation). For each plant species, I measured seed mass and length of the longest

axis from a random sample of 20 individuals (Table 2.2). To determine if the probability of a seed encounter was related to seed mass or seed length for each exclosure treatment, I fitted GLMs with seed encounter as the response variable and seed mass or seed length as the explanatory variable using a logit link and binomial errors. To determine if seed exploitation was related to seed mass or seed length for each exclosure treatment, I fitted polynomial regressions. For all analyses, the mean seed encounter and seed exploitation rate per plant species were used. Seed mass was $\log_{10}$-transformed to normalise the data.

To examine which of the measured habitat characteristics of the experimental units may influence seed exploitation, I initially used a regression tree (Crawley 2002). The regression tree analysis uses an algorithm to partition the response variable into 'branches' or nodes. During the construction of a node, the explanatory variable which explains the greatest amount of the deviance of the response variable is selected and then the analysis decides whether a node should be terminal or should be subject to further splits. This results in a 'tree' type explanation of the data indicating potential high order interactions. Regression tree analysis was concluded using the TREE package for R. Although regression trees indicate important explanatory variables, they do not show their significance to the response variable (Crawley 2002). Therefore to determine which habitat characteristics explained significant proportions of the variation in the cafeteria experiment data, the habitat characteristics selected in the regression tree were used as explanatory variables in a GLM. My response variable in the GLM was seed exploitation (the proportion of seeds preyed upon once a depot has been encountered by a predator). As the model was over-dispersed, significance testing was conducted using F–tests rather than Chi-square tests.

To investigate whether or not exotic mammals and native invertebrate seed predators respond differently to increases in seed density, I focused on two components of post-dispersal seed predation: 1) seed encounter (the probability of at least one seed being prey upon in a depot) and 2) overall seed predation (the proportion of seed preyed upon per 7 days). Each plant species was analysed separately. I used logistic regressions to investigate if seed encounter was related to seed density, while I used a weighted regression to investigate the role of seed density on the proportion of seed preyed upon. The use of weighted regressions ensures that the proportion of seed preyed upon at low seed densities does not have undue influence on the value of the slope (Crawley 2002). For both analyses, I used the 'glm' function with binomial errors within R statistical analysis software, to identify variables that might explain variation

in the response variables. As explanatory variables, I included seed density (1, 5, 10 and 15 seeds), exclosure treatment ('Possums, rodents and invertebrates access', 'Rodents and invertebrates access' and 'Invertebrates access only', habitat type (open, and continuous canopy), and all interactions (up to three-way) as explanatory variables.

2.3 Results

2.3.1 Identification of seed predators

A total of 61 predation events were observed from 1,152 hours of time-lapse video footage. All but two of these predation events occurred between dusk and dawn. By using the ratio of tail to body-head length (see Cunningham and Moors 1996) obtained from time-lapse video footage, I concluded that ship rats were the dominant exotic mammalian seed predator in this time-lapse video experiment, with ship rats comprising 40% of all mammalian predation events (Table 2.4). Brushtail possums were an important seed predator of *H. arborea* (the largest seeded plant species studied), being responsible for 46% of all predation events for this plant species, while house mice were observed occasionally preying upon all four plant species (Table 2.4). Seeds in the 'large-bodied predators' camera setup would have been accessible to birds, and although exotic ground-feeding bird species were present at low densities throughout the study, and were observed on video foraging near a monitored seed depot, no evidence of seed predation by these species was recorded.

The main predators of the two smallest seeds observed using time-lapse video were invertebrates; accounting for 63% of all predation events for these two species (Table 2.4). However, due to interference of depots by larger predators, the importance of invertebrates as seed predators of the other two larger-seeded plant species may be underestimated. A species of Staphylinidae (Coleoptera) was identified as the main predator of *S. digitata* but due to poor quality footage attempts to identify other invertebrate seed predators were unsuccessful and these remain unknown.

2.3.2 Determination of seed predation rates

Only 15 (0.3%) of the 4920 seeds placed in control exclosures as part of the cafeteria experiment disappeared. This implies that abiotic factors (e.g. wind, rain) are not responsible

Table 2.4: *Number of predation events identified to specific predators during the time-lapse video experiment. Each camera setup was carried out for 144 hours per plant species. Camera setup 1= 'large-bodied' seed predators, setup 2 = 'invertebrate' seed predators.*

Plant Species	*S. digitata*		*M. ramiflorus*		*C. rotundifolia*		*H. arborea*	
Seed size	Small		Small		Medium		Large	
Camera set up	1	2	1	2	1	2	1	2
Predator								
Invertebrate	-*	9	-*	8	-*	2	-*	0
Mice	4	1	2	1	2	1	1	2
Ship rat	1	0	0	} 1†	5	} 4†	6	} 2†
Brushtail possum	1	0	0		3		6	
Blackbird	0	0	0	0	0	0	0 ‡	0
Total predation events observed	6	10	2	9	9	3	13	2

† Large-bodied predators disturbed depot but due to camera setup identification of predator was not possible
‡ Blackbirds were observed near a seed depot on 3 occasions but no direct seed predation was recorded
* Camera setup did not allow for invertebrate predator identification

for seeds disappearing from the other exclosure treatments, instead I assume that disappearance from the other exclosures are almost exclusively due to seed predators.

A summary of the raw cafeteria data is located in Appendix One. The analyses indicated that exclosure treatment and plant species were significant explanatory variables in all three GLM models and the interaction between these two factors was significant for the overall predation and encounter models (Table 2.5). Habitat type was only a significant explanatory factor in the model of seed exploitation once the seed depots were encountered (Table 2.5). The explanatory variable, field-season and all other interactions were not significant factors in explaining variation in any of the three GLMs.

A significant interaction between exclosure treatment and plant species was observed in both overall seed predation and seed encounter models (Table 2.5). Although exclosure treatments allowing more predators access had consistently higher rates of seed encounter and seed exploitation across all studied plant species, the differences between exclosure treatments also varied among species (Figure 2.1). For four of the nine studied plant species, seed predation increased significantly when rodents had access to the depots, and all nine studied plant species were observed having a significant increase in the proportion of seed preyed upon when all predators had access to the seed depots (Figure 2.1).

A) Overall seed predation *(n = 63 per exclosure per species)*
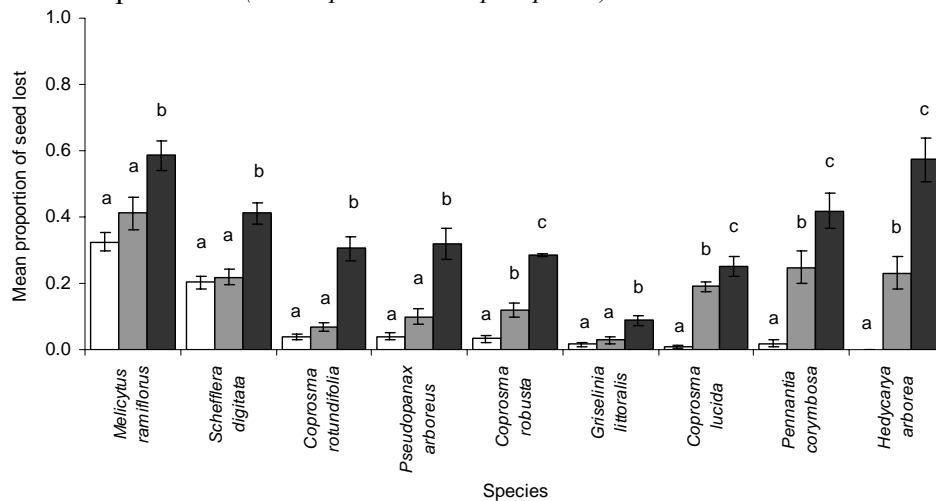
B) Seed depots encountered
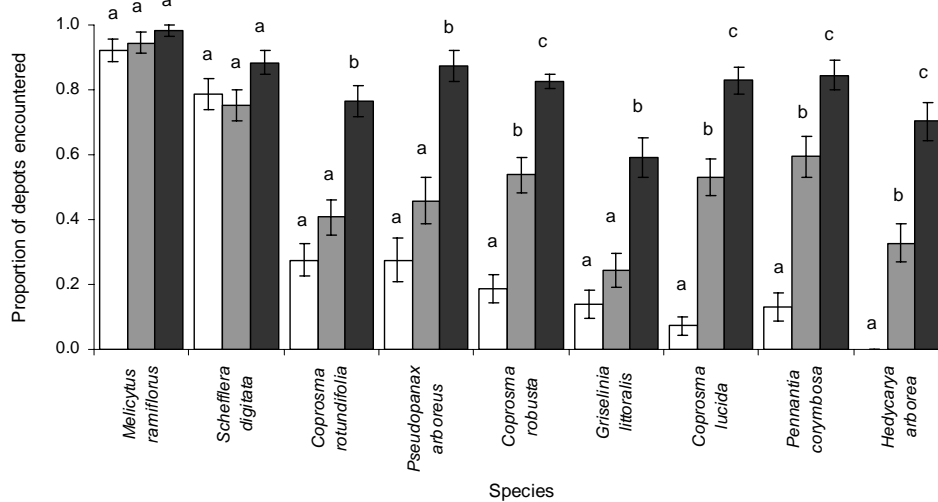
C) Seed exploitation once encountered
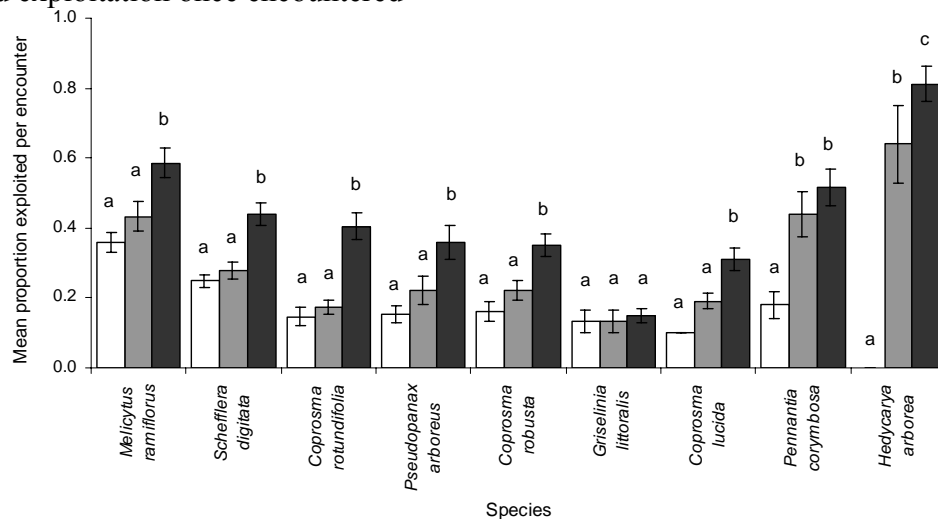
Figure 2.1: *Comparison between exclosure treatments for A) the overall seed predation levels observed in the cafeteria experiment, B) the proportion of depots encountered during the experiment and C) the mean proportion of seed exploited once encountered for each of the nine studied plant species. Species ordered by increasing seed length (from left to right). Different shaded bars represent the different exclosure treatments: white bars = "Invertebrates access only", grey bars = "Rodents and invertebrates access only" and black bars = "Possums, rodents and invertebrates access" treatment. Different letters within each plant species indicates a significant difference (P <0.05) between exclosure treatments calculated using Tukey's honestly significant difference tests. Error bars = 1 std error. Experimental unit and habitat have been pooled.*

Table 2.5: *Results of the generalised linear models of the overall seed predation (the proportion of seed preyed upon over 15-days) from the cafeteria experiment against explanatory variables. Overall seed predation has been further presented as 'seed encounter', which describes the probability of at least one seed being removed by a predator, and 'seed exploitation', which describes the proportion of seed preyed upon once a depot has been encountered by a predator. Explanatory variables used in the models are: E = exclosure treatment, F = field-season, H = habitat type and S = plant species. Because the models for overall seed predation and seed exploitation were over-dispersed, significance testing was conducted using F-tests. Seed encounter is binary, so significance testing was conducted using χ^2 tests. N.S. Not significant, *P<0.05, **P<0.01, *** P<0.001*

| Explanatory variable | Overall seed predation | | | Overall seed predation separated | | | | | |
| | | | | Seed encounter | | | Seed exploitation | | |
	d.f.	F	P	d.f.	Chisq	P	d.f.	F	P
E	3	493.76	***	3	1000.60	***	3	36.67	***
F	2	2.50	N.S.	2	0.27	N.S.	2	2.9	N.S.
H	2	0.98	N.S.	2	0.77	N.S.	2	3.26	*
S	8	47.55	***	8	200.93	***	8	25.99	***
E x H	6	0.66	N.S.	6	2.95	N.S.	6	0.22	N.S.
E x S	24	6.72	***	24	44.76	**	17	0.73	N.S
H x S	16	1.50	N.S.	16	19.76	N.S.	16	1.64	N.S.
E x H x S	48	0.50	N.S.	48	30.45	N.S.	29	0.47	N.S.
Residual	1889			1889			731		

2.3.3 Predator responses to habitat variation

Habitat type was a significant explanatory variable for the GLM for seed exploitation. I found weak support for my hypothesis that seed predation would be greater as the structural complexity of the habitat increased (Figure 2.2). To determine which of the 18 measured habitat characteristics might drive this general habitat trend, the regression algorithm selected five habitat characteristics to be part of the constructed tree (Figure 2.3). These characteristics were: percentages of canopy cover, ground vegetation, litter cover, and moss cover, and the distance to the nearest canopy tree. The GLM incorporating these five habitat characteristics as explanatory variables indicated that litter cover and ground vegetation density were the only variables that explained a significant component of the variation in seed exploitation at each depot site (Table 2.6). Generally seed exploitation was positive related to increasing litter cover and ground vegetation density.

2.3.4 Predator responses to seed characteristics

In determining if exotic mammalian seed predators target larger-seeded species than native invertebrate seed predators, both the seed mass and seed length analyses indicated a similar seed predator : seed characteristic trend. The probability of a seed encounter was negatively correlated to both seed mass and seed length for all exclosure treatments. Native invertebrate
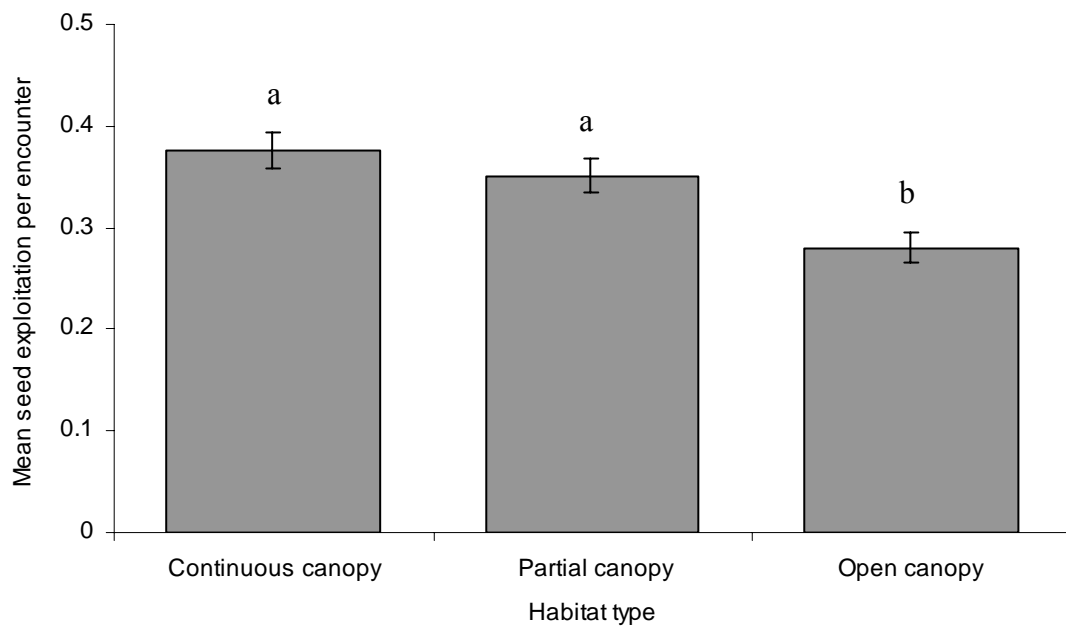
Figure 2.2: *Mean seed exploitation (the mean proportion of seed preyed upon once a depot had been encountered) in the three different habitat types used in the cafeteria experiment at Peel Forest. Habitat types are based on canopy cover. Plant species has been pooled. Different letters within each plant species indicates a significant difference (P <0.05) between exclosure treatments calculated using Tukey's honestly significant difference tests. Error bars are 1 std error.*

Percentage of ground
vegetation cover
<12.5%

0.401

Percentage of moss cover
<25%

Percentage of litter cover
<65%

0.449

Percentage of canopy cover
<25%

0.294

Distance to nearest canopy tree
<2.25m

0.389

0.311 0.351
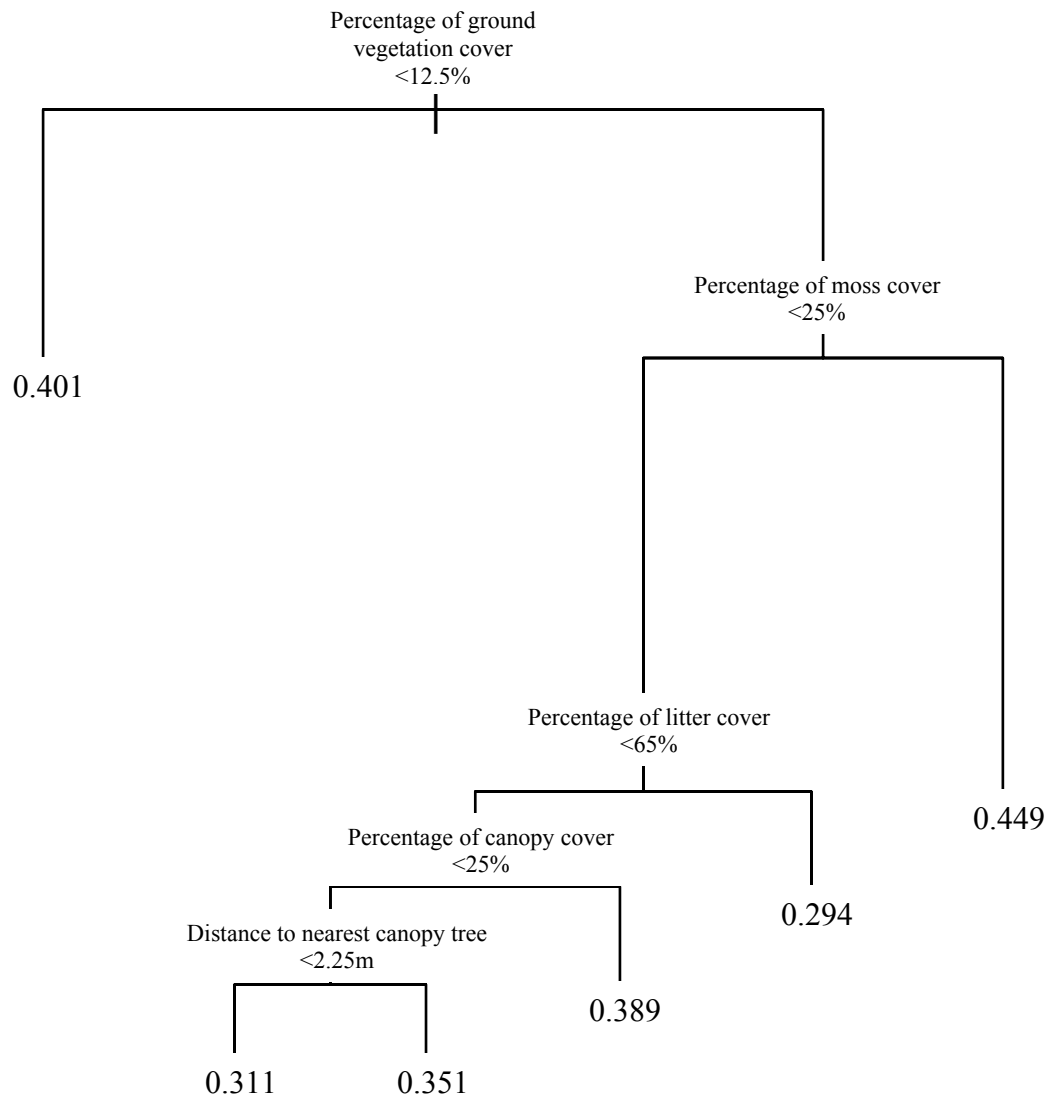
Figure 2.3: *Fitted regression tree of the effect of habitat characteristics on the levels of seed exploitation observed across the 24 experimental units used in the cafeteria experiment. The partition defining each split is shown at the corresponding node. Each split is represented as an inequality. If the inequality is true, proceed to the left branch of the node; otherwise proceed to the right branch. The number at the terminal of each node is the mean proportion of seed preyed upon within that habitat grouping.*

Table 2.6: *Results of the generalised linear model of seed exploitation (the proportion of seed preyed upon once a depot had been encountered by a predator) against habitat explanatory variables. Habitat explanatory variables used in the model were selected from 18 measured habitat characteristics (Table 2.3) by exploratory analysis using a tree regression (Figure 2.3). As the model was over-dispersed, significance testing was conducted using F-tests. Significant variables are in bold.*

Explanatory variable	d.f.	Deviance	F	P
Distance to the nearest canopy tree	1	8.73	2.60	0.107
Percentage of canopy cover	1	0.91	0.27	0.602
Percentage of ground vegetation cover	**1**	**17.32**	**5.16**	**0.023**
Percentage of litter cover	**1**	**16.00**	**4.77**	**0.029**
Percentage of moss cover	1	8.46	2.52	0.113
Residual	804	2997.30		

seed predators are only major predators of the two smallest seeded species studied (*S. digitata* and *M. ramiflorus*), and both the probability of seed encounter and seed exploitation for the 'Invertebrates access only' exclosure treatment declined dramatically as both seed mass and seed length increased (Figure 2.4). Though the probability of a seed encounter for the 'Possum, rodents and invertebrates access' and the 'Rodents and invertebrates access only' exclosure treatments also declined as both seed mass and seed length increased, the reduction in the probability of an encounter was less dramatic than the 'Invertebrates access only' exclosure treatment (Figure 2.4), implying that at least one species of exotic mammal was locating seed of larger size. While the increasing divergence in seed exploitation between the two exclosures allowing mammals' access and the 'Invertebrate access only' exclosure treatment implies that the importance of mammals as seed predators is positively related to seed size (Figure 2.4). This divergence between exclosure treatments continued to the extent that the largest seeded species studied, *H. arborea,* recorded the highest seed exploitation per encounter (81.2%) in the 'Possum, rodents and invertebrates access' exclosure treatment, while no seed encounters or seed exploitation was recorded in the 'Invertebrates access only' exclosure treatment for this plant species (Figure 2.1). However, this trend was not consistent for all species. *Griselinia littoralis* (a relatively large seed) experienced the lowest seed losses for the 'Possums, rodents and invertebrate access' and 'Rodents and invertebrates access only' exclosure treatments (Figure 2.1).

2.3.5 Predator responses to seed density

In investigating whether native invertebrates and exotic mammals respond differently to initial seed density, the GLM models indicated that all explanatory variables and several two-way interactions were significant in either the probability of a seed encounter or the level of

A) Seed encounter

B) Seed exploitation
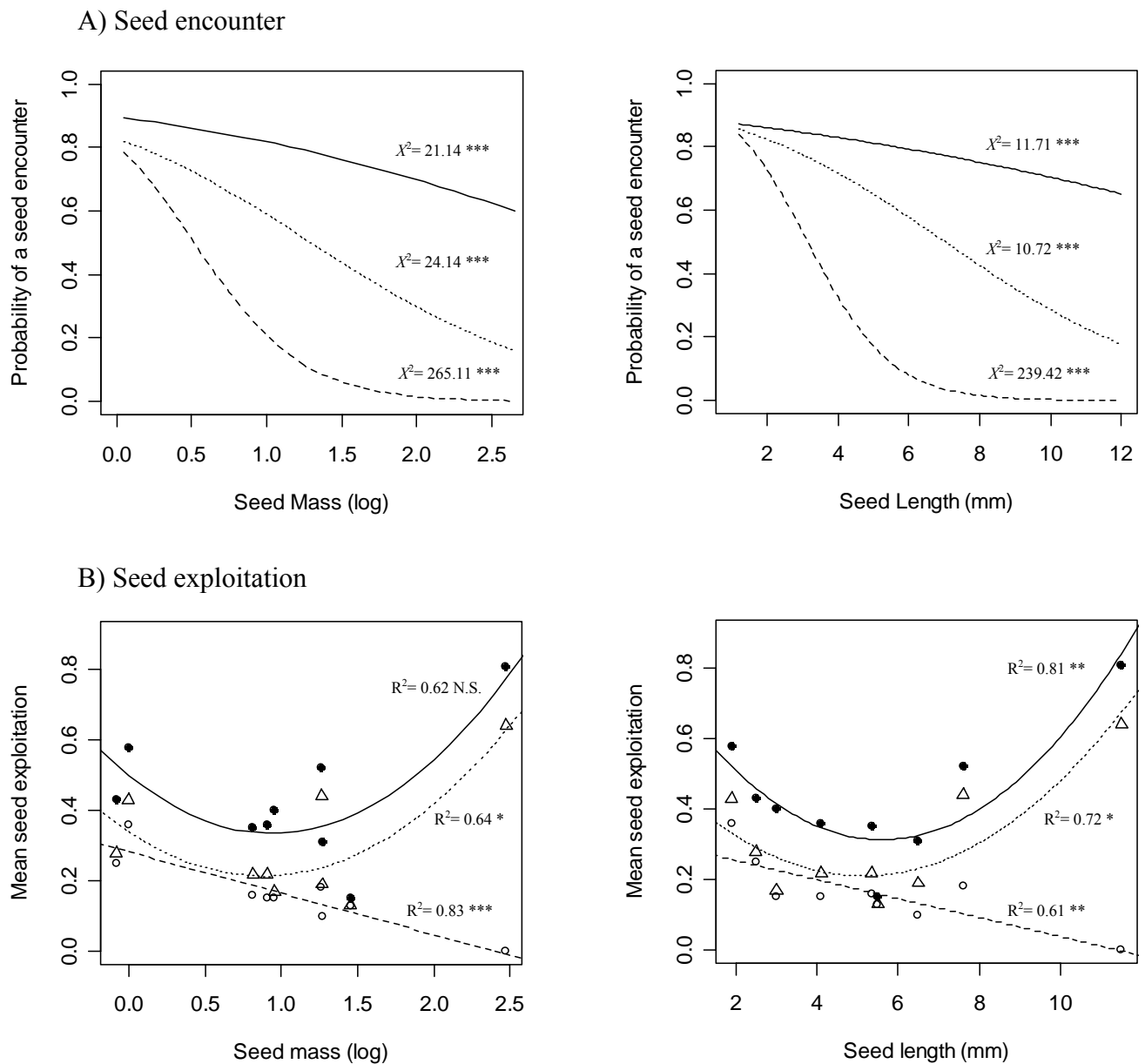
Figure 2.4: *The relationship between seed mass and seed length and A) seed encounter (the probability of at least one seed being preyed upon) and B) seed exploitation (the proportion of seed exploited per encounter) observed in the "Possum, rodents and invertebrates access" treatment (—●—), "Rodents and invertebrates access only" treatment (····Δ····) and the "Invertebrates access only" treatment (---○---). Significance determined by logistic regression for seed encounter and polynomial regression for seed exploitation. N.S. Not significant, *P<0.05, **P<0.01, ***P<0.001.*

Polynomial regression equations for seed exploitation: Seed mass – 'Possums, rodents and invertebrates access': Y = 0.50 – 0.35(log(mass)) + 0.19(log(mass))^2; Rodents and invertebrates access': Y = 0.34 – 0.29(log(mass)) +0.16(log(mass))^2; 'Invertebrates access only': Y = 0.28 – 0.12(log(mass)). Seed length – 'Possums, rodents and invertebrates access': Y = 0.79 – 0.17(length) + 0.02 (length)^2; 'Rodents and invertebrates access': Y= 0.51 – 0.12(length) + 0.01(length)^2; 'Invertebrates access only': Y = 0.31 – 0.03(length).

overall seed predation for at least one of the studied plant species (Table 2.7). A summary of the raw density experiment data is located in Appendix Two.

As with the cafeteria experiment, habitat type and exclosure treatment were significant variables in both seed encounter and overall seed predation models (Table 2.7). The probability of a seed encounter and the level of overall seed predation of all three studied species increased as more seed predators had access to the depots (Figure 2.5).

The initial seed density was a significant explanatory variable in the seed encounter models for *S. digitata* and *C. robusta* with the probability of a seed encounter increasing with seed density (Figure 2.5). Though a slight increase in the levels of seed lost to predators was apparent (Figure 2.5), initial seed density was only a significant variable for the level of overall seed predation for *C. robusta* (Table 2.7). There was little indication that native invertebrate and exotic mammalian seed predators responded differently to initial seed density as a significant interaction between seed density and exclosure treatments was only observed for *G. littoralis* (Table 2.7). For this plant species, as seed density increased, the divergence between the levels of seed predation within different exclosure treatments increased (Figure 2.5).

2.4 Discussion

2.4.1 Predators involved in post-dispersal seed predation events at Peel Forest

Both the time-lapse video and cafeteria experiments provide clear support for my hypothesis that exotic mammals are responsible for the majority of post-dispersal seed predation events at Peel Forest. Several previous New Zealand studies on mammal diets have indicated seeds are important dietary components so indirectly support my observations (e.g. Campbell 1978; Badan 1986; Williams et al. 2000). Ship rats are the dominant mammalian post-dispersal seed predators in this study. In New Zealand forests, ship rats eat both plant and animal foods, with seeds and fruit forming an important dietary component when available (Best 1969; Campbell 1978). Ship rats are traditionally believed to be principally an arboreal foraging rodent in New Zealand (Innes 1990), but research both in New Zealand and Australia indicate that ship rats appear to spend the majority of time foraging on the ground rather than in shrubs or trees, and probably obtain a substantial proportion of their food there (Dowding and Murphy 1994; Cox et al. 2000). So my findings that ship rats are major post-

Table 2.7: *Results of the generalised linear models examining the effects of explanatory variables on seed encounter (the probability of at least one seed being preyed upon) and overall levels of seed predation observed over 7 days of the three plant species used in the density experiment. To ensure the observations at low seed densities do not over influence the analysis, the explanatory variable 'seed density' has been included in the models as a continuous factor. Significance testing for the models was conducted using χ^2 tests. N.S. Not significant, *P<0.05, **P<0.01, ***P<0.001*

Explanatory variable	d.f.	*Schefflera digitata*				*Coprosma rotundifolia*				*Griselinia littoralis*			
		Seed encounter		Overall seed predation		Seed encounter		Overall seed predation		Seed encounter		Overall seed predation	
		χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P
Seed density	1	37.29	***	0.01	N.S.	12.58	***	5.01	*	1.55	N.S.	0.24	N.S.
Habitat type	1	0.60	N.S.	3.83	*	0.05	N.S.	6.10	*	0.47	N.S.	1.58	N.S.
Exclosure treatment	2	3.90	N.S.	25.76	***	9.06	*	38.83	***	6.13	*	55.82	***
Density x habitat	1	0.06	N.S.	0.02	N.S.	0.01	N.S.	9.55	*	0.01	N.S.	0.09	N.S.
Habitat x exclosure	2	4.22	N.S.	4.75	N.S.	1.61	N.S.	0.64	N.S.	4.59	N.S.	3.54	N.S.
Density x exclosure	2	0.79	N.S.	2.31	N.S.	1.02	N.S.	1.27	N.S.	0.81	N.S.	15.41	***
Density x habitat x exclosure	2	2.20	N.S.	2.92	N.S.	0.77	N.S.	5.74	N.S.	1.32	N.S.	1.83	N.S.
Residual	143												
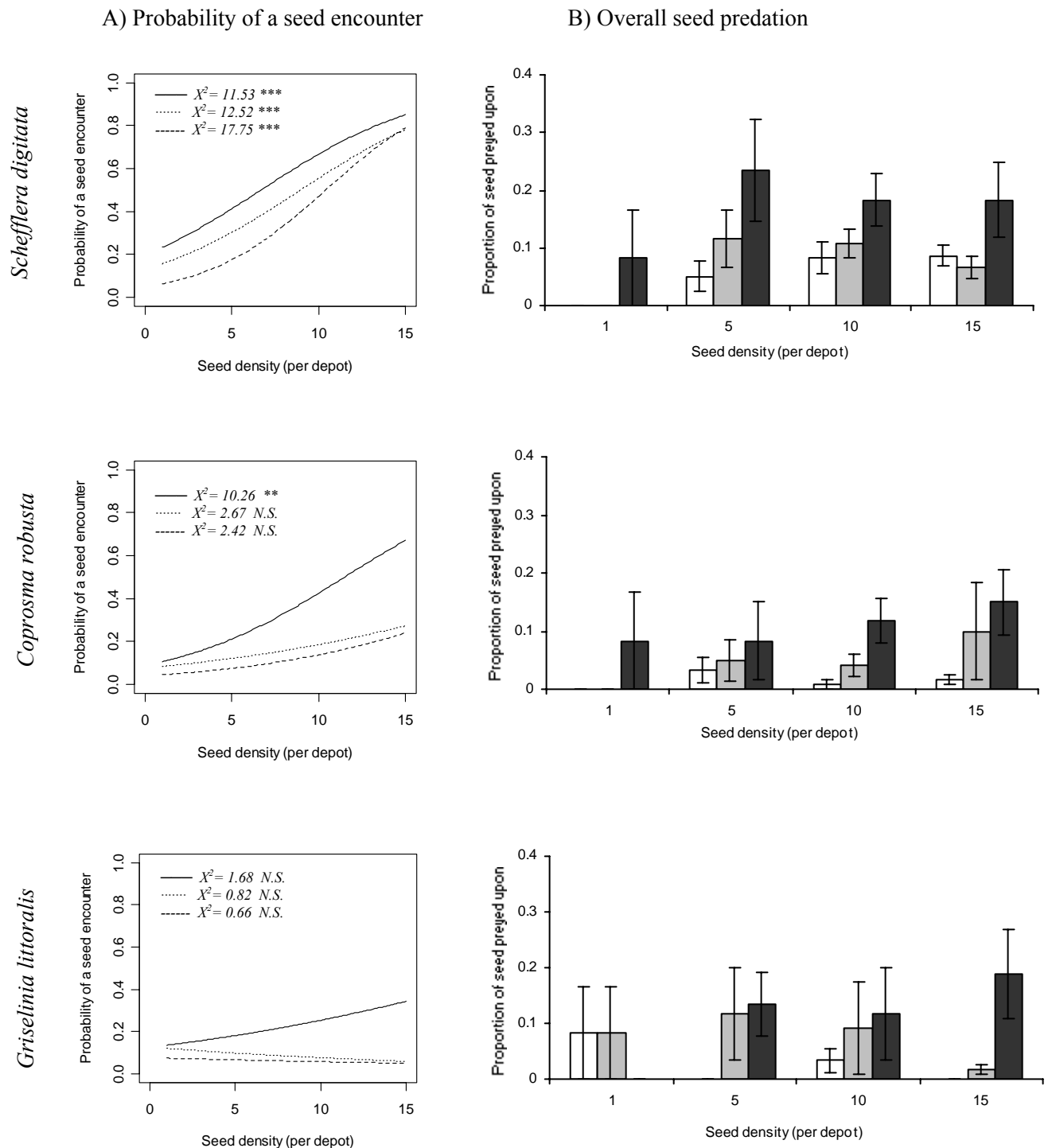
Figure 2.5: *The importance of initial seed density on A) probability of seed encounter, B) overall seed predation (the proportion of seed preyed upon per 7 days) for* Coprosma robusta, Griselinia littoralis *and* Schefflera digitata. *Species are ordered by increasing seed size. Different lines and shaded bars represent the different exclosure treatments:* ⎯ / black bars = 'Possums, rodents and invertebrates access', ⋯⋯ / grey bars = 'Rodents and invertebrates access only' and ------- / white bars = 'Invertebrates access only' exclosure treatments. Error bars are 1 std error. Significance determined by logistic regression for seed encounter. N.S. Not significant, * P<0.05, ** P<0.01, *** P<0.001.*

dispersal seed predators foraging on the forest floor is not unexpected. Time-lapse video coupled with the seed remains remaining after predation events in the cafeteria experiment indicate that brushtail possums are also important as seed predators at Peel Forest. Brushtail possums are known to feed extensively on the forest floor (Cowan and Clout 2000), usually feeding on low growing herbs, grasses, fallen leaves and invertebrates (Cowan and Moeed 1987; Nugent et al. 2000). Seeds are regularly observed in the possum diets but are used as an indicator of fruit consumption (e.g. Coleman et al. 1985; Nugent et al. 2000; Dungan et al. 2002). However, as I focused on 'cleaned' seeds only (representing avian dispersed seeds), my study provides evidence that possums specifically target seeds as well as complete fruit. House mice were also responsible for some predation events observed in the time-lapse video experiment. House mice are known to be seed predators (e.g. Murphy and Pickard 1990; Fitzgerald et al. 1996) so this finding is not unexpected. No evidence of seed predation by exotic avian species was recorded in any experiment conducted as part of my study even though previous studies in New Zealand have recorded exotic bird species foraging on seed on the forest floor (e.g. Beveridge 1964).

I have assumed that due to the limited success of exotic invertebrates in establishing in New Zealand forests (Harris and Burns 2000), the invertebrates involved in post-dispersal seed predation events in my study are native species. Generally the time-lapse video footage obtained was not of sufficient quality to identify invertebrate predators, apart from a species of Staphylinidae. In the cafeteria experiment the remains of *M. ramiflorus* were regularly found as a hollow husk with a single hole piercing the outer seed coat. Damage of this nature is most likely caused by beetle larvae (Lövei and Sunderland 1996). None of the seeds used in the control treatments of the cafeteria experiment were similarly affected, suggesting that the damage was inflicted post-dispersal rather than from a pre-dispersal infestation. However, in general very little is known about the diet and behaviour of ground dwelling invertebrates in New Zealand conifer-broadleaf forests (Howarth and Ramsay 1991) and this requires further investigation.

2.4.2 Predator responses to seed characteristics

My study provides support for the hypothesis that at Peel Forest exotic mammalian seed predators target larger seeded species than remnant native invertebrate seed predators. Though probably quite fluid, there appears to be a division of the seed based food resource

among predator types. Both the encounter rates and the exploitation level for invertebrates declined as seed size increased suggesting that, at Peel Forest, invertebrates are primarily post-dispersal seed predators of small seeds. In a similar forest type, Moles and Drake (1999) also found a low level of invertebrate predation in their study of large-seeded tree species. The seed encounter rates for the two smallest seeds, *S. digitata* and *M. ramiflorus*, were not significantly higher when mammals had access to the depots and seed exploitation between exclosure depots were similar (Figure 2.1), implying that invertebrates are the major seed predators of these two species. The encounter rates by invertebrates for these two species (82% and 90% respectively) were extremely high when compared to the seven larger seeded species used in this study which all experienced encounter rates less than 27%, and to overseas studies which report encounter rates for invertebrates of less than 25% (Hulme 1994; Hulme and Borelli 1999; Hulme and Hunt 1999).

The divergence between the 'Invertebrates access only' and 'Rodents and invertebrates access only' exclosure treatments indicates that post-dispersal seed predation by rodents was positively related to seed size for both seed encounter and seed exploitation. While the additional divergence in the proportion of seed preyed upon between the 'Rodents and invertebrates access' and the 'Possums, rodents and invertebrates access' exclosure treatments for the larger seed sizes indicates additional post-dispersal seed predation by brushtail possums (Figure 2.4). The largest seed studied, *H. arborea,* was recorded with the highest average seed exploitation in the 'Possums, rodents and invertebrates access' exclosure treatment. This combined with the fact that no seed predation events were recorded in the 'Invertebrates access only' exclosure treatment indicates that mammalian species are the only post-dispersal seed predators of this species. Time-lapse video captured house mice, ship rats and brushtail possums preying upon this plant species (Table 2.3). Previous studies of seed size selection by mammals agree with my findings, that larger seed may suffer a higher predation rate (Mittelbach and Gross 1984; Kelrick et al. 1986; Reader 1993). However this may not be always the case as the only other study of this type in New Zealand found no relationship between seed removal and seed size (Moles and Drake 1999), though their study was a preliminary study conducted under one habitat type, over one field-season with limited replication.

The apparent limited exploitation of seeds between 4 to 7 mm in length suggests that while these seeds may be too large for remnant invertebrate seed predators, they are also too small

for exotic mammalian seed predators to prey upon. Whether they are too small to locate on the forest floor or the net gain is too small for a mammalian seed predator to actively select this size of seeds is unknown. However, the plant species, whose seeds appear not to be preyed upon, are likely to be experiencing release from predator pressure as it is assumed that due to the introduction of mammals, either the native seed predators (the large invertebrate or avian species) which would have potentially targeted seeds of this size are to now be extinct at Peel Forest and /or the defences evolved as in response to these native post-dispersal seed predators over time may also be effective against the newer exotic mammals (Sherbrooke 1976; Ruscoe et al. 2005).

Theoretically, larger seeds should be easier to locate on the forest floor so one might expect that encounter rates would increase with seed size. However, while the amount of seed preyed upon differed between exclosure treatments increased with seed size, seed encounter for all exclosure treatments decreased (Figure 2.4) and the reason for this remains unknown. One contributing factor to this observation may be the response 'seed encounter' itself. For a seed encounter to be recorded, at least one seed needed to be removed. Hence this requirement does not account for occasions when depots were discovered by a predator but no seeds were removed, leading to an underestimate of actual encounter events. Having said that, from the plant perspective, if no seeds were removed in an encounter then it is as though the depot was not discovered by the predator (Hulme 1994).

2.4.3 Predator responses to habitat variation

The lack of a significant habitat : exclosure treatment interaction with respect to any of the three response variables relating to the cafeteria experiment, suggests that both native invertebrate and exotic mammalian seed predators forage in similar habitats, providing support for my hypothesis. I also found limited support for the hypothesis that seed exploitation was positively related to the density of ground-layer vegetation and the amount of leaf litter present. My findings that seed losses to predators are often greatest in areas of high structural complexity compared with more open habitats agrees with Cox et al. (2000) who reported that in Australian forests, ship rats preferentially used habitats with dense understorey, numerous vertical stems and dense litter cover. My results may be a consequence of vegetation cover contributing to anti-predator strategies of the seed predators

(Dickman 1992; Cox et al. 2000), or the use of cover maybe a result of competition with other animals (Falkenberg and Clarke 1998).

2.4.4 Predator responses to seed density

I hypothesised that native invertebrate and exotic mammalian seed predators would respond differently to changes in seed density, but I found little support for this prediction. In the density experiment, I focused on two components of seed predation, and I found that both native and exotic seed predators had similar responses to changes in seed density. Overall, the probability of a seed encounter increased with initial seed density. This trend was apparent in all exclosure treatments for the three plant species studied, indicating that with respect to seed encounter, both native and exotic seed predators had a density-dependent response.

Although the probability of a seed encounter increased, no increase in the overall amount of seed preyed upon was observed for any exclosure treatment. This suggests that both predator types (invertebrate and mammalian) consumed a constant proportion of seeds irrespective of the seed density; a density-independent response. Mittelbach and Gross (1984) found a similar result in their study of old-fields of North America and suggested that predators were treating each depot as a single prey clump regardless of density. This pattern of predation may account for the general lack of seed density effects observed in this study.

2.4.5 Other factors affecting predator behaviour

With two distinct types of seed predators at Peel Forest, native invertebrates and exotic mammals, the responses of these predators to different seed morphological traits result in variable seed survival amongst plant species. However, the variation in mammalian seed exploitation between seeds of a similar size in this study suggests that seed size is only one of a number of variables underlying mammalian seed preferences. In the cafeteria experiment, *G. littoralis* recorded low levels of seed predation for all exclosure treatments (Figure 2.1), implying that mammals did not utilise this species as much as species with similar seed dimensions (i.e. *C. lucida* or *Pennantia corymbosa*). Due to their high nutritional value, seeds often receive a greater investment in anti-herbivore defence than vegetative tissue (Janzen 1971). Seeds may be poisonous or have a large amount of secondary compounds that either impair digestibility or just make them unpalatable (Campbell 1978; Kollmann et al. 1998).

Common chemical defences include non-protein amino acids, cyanogenic glycosides and protease inhibitors (Thompson and Hagen 1999; Hulme and Benkman 2002). How effective these defences are against exotic mammalian post-dispersal seed predators is unknown and requires more in-depth experiments than performed here. These defences may be effective against mammals, but it is unlikely there has been sufficient time for plants to have adapted their seed defences to become effective against any new seed predation pressure from exotic mammals (Ruscoe et al. 2005).

To conclude, the introduction of mammals has had a major affect on the dynamics of seed predation in New Zealand conifer-broadleaf forests, exotic mammals are themselves major post-dispersal seed predators. My study clearly supports the hypothesis that exotic mammals have replaced native species as the dominant post-dispersal seed predators at Peel Forest. Ship rats were found to be the major post-dispersal seed predator, while brushtail possums and house mice were also important post-dispersal seed predators. And though, many native predators are now extinct at Peel Forest, remnant invertebrates are still important post-dispersal seed predators for several plant species. Clearly the most conspicuous difference between the exotic mammals and remnant native invertebrate seed predators is their body size, and I found support for my hypothesis that the larger mammalian seed predators target larger seeded plant species than remnant native invertebrate predators. But if you focus on their prey (i.e. individual seeds), exotic mammalian seed predators share similarities with remnant native invertebrate seed predators in many of their foraging behaviours. As predicted, I found that both remnant native invertebrate and exotic mammalian seed predators forage in similar habitats, preferring to prey upon seeds in more structurally complex, closed habitats. But I found no evidence that these exotic and native seed predators responded differently to changes in seed density. For all seed predators, while the probability of a seed encounter was positively correlated to seed density, I observed no change in the proportion of seed preyed upon, indicating that both native and exotic predators exhibit a density-dependent response to changes in seed density.

Chapter Three: The role of exotic mammalian post-dispersal seed predators in controlling seedling establishment in a conifer-broadleaf forest remnant, Canterbury, New Zealand

3.1 Introduction

3.1.1 Mammals as post-dispersal seed predators

Since the arrival of humans to New Zealand approximately 800 years ago the mammalian fauna has changed dramatically resulting in a unique mixture of species from both temperate and tropical climates (King 1990). These exotic mammals have had a dramatic effect on the native flora and fauna and the environment in which they evolved (King 1984; Wodzicki and Wright 1984). While impacts on native fauna are well documented (see Worthy and Holdaway 2002 for a review), our understanding in New Zealand of the role of these exotic mammals in many aspects of forest plant dynamics is limited (Halloy 1995).

Although large bodied mammals are known to have significant effects on plant communities through selective removal of biomass and death of established individuals (see Augustine and McNaughton 1998 for a review), it is principally at the seed and seedling stages that animals influence plant mortality (Harper 1977; Clark et al. 1998; Zobel et al. 2000) and it is at this stage that the parent plant has the fewest options to compensate for seed losses (Blaney and Kotanen 2001). Consequently at the seed and seedling stages, animals have the greatest impact on plant communities (Crawley 2000). Mammalian post-dispersal seed predators are responsible for considerable seed mortality in temperate (Webb and Willson 1985; Hulme and Hunt 1999; Hulme and Benkman 2002) and tropical (Holl and Lulow 1997) plant communities. As a result of human introductions, a new suite of ground foraging mammals has become established in New Zealand. These include four species of rodent (kiore (*Rattus exulans*), Norway rat (*R. norvegicus*), ship rat (*R. rattus*) and the house mouse (*Mus musculus*), and the brushtail possum (*Trichosurus vulpecula*)(King 1990). These mammals are omnivores, polyphagous feeders, whose diets have been known to contain seeds (Beveridge 1964; Campbell 1978; Miller and Miller 1995; Nugent et al. 2000). In Chapter Two, I presented results of the first comprehensive, specifically designed study to assess the role of exotic mammals as post-dispersal seed predators within a conifer-broadleaf forest on the mainland New Zealand. Ship rats were found to be the dominant post-dispersal seed predator, while brushtail possums, house mice and remnant native invertebrates were also

found to be important post-dispersal seed predators. Through use of time-lapse video and cafeteria experiments I found that exotic mammalian seed predators, when compared to native invertebrate seed predators, preyed upon larger-seeded plant species and could potentially cause considerable seed losses of several tree species.

3.1.2 Influence of mammals on seedling establishment

Elsewhere, mammalian post-dispersal seed predators have been shown to exert a strong influence on plant populations by altering rates and patterns of plant establishment (Crawley 1992; Danell and Bergstrom 2002), spatial distribution (Webb and Willson 1985) colonisation ability (Schupp et al. 1989; Myster and Pickett 1993) and may even exclude some species from the community (Hulme and Benkman 2002). However, the nature of these effects depends chiefly on the seed predator assemblage present. Rodents are major post-dispersal seed predators and are known to significant reduce seedling establishment of plant species in deserts (Inouye et al. 1980; Heske et al. 1993) and in old-fields of North America (Mittelbach and Gross 1984). Although I am unaware of any studies focusing on the link between post-dispersal seed predation and seedling establishment in New Zealand conifer-broadleaf forests, recent studies focusing solely on the presence of small mammals in relation to plant dynamics in New Zealand are inconclusive. Both Allen et al. (1994) and Campbell and Atkinson (2002) concluded that rodents had a negative effect on the recruitment of several plant species on islands, while Campbell (2002) and Wilson et al. (2006) were unable to separate the benefit of removing rodents on seedling establishment from that of natural variation (see Chapter One for a full summary).

Mammalian post-dispersal seed predators do not influence seedling establishment in isolation. Mammals are selective in the way they forage within habitats; mammalian post-dispersal seed predation is often greatest in areas of high structural complexity compared with more open habitats (Myster and Pickett 1993; Manson and Stiles 1998; Holl 2002). In Chapter Two, though I found no significant variation in the probability of a seed encounter between habitats, the proportion of seed preyed upon was positively related to the percentage cover of litter and ground vegetation. If suitable germination sites are uncorrelated between plant species, and these sites experience sufficient variation in the intensity of mammalian foraging pressure then mammalian post-dispersal seed predation may contribute to the maintenance of overall

species diversity within a community by altering the distribution of 'safe' germination sites (Schupp 1988; Meiners and Stiles 1997; Rey et al. 2002).

I have previously discussed evidence that exotic mammals are selective in the seeds they prey upon and forage across a variety of habitats within New Zealand conifer-broadleaf forests (see Chapter Two). Combining these results with the limited ability of plants to compensate for post-dispersal seed losses, the potential for small mammals to have a considerable impact on seedling establishment exists. However, the influence of mammalian post-dispersal seed predators on plant dynamics within New Zealand conifer-broadleaf forests remains poorly understood. If in fact the discriminatory mammalian post-dispersal seed predation observed in Chapter Two does have a flow on effect on seedling establishment, in this chapter, I hypothesise that:

1. The presence of exotic mammals will lower overall plant species diversity and abundance of seedlings establishing within the conifer-broadleaf forests,

2. The influence of mammals on seedling establishment will be greater under a continuous canopy than in open canopy habitats, and

3. Any changes in seedling establishment accredited to the presence of mammals will be due to these mammals acting as post-dispersal seed predators.

To addresses these hypotheses, I monitored natural seed germination over a three-year period within permanently marked seedling plots under two levels of canopy cover. The importance of different mammalian post-dispersal seed predators was determined by monitoring seed germination within exclosures utilising wire-mesh that excluded mammalian species of different sizes.

3.2 Materials and Methods

3.2.1 Study area

This study was conducted at Mount Peel Forest Park Scenic Reserve which lies along the southern edge of the Rangitata River in South Canterbury, New Zealand (43°54'S, 171°15E). Peel Forest has a mild, moist temperate climate (Molloy 1983), with an annual precipitation of 1160mm (Massam 1986). The experiment was carried out in a 60-hectare section of conifer-broadleaf forest spanning an altitudinal range of 300 to 360 metres. The majority of the forest was selectively logged for conifer species between 1860-1900 (Kerr 1972; Massam 1986), resulting in a regenerating secondary forest dominated by broadleaf species with a few

emergent conifers. A dense shrub tier is present and ferns and graminoids dominate the ground layer (see Chapter One for a full description of the study area). Tracking tunnels and time-lapse video footage identified ship rat, house mouse and brushtail possum were present in Peel Forest and were observed consuming seeds on the forest floor (see Chapter Two).

3.2.2 Field experiment setup

To investigate if the discriminatory post-dispersal seed predation by mammals observed in Chapter Two has a flow on effect on seedling establishment an experiment was designed to monitor natural seedling establishment at Peel Forest. A total of 14 experimental units were established in April 2000. To determine if the presence of different mammalian species on seedling establishment was greater under a continuous canopy, each experimental unit was situated under one of two habitat types, based on canopy cover: (1) open canopy (within a single tree-fall gap) and (2) under continuous canopy at least 20 metres from the nearest tree-fall gap. To locate experimental units situated with open canopy sites, all single treefall gaps within the study area were mapped and then I randomly selected seven for my experiment. With all single treefall gaps located, the seven experimental units under a continuous canopy were randomly allocated within areas away from treefall gaps.

At each experimental unit three seedling plots (1.0 × 0.75m) were placed within a 3m radius circle. The seedling plots were placed at least 1m away from trees greater than 5cm dbh, however large ground ferns (*Blechnum discolor* and *Polystichum vestitum*) were left inside the seedling plots as they were common throughout the study area. As the plot was established, all seedlings present were removed while minimising the amount of soil disturbance. One assumption of this experiment is that any seedlings that emerged during the experiment were available to seed predators prior to germination. I used germination as a measure of realised survival from seed predation; it is expected that this will under-estimate the actual seed survival as some seeds that survived possible post-dispersal predation may not have germinated for other reasons.

Previously, I found three guilds of seed predators were present at Peel Forest: brushtail possums, rodents and invertebrates (see Chapter Two). To investigate if the discriminatory post-dispersal seed predation these mammals has a flow on effect on seedling establishment, I used wire exclosures to control the access of certain mammalian species to the seedling plots.

Each exclosure was 1.2 × 0.9m consisting of 0.6m high wire walls and a mesh roof. This area was larger than the seedling plot to allow for a 'buffer' zone from the edge of the wire walls. The three types of exclosures used were:

(1) *'Possums, rodents and invertebrates access':* An open treatment where no predator exclusion method was used; seeds were available to all mammalian predators.

(2) '*Rodents and invertebrates access only'*: 50mm hardware wire mesh cages buried 10cm deep with a mesh roof to prevent predators that climbed up the sides of the cage from entering and consuming the seeds. Seeds were available to rodents but brushtail possums were excluded.

(3) *'Invertebrates access only'*: A control exclosure. Similar to the 'Rodents and invertebrates access only' exclosure treatment but consisting of 12mm wire. All mammals were excluded.

Tracking tunnels indicated that rodents were not present inside the 'Invertebrates access only' exclosure treatment but were entering both exclosures that allowed rodents access. The mesh diameters used were based on research done at the Karori Wildlife Sanctuary, Wellington (Hitchmough 1994). All exclosure treatments were open to natural seed- and litter-fall, but the smaller mesh used in the 'Invertebrates access only' exclosure treatment blocked larger litter items which collected on the roof. Every month, the exclosures were monitored and any litter that accumulated on the roofs was placed haphazardly within the exclosures.

The experiment was established in April 2000. Seedling plots were surveyed every six months until April 2003. As I used seed germination as a measure of realised survival from post-dispersal seed predation, within each seedling plot, I removed each dicotyledonous seedling once it had been identified to species level.

3.2.3 Data analysis

All analyses were performed using the statistical analysis package R version 1.9.1 (R Development Core Team 2004).

To determine if the presence of mammals lowers overall plant species diversity and seedling abundance and to investigate if the influence of mammals was greater under a continuous canopy, I used as my response variables the 'number of plant species' and the 'number of seedlings' observed in each seedling plot during the three years. To identify factors that

might explain variation in these response variables, I included canopy cover (open and continuous), exclosure treatment ('Possums, rodents and invertebrates access', 'Rodents and invertebrates access only' and 'Invertebrates access only') and their interactions as explanatory variables. As the exclosure treatments were grouped together within 14 experimental units, I fitted a nested analysis of variance with the factor 'experimental unit' included as an additional error term. The response variable 'number of seedlings observed' was square-root transformed to normalise the data.

To further investigate the importance of the presence of mammals on the variation in plant species composition and seedling density, I examined the data using non-metric multidimensional scaling (NMDS). NMDS is a nonparametric dimension reduction technique that works without assumption of a linear or unimodel response variable (Kenkel and Orloci 1986) and was applied using the Bray-Curtis dissimilarity coefficient measures. The level of 'stress' (the level of mismatch between the rank order of distances in the data, and the rank order of distances in the ordination model) was used to determine the strength of the model. Species data was not standardized or transformed prior to analysis. NMDS analysis was accomplished by using the isoMDS package MASS and the VEGAN package for R.

To determine the effect of the presence of specific mammals on seedling establishment of individual plant species, I calculated a 'seedling ratio'. The 'seedling ratio' provides a measure of the relative difference in seed survival between exclosure treatments within an experimental unit for the particular plant species. It was calculated using the following equation (see Wilson et al. 2003).

$$SR = \frac{S_{TF}}{\sum S_{TF} + S_{TM}}$$

SR = Seedling ratio
S_{TF} = Total number of seedlings germinating in the plot allowing fewer mammals access
S_{TM} = Total number of seedlings germinating in the plot allowing more mammals access

Seedling ratios can range from 0 – 1.0 with 0.5 indicating the number of seedlings observed if two exclosure treatments were the same. A seedling ratio <0.5 indicates that the exclosure treatment allowing fewer mammalian species access had less seedlings than the treatment allowing more mammalian species, and >0.5 indicates the reverse. For each plant species, the

seedling ratios were calculated for each experimental unit and then bootstrapped 10,000 times
to provide mean and 95% confidence intervals. I considered two exclosure treatments to be
significantly different if the 95% confidence interval did not include 0.5.

To investigate if the changes in seedling establishment accredited to the presence of mammals
were due to these mammals acting as post-dispersal seed predators, I compared the seedling
ratios of seven plant species (obtained in this experiment) with the proportion of seed preyed
upon attributed to mammals observed in the cafeteria experiment for these plant species
(discussed in Chapter Two). As both factors are measured with errors I performed a non-
parametric Spearman's rank correlation. The proportion of seed preyed upon by mammals
from the cafeteria experiment is defined as the difference in the proportions of seed preyed
upon observed in the 'Invertebrate access only' and the 'Possums, rodents and invertebrates
access' exclosure treatments within the same experimental unit.

3.3 Results

3.3.1 Overall plant community response to the presence of mammals

Habitat type (i.e. canopy cover) was the only factor that explained a significant proportion of
the variation in plant species richness, while habitat type and exclosure treatment were
significant explanatory variables in the seedling abundance model (Table 3.1). The
interaction terms between habitat type and exclosure treatment are not significant in either
model. A summary of the seedlings observed within each experimental unit is located in
Appendix Three.

The presence of mammals did not lower the overall species diversity within the seedling plots,
however, the presence of mammals did significantly influence the abundance of seedlings
observed within the seedling plots over the three years. Under an open canopy cover, the
exclosure treatment preventing mammalian access (i.e. 'Invertebrates access only' treatment)
had consistently higher seedling abundances when compared to the other exclosure
treatments. Though a similar relationship was observed under a continuous canopy, the
differences between exclosure treatments was less defined (Figure 3.1). Habitat type affected
both the species diversity and abundance of seedlings within seedling plots, as the both
species richness and seedling abundance recorded under a continuous canopy were

A) Number of species observed
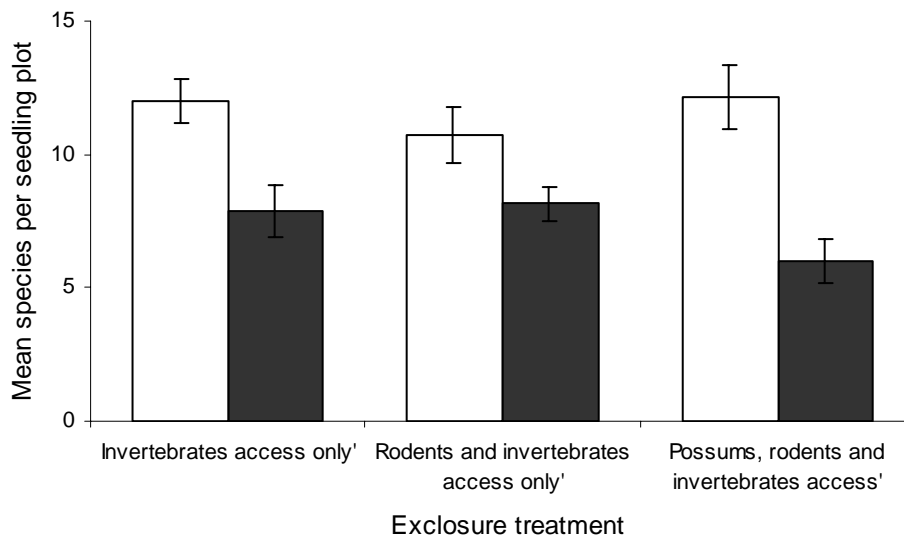
B) Number of seedlings observed
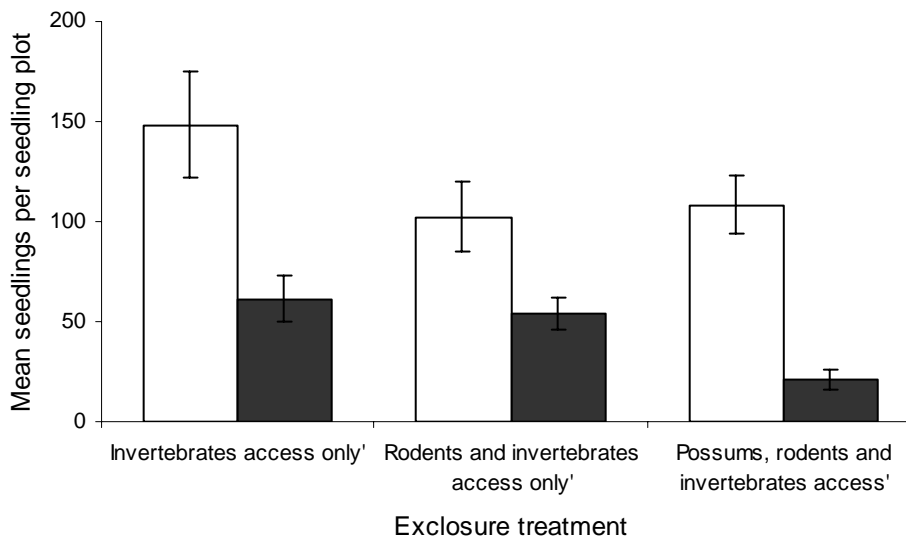
Figure 3.1: *Mean number of A) plant species and B) seedlings observed per exclosure treatment over a three-year period. Different shaded bars represent the studied habitat types at Peel Forest. White bars = open canopy habitat, black bars = continuous canopy habitat. n = 7 per exclosure treatment per habitat type. Error bars are ± 1 standard error.*

consistently lower than in the corresponding seedling plots under an open canopy (Figure 3.1).

However, the NMDS ordination does not support the hypothesis that the presence of mammals consistently lowers species diversity and seedling abundance at Peel Forest. Though the analysis found two convergent axes after 16 attempts, the stress obtained is high (20.38) meaning the resulting second axis is unlikely to be useful in explaining the species composition and density within the seedling plots. If the presence of mammals was as influential in seedling establishment as indicated by the nested ANOVA, then the plot of the NMDS should show a consistent directional shift between exclosure treatments across each experimental unit. While the NMDS plot indicates a similarity between exclosure treatments within an experimental unit, no consistency in the relative positioning of an exclosure treatment with respect to the other exclosure treatments was observed. This implies that the experimental unit is a critical factor in determining seedling abundance within the seedling plots rather than the exclosure treatments (Figure 3.2).

Table 3.1: *Results of the nested analysis of variance of the effects of experimental variables on A) number of plant species and B) number of seedlings observed per seedling plot. As the exclosure treatments were grouped together within experimental units, experimental unit was included as an additional error term. The 'number of seedlings per seedling plot' was square-root transformed to normalise the data. d.f. = degrees of freedom, SS = Sum of squares and SM = Mean square*

A) Number of plant species per seedling plot

Source of variation	d.f.	SS	MS	F	P
Error: Among experimental unit					
Habitat	1	192.86	192.79	16.82	0.002
Habitat: experimental unit	12	137.62	11.47		
Error: Within experimental unit					
Exclosure	2	5.20	2.60	0.70	0.504
Habitat: Exclosure	2	22.42	11.21	3.05	0.066
Residuals	24	88.38	3.68		

B) Number of seedlings per seedling plot

Source of variation	d.f.	SE	ME	F	P
Error: Among experimental unit					
Habitat	1	192.47	192.47	67.00	<0.001
Habitat: experimental unit	12	34.41	2.87		
Error: Within experimental unit					
Exclosure	2	40.18	20.08	4.16	0.028
Habitat: Exclosure	2	17.49	8.75	1.81	0.19
Residuals	24	115.92	4.83		
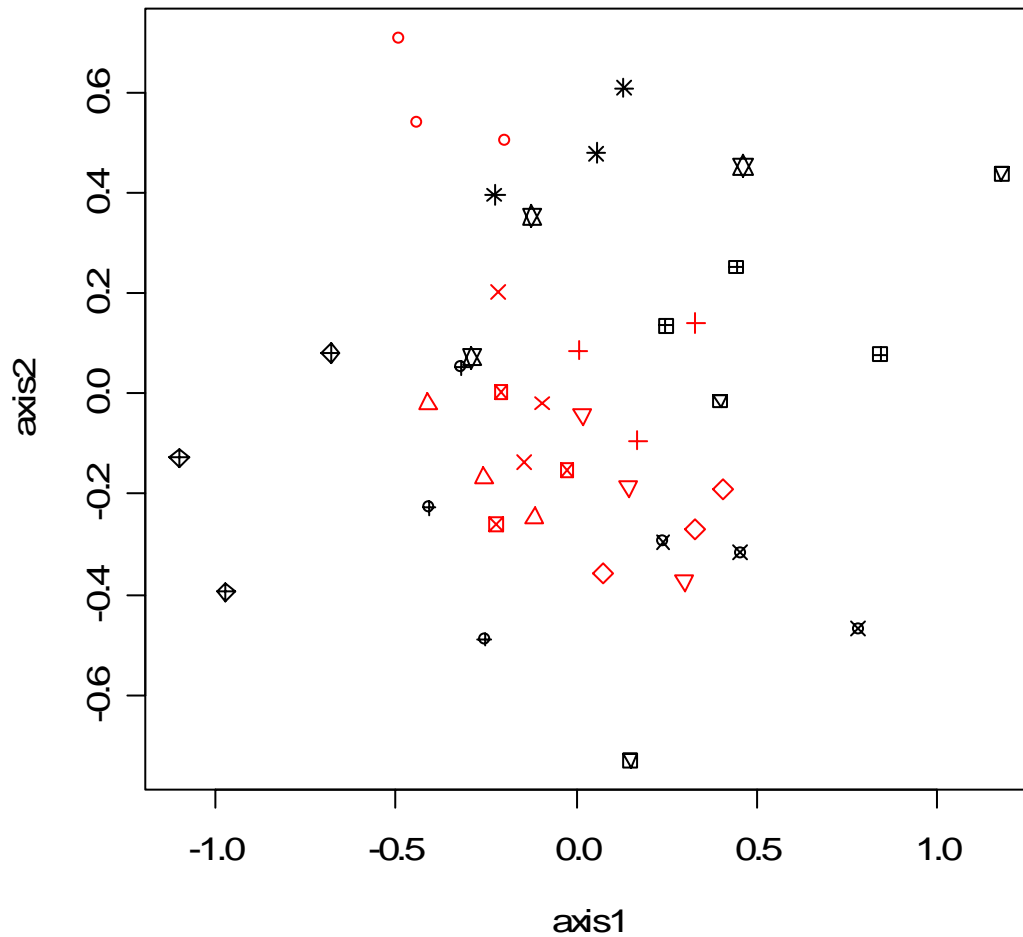
Figure 3.2: *Ordination plot of the non-metric multidimensional scaling analysis of exclosure treatments per experimental unit. A stress value of 20.38 was obtained. Analysis based on seedling composition and density of 15 plant species within exclosure treatment. Exclosure treatments within the same experimental unit have the same symbol. Coloured symbols represent the two habitat types used in this study: Red = open canopy (within a single tree-fall gap) and Black = under a continuous canopy.*

3.3.2 Individual plant species responses to the presence of mammals

Fifteen dicotyledonous species where considered to have sufficient numbers of seedlings germinating in each seedling plot to allow a seedling ratio to be calculated (Appendix Three, Table 3.2). Eight plant species had significant seedling ratios indicating a positive response to the exclusion of all mammals (i.e. 'Invertebrates access only' exclosure treatment versus 'Possums, rodents and invertebrates access' exclosure treatment), while three species (*Dacrycarpus dacrydioides*, *Griselinia littoralis* and *Pittosporum eugenioides*) showed a significant negative response to the exclusion of all mammals from the seedling plots (Table 3.2).

Table 3.2: *Seedling ratios for 15 plant species to the exclusion of different guilds of mammals under the two habitat types (based on canopy cover). Ratios range from 0 to 1: 0.5 = no difference between exclosure treatments, >0.5 more seedlings when less mammals have access, <0.5 more seedlings when more mammals have access. Significant seedling ratios were determined by bootstrapping of seedling ratios of each experimental unit 1000 times to obtain 95% confidence intervals. Bold indicates a significant difference between exclosure treatments if confidence interval does not cut 0.5.*

Exclosure treatments compared:	Exclusion of all mammals 'Invertebrates access only' versus 'Possums, rodents and invertebrates access'		Exclusion of rodents only 'Invertebrates access only' versus 'Rodent and invertebrates access only'		Exclusion of possums only 'Rodents and invertebrates access only' versus 'Possums, rodents and invertebrates access'	
Habitat type (canopy cover):	Open	Continuous	Open	Continuous	Open	Continuous
Aristotelia serrata	0.58	**0.84**	**0.64**	**0.67**	0.43	0.73
Carpodetus serratus	0.44	0.50	**0.71**	0.43	**0.29**	0.57
Coprosma rotundifolia	0.62	**0.62**	0.64	0.61	0.54	0.78
Coprosma spp.	0.50	**0.54**	0.62	0.44	0.34	**0.60**
Dacrycarpus dacrydioides	**0.34**	**0.28**	**0.34**	**0.43**	0.49	0.35
Fuchsia excorticata	0.52	**0.67**	0.53	0.74	0.41	0.56
Griselinia littoralis	**0.32**	0.41	0.62	0.51	**0.27**	0.44
Hoheria angustifolia	0.45	**0.56**	0.48	0.47	0.46	0.54
Melicytus ramiflorus	0.62	0.76	0.56	**0.70**	0.58	0.57
Pennantia corymbosa	**0.77**	**0.63**	0.55	0.35	0.66	**0.79**
Pittosporum eugenioides	**0.26**	**0.39**	0.39	0.48	0.43	0.41
Plagianthus regius	0.62	0.63	0.59	0.47	0.59	**0.69**
Pseudopanax arboreus	0.42	**0.81**	0.41	0.62	0.56	0.68
Pseudowintera colorata	**0.69**	**0.74**	0.63	0.56	0.53	0.64
Schefflera digitata	0.42	0.52	0.61	0.40	0.26	0.62
All seedlings combined	0.56	**0.74**	0.58	0.53	0.47	**0.70**

Although no significant interactions between exclosure treatment and canopy cover were detected in the nested ANOVAs, apparent interactions between exclosure treatments and habitat type were noticeable for individual plant species. Only four species showed a significant response to the exclusion of mammals under both canopy covers; *Pennantia corymbosa* and *Pseudowintera colorata* had a positive response while *Pittosporum eugenioides* and *Dacrycarpus dacrydioides* had a negative response. The majority of plant species had a significant response in one habitat type only. Under continuous canopy cover, eight of the ten species with a significant response to the exclusion of mammals, had a positive response. While under an open canopy, only two of the five species with a significant response, had a positive response. These results imply that the influence of mammals on seedling establishment is greater under a continuous canopy (Table 3.2).

The seedling ratios investigating specific mammals indicate that the presence of either brushtail possums or rodents affected the seedling establishment of several plant species. The exclusion of rodents increased seedling germination of three plant species, while two species showed a negative response of the exclusion of rodents. The exclusion of brushtail possums also had a similar effect on the seedling establishment, with three and two plant species having a positive and negative response respectively (Table 3.2).

3.3.3 Importance of mammalian post-dispersal seed predation

Seven plant species were used in both the cafeteria experiment (discussed in Chapter Two) and had sufficient seedlings observed in the current study to allow investigation into whether or not the changes in seedling establishment accredited to the presence of mammals were due to these mammals acting as post-dispersal seed predators. Seedling ratio and the proportion of seeds preyed upon by mammalian predators (from the cafeteria experiment) were positively correlated (Figure 3.3; Spearman's rank = 0.8571, $P = 0.024$).

3.4 Discussion

3.4.1 Exotic mammals' influence on overall seedling recruitment

In Chapter Two, I found evidence that exotic mammals are not only post-dispersal seed predators at Peel Forest but are responsible for the majority of predation events observed although this varied among plant species. But a major obstacle in assessing the role of seed predation in plant recruitment is demonstrating the impact of a predator on plant population
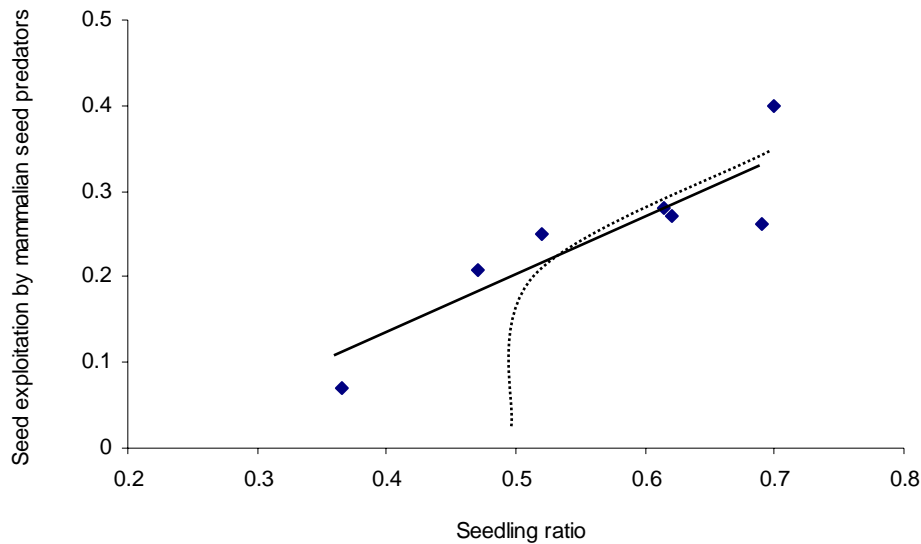
Figure 3.3: *The correlation between the seedling ratio for 'Invertebrates access only' versus 'Possums, rodents and invertebrates' exclosure treatments (see Table 3.2) and seed exploitation (proportion of seed preyed upon) by mammalian post-dispersal seed predators for seven plant species. Seed exploitation is defined as the difference in the proportion of seed preyed upon in the 'Invertebrates access only' and 'Possums, rodents and invertebrates access' exclosure treatments in the cafeteria experiment discussed in Chapter Two. A positive correlation between variables was observed (Spearman's rank = 0.8571, P = 0.024). The solid line represents the line of best fit for the observed correlation, while the dotted line represents the expected relationship if mammalian post-dispersal seed predation was the sole factor influencing seedling establishment at Peel Forest.*

demography or community structure (Crawley 1989). The potential impact of post-dispersal seed predation on plant recruitment is determined in part by whether or not the predator is capable of affecting functional or numerical changes in plant abundance (Hulme and Benkman 2002; Ruscoe et al. 2005). So even though in Chapter Two, I discussed evidence of differential seed predation by exotic mammals, this predation may have little effect on plant recruitment at Peel Forest. To access the importance of mammals as post-dispersal seed predators, I used germination as a measure of realised survival from seed predation. Though this method underestimates true survival from post-dispersal seed predation, it provides comparable results between exclosures treatments within the same experimental unit.

It has been shown that large-seeded species have an advantage over smaller-seeded species during seedling establishment (Turnbull et al. 1999; Dalling and Hubbell 2002; but see Moles and Westoby 2004 for a review) and therefore may dominate and limit species diversity. If mammalian seed predators are to promote plant diversity they must differentially affect these dominant plant species since predation of competitively inferior species will tend to decrease diversity. After three years, while the numbers of seeds germinating were significantly higher in the absence of mammalian seed predators, I found no evidence to support my hypothesis that the presence of mammals significantly altered the overall species richness significantly suggesting that exotic mammals are not a major factor in controlling species richness at Peel Forest.

Canopy gaps create fine-scale variation in light intensity within the forest environment (McAlpine and Drake 2002) and their importance for forest tree regeneration has been recognized globally in both temperate and tropical forests (Coley 1993). Within New Zealand conifer-broadleaf forests, the importance of canopy gaps in tree species regeneration is also well accepted (Ogden 1985; McDonald and Norton 1992; Smale and Kimberley 1993; Stewart 2002). In my study, the canopy cover was a significant factor in both the species richness and number of seeds germinating. The NMDS analysis indicated that the exclosure treatments within an experimental unit are loosely grouped together, implying that the actual experimental unit is a driving factor in seedling recruitment observed not the exclusion of mammals. When selecting sites for use in this experiment, I attempted to utilise sites that appeared to be uniform across experimental units, however subtle differences in either abiotic (e.g. soil, moisture) or biotic (seed source) factors appear to heavily influence seedling establishment within each experimental unit.

But the importance of canopy gaps and the resulting light regime to plant regeneration may be over-estimated in New Zealand as the interaction between mammalian seed predators and abiotic factors are not generally considered by researchers. Although both the nested ANOVA and NMDS analyses indicated that at the broad plant community level, no interaction between habitat and exotic mammals occurred and no significant differences in seed predation across habitat types were observed for the tree species studied in the cafeteria experiment (see Chapter Two), I did find evidence that mammals interacted with habitat to influence seedling establishment for individual plant species in my study. Under an open canopy (i.e. within a single treefall gap), the majority of dicotyledonous species showed no significant response to the presence of mammals but under continuous canopy cover, eight of the 15 species studied showed a positive response in seedling numbers to the removal of exotic mammals (Table 3.2). Consequently, even though the cafeteria experiment implied there was no significant difference in the overall amount of seed preyed upon under the two canopy conditions, the less favourable microsite conditions for germination under an intact continuous canopy allows mammals the opportunity to exacerbate habitat-related patterns of seed mortality and have a noticeable effect on seedling establishment in the natural recruitment experiment. Thus increasing the apparent variation in seedling establishment between canopy habitats that are commonly accredited to the influence of light alone.

3.4.2 Influence of mammalian post-dispersal seed predators on individual plant species

There are two common approaches used to determine the influence of mammals on seed survival and subsequent seed germination. As an indicator of actual or potential changes to seedling dynamics, researchers can focus either on seedling establishment (i.e. the prey) or focus on the diet of mammals (i.e. the predator). Studies focusing on seedling establishment in New Zealand conifer-broadleaf forests exist (e.g. Williams et al. 2000; Wilson et al. 2003; Wilson et al. 2006) and the use of cafeteria experiments to focus on the predator is relatively common overseas (see Crawley 2000 for a review). My study however, is one of the first to attempt to link results of a manipulative experiment focusing on the predators to differences in seedling abundance in the field. This was carried out in an effort to validate the use of cafeteria experiments to predict the long-term effect of post-dispersal seed predation on plant dynamics. Seven plant species allowed this comparison to occur and a strong correlation was observed. This suggests the results of the cafeteria experiment (discussed in Chapter Two) do

flow on to seedling establishment and implies that the level of post-dispersal seed predation by mammals determined by the cafeteria experiment provides an excellent predictor of influence of mammals on seedling establishment.

Several tree species clearly demonstrate this relationship between the cafeteria experiment and the current experiment. *Pennantia corymbosa* and *C. rotundifolia* were observed being heavily preyed upon by mammals in the cafeteria experiment (Chapter Two) and in the current experiment I observed seedlings of these species showing a significant positive response to the exclusion of mammals (Table 3.2).

However, if the observed relationship between the seedling ratios and the cafeteria results is plotted then the relationship appears to be linear (as shown by the solid line in Figure 3.3). But if seedling abundance at Peel Forest was related solely to the level of post-dispersal seed predation, then two types of plant responses would be expected. For plant species experiencing low levels of mammalian seed predation, the exclusion of mammals would have little effect on seedling recruitment, so their seedling ratios might be expected to equal 0.5 (i.e. no difference between exclosure treatments). While plant species with a high proportion of seeds preyed upon by mammals, the exclusion of mammals would benefit the plant species, resulting in a seedling ratio greater than 0.5. Hence if plotted these two responses would form a curved relationship between the seedling ratios and the results of cafeteria experiment would be expected (shown as a dotted line in Figure 3.3).

A possible explanation for this lack of a curve for the plant species with low mammalian seed predation is that exotic mammals have both direct and indirect influences on early plant recruitment. Apart from directly influencing seed survival through selective seed predation, plant species not targeted by mammals may also benefit from competition release from seedlings of other species that are more heavily preyed upon by mammals. I had previously found that *G. littoralis* was not utilised by mammals as much as species with seeds of similar dimensions used in the same experiment (see Chapter Two). And in the current experiment significantly more *G. littoralis* seedlings were observed in the presence of mammals. This positive response to the presence of mammals was also observed for *D. dacrydioides* and *Pittosporum eugenioides,* though these species were not used in the cafeteria experiment (Table 3.2). Even though I removed seedlings from the plots every survey, the time between surveys (6 months) may have been sufficient to allow seedlings to benefit from reduced

seedling competition (see Silvertown and Bullock 2003 for a review). As my focus is post-dispersal seed predation and I used seedlings as a measure of realised survival from post-dispersal seed predation, I'm unable to determine what importance (if any) competition played between the seedlings observed in this study.

While I was able to identify individual plant species responses to the broad presence of mammals, my attempt to differentiate the impact of brushtail possums versus rodents on seedling numbers was less successful as the influence of specific guilds of mammals on seedling establishment is complex. For example, under an open canopy, *Carpodetus serratus* had a significant negative response to the exclusion of brushtail possums while also having a positive response to the exclusion of rodents (Table 3.2). Also despite the fact that in Chapter Two, I found *Melicytus ramiflorus* being heavily preyed upon by invertebrate post-dispersal seed predators (with limited seed lost to mammals) this species showed a significant negative response to the presence of rodents under a continuous canopy in this study (Table 3.2). Therefore, though my study provides an insight into the influence of individual mammal species, a more robust method of separating mammal species is needed to further investigate these relationships.

3.4.3 Consequences of mammalian post-dispersal seed predators

In Chapter Two I discussed evidence that mammals are major post-dispersal seed predators at Peel Forest and in the current study while the presence of mammals significantly reduced overall seedling abundance at Peel Forest, the presence of mammals appeared not to influence species richness across either habitat studied. This study found evidence that the presence of mammals has a significant impact on the early seedling establishment of several tree species. Though some species benefited for the presence of mammals, the majority of species had a negative response and this was more evident under a continuous canopy. And I also found support that the results of the cafeteria experiment focusing on mammalian post-dispersal seed predation could be used as an indicator of the importance of mammals on seedling establishment for individual tree species.

However, the impact of exotic mammalian post-dispersal seed predators on early plant recruitment may be irrelevant by the time of plant maturation (Edwards and Crawley 1999). The extent that seed predators actually affect vegetation diversity will depend on the

importance of seed-based regeneration to the plant community (Hulme 1996). Here I reported that seedlings of *G. littoralis* benefited from the presence of exotic mammals. Stewart & Veblen (1982) also reported abundant *G. littoralis* seedlings in their study of plant regeneration in a Westland forest. However, Stewart & Veblen observed only a few saplings of *G. littoralis* in the same study. *Griselinia littoralis* is known to be a preferred food of many large ungulates (Forsyth et al. 2002; Husheer et al. 2003) and hence these herbivores appear to be more influential than post-dispersal seed predators in determining adult *G. littoralis* abundance. This highlights the problem with extrapolating results from short-term experiments on long-lived species. To fully understand the impact of post-dispersal seed predation on individual plant species regeneration and overall community structure, the shifts in species composition and relative seedling densities observed in this study need to be followed through each stage of plant recruitment until maturity. Unfortunately this has yet to be attempted in any New Zealand landscapes affected by the introduction of mammals.

Chapter Four: Determining the impact of post-dispersal seed predation on seedling establishment of avian-dispersed tree species: the significance of plant recruitment limitations

4.1 Introduction

Since humans colonised New Zealand, the post-dispersal seed predator fauna has changed with the addition of five ground foraging mammalian species and the extinction of several native seed predators (King 1984; Worthy and Holdaway 2002 but see Chapter Two for a summary). In Chapter Two, I presented evidence that exotic mammals are the major post-dispersal seed predators within a conifer-broadleaf forest remnant. Ship rats (*Rattus rattus*) were found to be the main post-dispersal seed predator, while brushtail possums (*Trichosurus vulpecula*), house mice (*Mus musculus*) and remnant native invertebrates were also found to be important post-dispersal seed predators. Mammalian post-dispersal seed predators are responsible for considerable seed mortality in temperate (Webb and Willson 1985; Hulme and Hunt 1999; Hulme and Benkman 2002) and tropical (Holl and Lulow 1997) plant communities and have been shown to exert strong impacts on plant populations dynamics (Crawley 1992; Danell and Bergstrom 2002). I have also discussed evidence that exotic mammalian seed predators, when compared to remnant native seed predators, preyed upon larger seeded plant species, and were responsible for considerable seed losses of several plant species. In Chapter Three, I found that exotic post-dispersal mammalian seed predators have a strong influence on the seed germination of many broadleaf tree species at Peel Forest. However despite my findings, the role of exotic mammals in controlling plant recruitment remains unclear. To fully gauge the impact of mammalian post-dispersal seed predators on plant recruitment, the conditions of seed abundance and habitat disturbance, under which plant populations experience recruitment limitations needs to be considered with relation to post-dispersal seed predators (Anderson 1989).

4.1.1 The importance of recruitment limitation to plant dynamics

The identification of factors that determine recruitment rates of plant species is fundamental for understanding plant population dynamics (Grubb 1977; Harper 1977). Although a combination of abiotic and biotic factors act throughout the life of the plant controlling plant survival, these factors are most influential in the germination and early establishment phases (Clark et al. 1998; Zobel et al. 2000) and can be broadly divided into two types of recruitment

limitations. The failure of seeds to be produced and dispersed in sufficient numbers to saturate all suitable germination sites consequently limiting population growth rates and abundance, is a phenomenon called 'seed limitation' (Eriksson and Ehrlén 1992). However, when sufficient seeds are dispersed, either intense biotic interactions for access to suitable germination sites or unsuitable abiotic conditions for germination may prevent or reduce germination and establishment, slowing population growth and expansion. In this situation the plant population is considered to be experiencing 'microsite limitation' (Crawley 1989; Gross et al. 2005; Zeiter et al. 2006).

The level of seed and microsite limitation experienced by a plant species may be determined by factors such as seed size, light intensity or soil disturbance (Eriksson and Ehrlén 1992). Seed size is perhaps the most important life-history character influencing recruitment success (Turnbull et al. 1999; Henery and Westoby 2001). Large-seeded species are unlikely to be microsite limited (Coomes and Grubb 2003); these species generally develop large seedlings which are relatively resistant to environmental stresses that may limit seedling establishment. (i.e., low light (Foster and Janson 1985; Seiwa and Kikuzawa 1996) and dense litter (Gross 1984; Molofsky and Augspurger 1992; Gillman et al. 2004)). However as the number of seeds a plant can produce for a given amount of energy is inversely related to the mass of the seeds produced (Jakobsson and Eriksson 2000; Henery and Westoby 2001), there is the potential for large-seeded species to experience some level of seed limitation. Alternately, small-seeded species are considered to be superior dispersers and as the parent plant is able to produce more seed the likelihood of these species being seed limited is lower (Foster and Janson 1985; Coomes and Grubb 2003; Moles et al. 2004). But without the energy reserves invested into the seed to ensure large seedlings, small-seeded species are commonly observed to be experiencing microsite limitation (Seiwa and Kikuzawa 1996; Dalling and Hubbell 2002).

The extent to which regeneration of tree species is seed or microsite limited remains poorly understood (Hulme 1996). Crawley (1992) suggests that plants inhabiting forest would be more likely to experience microsite limitation than plants in grasslands, however, both Eriksson and Ehrlén (1992) and Turnbull et al. (200) consider the importance of seed limitation in tree populations has been underestimated. Seed addition experiments have been regularly used to test for recruitment limitations, and recent studies have shown that many communities are unsaturated by plant species, indicating that species richness within these

communities are constrained by a mixture localised processes and the availability of seeds (e.g. Zobel et al. 2000; Foster and Tilman 2003; Zeiter et al. 2006). In New Zealand, the availability of suitable microsites for germination (McDonald and Norton 1992; McAlpine and Drake 2002) and/or seed availability at or around the time of a habitat disturbance event (Stewart and Veblen 1982) are considered to play an important role in forest plant recruitment. However, overall the extent to which tree species within New Zealand conifer-broadleaf forests experience recruitment limitations remains poorly understood.

4.1.2 Interaction with mammalian post-dispersal seed predation

Understanding the impact of post-dispersal seed predators on individual plant species depends on both seed density and the environmental conditions necessary for successful germination (Grubb 1977; Anderson 1989). Post-dispersal seed predators may exacerbate or counteract the impact of recruitment limitations. When conditions are favourable for germination but seed supply is low, post-dispersal seed predators can have a significant impact on early plant recruitment further increasing the level of seed limitation experienced by the plant species (Anderson 1989; Louda and Potvin 1995). This occurs because at low seed densities there is no opportunity for compensatory reductions in other mortality factors (Crawley 1992). If plant recruitment is limited by factors other than seed availability (i.e. microsite limited) then seed losses to predators may have no impact, as the seeds may never have contributed to the population as eventually other factors would have lead to the death of the seed (Edwards and Crawley 1999; Turnbull et al. 2000).

I have previously discussed evidence that mammalian post-dispersal seed predators present in New Zealand are selective in the size of seed they prey upon (see Chapter Two). Combine this mammalian preference for larger seeds with overseas research demonstrating a link between seed size and seed limitation (i.e. Coomes and Grubb 2003; Moles and Westoby 2004), then in New Zealand conifer-broadleaf forests exotic mammals may be increasing seed limitation and further restricting plant recruitment of many species. Conversely mammalian post-dispersal seed predators are unlikely to influence seedling establishment of small seeded species as recruitment of these plant species is likely to be microsite limited rather than seed limited.

This preliminary study is an extension of earlier work I performed on early plant recruitment within a conifer-broadleaf forest remnant (see Chapter Three). For this experiment I manipulated seed densities of four broadleaf tree species to investigate the interaction of recruitment limitation and post-dispersal mammalian seed predators and I tested the following hypotheses:

1. The type of recruitment limitation a plant species experiences will be correlated with its seed size; with large seeded species experiencing seed limitation while small seeded species will experience microsite limitation; and

2. Mammalian post-dispersal seed predators will further reduce early plant recruitment of seed limited plant species while having no effect on species experiencing microsite limitation.

To address these hypotheses, I combined seed additions and predator exclosures to create experimental patches which were monitored for 13 months. Four tree species were selected represented a range of seed size. To investigate the importance of microsite limitation the experimental patches were established under two levels of canopy cover. Mesh cages were used to exclude mammalian post-dispersal seed predators from half of these plots.

4.2 Material and Methods

4.2.1 Study area

This study was conducted at Mount Peel Forest Park Scenic Reserve which lies along the southern edge of the Rangitata River in South Canterbury, New Zealand (43°54'S, 171°15E). Peel Forest has a mild, moist temperate climate (Molloy 1983), with an annual precipitation of 1160mm (Massam 1986). The experiment was carried out in a 60-hectare section of conifer-broadleaf forest spanning an altitudinal range of 300 to 360 metres. Most of the study area was selectively logged for conifer species between 1860-1900 (Kerr 1972; Massam 1986), resulting in a regenerating secondary forest dominated by broadleaf species with a few emergent conifers. A dense shrub tier is present and ferns and graminoids dominate the ground layer (see Chapter One for a full description of the study area). An earlier investigation indicated that house mice, ship rats and the brushtail possums were involved in post-dispersal seed predation events at Peel Forest (see Chapter Two).

4.2.2 Plant species studied

In this preliminary investigation focusing on the relationships between seed size, recruitment limitations, and mammalian post-dispersal seed predators, I selected four plant species: *Coprosma rotundifolia, Pennantia corymbosa, Pseudopanax arboreus* and *Schefflera digitata* (Table 4.1). These species represented the range of seed sizes present at Peel Forest and were earlier determined to experience varying levels of mammalian post-dispersal seed predation (see Chapter Two). By using plant species resident at Peel Forest, it is assumed that their regeneration niches exist within the study site and that abiotic conditions such as substrate and microclimate do not present a fundamental barrier to seedling recruitment. All seed used in this study was collected locally at Peel Forest from at least eight individuals. To resemble natural 'avian-dispersed' seeds, I removed all fleshy tissues from around the seeds. Seeds were stored at 4°C for up to 4 weeks before the experiment began while sufficient quantity of seed for the experiment was collected.

Table 4.1: *Level of mammalian post-dispersal seed predation, mean seed mass, estimated seedfall density and percentage germination in laboratory of the four species used in the seed addition experiment. Level of mammalian post-dispersal seed predation is based on a cafeteria experiment described in Chapter Two. Seed mass was calculated by weighing a sample of 20 seeds per species. Natural seed density for each species per year was estimated from seedfall data collected over a two year period prior the establishment of the experiment. Germination was determined for a random sample of 100 individuals germinated under a 12:12 hr light : dark photo-period and maintained at 20°C with 20% relative humidity over 5 months.*

Species	Level of mammalian post-dispersal seed predation	Mean seed mass (mg)	Estimated natural seed density (m^2)	Germination (%)
Schefflera digitata	Low	0.83	400	70
Pseudopanax arboreus	Medium	8.25	20	76
Coprosma rotundifolia	Medium	9.00	40	83
Pennantia corymbosa	High	18.30	10	14

4.2.3 Germination in the laboratory

Prior to the field component of this study, I determined the viability of the seed collected by germinating a random sample of 100 seeds per plant species within a controlled environment. Seeds were initially sorted under a microscope to exclude empty, damaged or diseased individuals. Immediately prior to the germination experiment the seeds were soaked in tap water for 24 hours. Seeds were germinated on two layers of filter paper, saturated with water, in glass petri dishes. Each dish contained 20 seeds of one species; five dishes per species. Dishes were placed in a controlled temperature room at Lincoln University with 12:12 hr

light:dark photo-period and maintained at 20°C with 20% relative humidity. Germinated seeds were counted and removed from the dishes for five months. Germination was considered to have occurred for *S. digitata* when splitting of the seed coat was observed and by radicale emergence for the other larger-seeded species. Seeds that rotted during the experiment period were considered to be nonviable and were removed.

4.2.4 Field experiment setup

To determine the type of recruitment limitation experienced by the studied plant species, I conducted a seed addition experiment at Peel Forest, based on the recommendations made by Turnbull et al. (2000) in their review of recruitment limitation experiments. The experiment was based on a combination of mammalian seed predator exclosure treatments, seed densities and habitat types based on canopy cover. The experiment was established in May 2002, with seedling plots re-surveyed in May 2003. To assess the importance of canopy disturbance to recruitment limitation, 40 experimental units was located under one of two habitat types: 1) open canopy (within a single tree fall gap) and 2) under continuous canopy (at least 20 metres from the nearest treefall gap). To locate the open canopy units, all single treefall gaps within the study area were located, and then I randomly selected a subset of 20 for my experiment. With all treefall gaps located, the 20 continuous canopy experimental units were randomly allocated within areas of the study area known not to contain canopy gaps. An effort was made to ensure that all experimental units classified as the same canopy condition were in similar light conditions. However, the distance to the nearest seed source was not managed. One studied plant species was randomly allocated to each experimental unit resulting in five experimental units per plant species per habitat type. Within each experimental unit six seedling plots (0.3 × 0.3m; permanently marked with two corner pegs) were randomly placed within a 4 × 4m area. These seedling plots were a factorial combination of two mammalian seed predator exclosure treatments and three seed densities.

To determine if a studied plant species was experiencing seed limitation at Peel Forest, three levels of seed density were used in this experiment: 1) no seed addition (plots contained the estimated natural seed density only; Table 4.1), 2) 5× natural (seed added until the total seed present equated to 5× the estimated natural level) and 3) 10× natural (seed added until the total seed present equated to 10× the estimated natural level). Natural seed densities for each species were estimated from two years of seedfall data obtained prior to the establishment of

the experiment (Table 4.1). Fourteen pairs of seed traps were placed under both open and continuous canopies throughout the study area. Each month these seed traps were cleared and the contents sorted. The seed traps were based on the methodology used by Moles and Drake in 1999 and sampled an area equating to $0.04m^2$. The field experiment started in May 2002 coinciding with the fruiting of the studied plant species and when naturally dispersed seeds would be available to the mammalian post-dispersal seed predators ensuring that the seed added were not foreign to the seed predators. I purposely added seed densities high enough to force saturation. This overcomes any seed limitation that may be present and allows the importance of microsites to appear. The seedling plots were resurveyed for seedlings in May 2003.

To determine if mammalian post-dispersal seed predators would further reduce recruitment of a plant species experiencing seed limitation while having no effect on species experiencing microsite limitation, I excluded mammalian species from half of the seedling plots by using wire exclosures. The two exclosures treatments were:

(1) '*Possums, rodents and invertebrates access':* An open treatment, with no mammalian exclusion method used. Seeds were available to all mammalian and invertebrate predators.

(3) '*Invertebrates access only':* a 12 mm wire mesh cage ($30 \times 30 \times 20$ cm) buried 10 cm deep. Cages included a mesh roof to prevent climbing predators entering and consuming seeds. All mammals were excluded; seeds were only available to invertebrates.

The wire mesh diameter used to exclude mammalian predators was based on research at the Karori Wildlife Sanctuary, Wellington (Hitchmough 1994).

4.2.5 Data analysis

All analyses were performed using the statistical analysis package R version 1.9.1 (R Development Core Team 2004).

Each plant species was analysed separately by fitting individual Generalised Linear Models (GLMs). My response variable was the 'proportion of seedlings observed' after 13 months and was modelled using a binomial distribution and logit link function (Crawley 2002). The proportion was derived from the number of seedlings observed within each seedling plot after 13 months with respect to the density of seed within each seedling plot at the beginning of the experiment. By using the 'proportion of seedlings observed' rather than the actual number of

seedlings observed, it ensures that the natural density plots (i.e. low seed density) do not have undue influence on the analysis (Crawley 2002). To identify factors that might explain variation in the proportion of seedlings observed, I included habitat type (open and continuous canopy), mammalian exclosure treatment ('Possums, rodents and invertebrates access' and 'Invertebrates access only'), and seed density (natural, 5× natural and 10× natural) as explanatory variables. An initial investigation of the raw data indicated low numbers of seedlings for three of the four studied plant species (*S. digitata*, *Pseudopanax arboreus* and *Pennantia corymbosa*; Table 4.2), limiting the power of the analysis. As a result only the main explanatory variables were included in the GLMs. However as numerous *C. rotundifolia* seedlings were observed, all possible interactions were also included as explanatory variables in the GLM. Experimental unit was included as an explanatory variable but due to the lack of replication it was not included in any interactions. Significance testing was conducted using Chi-square tests but as the models for *Pseudopanax arboreus* and *C. rotundifolia* were over-dispersed, significance testing was performed using F-tests.

Table 4.2: *Number of seedling plots observed with seedlings 13 months after the addition of seed. Species are ordered by increasing seed mass. Percentages represent the percentage of total seedling plots for each plant species. Habitat type, seed density and mammalian exclosure treatments have been pooled. Each seedling plot was 0.3 ×0.3m. n= 60 seedling plots per plant species.*

Species	Number of seedling plots observed with seedlings		
	6 or more seedlings	**1-5 seedlings**	**No seedlings**
Schefflera digitata	0 (0%)	20 (33%)	40 (66%)
Pseudopanax arboreus	0 (0%)	29 (48%)	31 (52%)
Coprosma rotundifolia	31 (52%)	24 (40%)	5 (8%)
Pennantia corymbosa	0 (0%)	13 (22%)	47 (78%)

4.3 Results

4.3.1 Germination in the laboratory

After five months, over 70% of *C. rotundifolia, Pseudopanax arboreus* and *S. digitata* seeds and 14% of *Pennantia corymbosa* had successfully germinated (Table 4.1). The majority (62%) of the *Pennantia corymbosa* seeds rotted within the first two-months of the germination experiment beginning.

4.3.2 Determination of recruitment limitation

Coprosma rotundifolia was the only species to be observed with a range of seedling densities and had the highest average number of seedlings per seedling density treatment (Table 4.2; Appendix Four). Low seedling numbers were observed for *S. digitata, Pseudopanax arboreus* and *Pennantia corymbosa* across all seed densities with an average of less than one seedling per plot (Appendix Four).

Seed density was a significant explanatory variable for the *Pseudopanax arboreus* model (Table 4.3). While this implies some level of seed limitation, only a small increase in seedlings with respect to seed addition was observed (Figure 4.1) suggesting the biological significance of this increase for *Pseudopanax arboreus* may be minimal. The actual numbers of *C. rotundifolia* seedlings observed within a seedling plot were positively correlated to seed addition, indicating this species experiences considerable seed limitation (Figure 4.1), but seed density was not a significant variable in the GLM (Table 4.3). Habitat type was also found to be a significant explanatory variable for *C. rotundifolia* (Table 4.3). Under an intact continuous canopy, lower numbers of seedlings were observed than in the corresponding seedlings plots under an open canopy (Appendix Four). As seeds were sown in densities high enough to force saturation (i.e. 10× natural) the lack of a response to seed addition by *S. digitata* suggests this species experiences microsite limitation at Peel Forest (Figure 4.1).

4.3.3 Influence of mammalian post-dispersal seed predators

The GLMs indicate that the exclusion of mammals was a significant explanatory variable in the *C. rotundifolia* model only (Table 4.3); more seedlings were observed in the 'Invertebrates access only' exclosure treatment than the corresponding 'Possums, rodents and invertebrates access' exclosure treatment (Figure 4.1). A slight increase in seedlings in the 'Invertebrates access only' exclosure treatments for *Pseudopanax arboreus* and *Pennantia corymbosa* was also apparent, while no consistent trend between the two mammalian exclosure treatments were observed for *S. digitata* (Figure 4.1).

A) *Schefflera digitata*

B) *Pseudopanax arboreus*

C) *Coprosma rotundifolia*

D) Pennantia corymbosa

Seed addition treatment
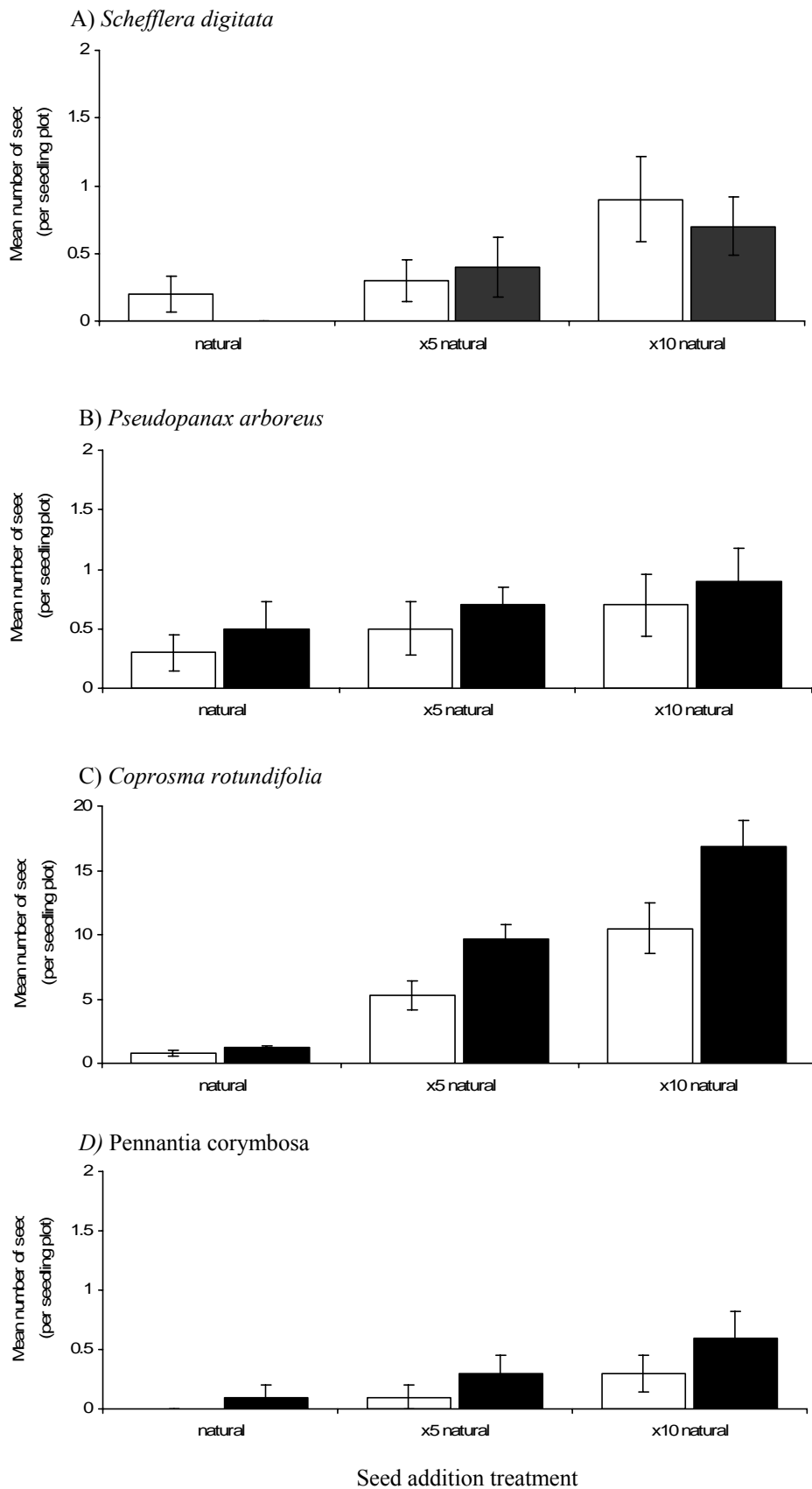
Figure 4.1: *Comparisons between the mammalian exclosure treatments for the mean number of seedlings observed within the different seed addition treatments for the four plant species. Plant species have been ordered by increasing seed mass. Different shaded bars represent the different exclosure treatments: White bars = 'Possums, rodents and invertebrates access' and black bars = 'Invertebrate access only' exclosure treatment. Habitat type has been pooled. N= 10 per exclosure treatment per seed addition treatment. Error bars = 1 std error.*

Table 4.3: *Results of the generalised linear models (GLMs) examining the influence of explanatory variables on the 'proportion of seedlings observed' for the four plant species used in the seed addition experiment. The 'Proportion of seedlings observed' was derived from the number of seedlings observed after 13 months with respect to the density of seed placed within each seedling plot at the beginning of the experiment. Due to a lack of seedlings, only the main explanatory variables were included in the GLMs for* Schefflera digitata, Pseudopanax arboreus *and* Pennantia corymbosa. *The explanatory variables are: EU = Experimental unit, H = Habitat type, E = mammal exclusion and S = sown seed density. Due to the lack of replication experimental unit was not used in any interactions. Significance testing was performed by Chi-square tests. However as the models for* Coprosma rotundifolia *and* Pseudopanax arboreus *were over-dispersed, significance testing was performed by F-tests. Residual degrees of freedom for* Coprosma rotundifolia *= 44 and the other three plants species = 51. Significant (P<0.05) explanatory variables are in bold*

Explanatory variable	*Coprosma rotundifolia*				*Schefflera digitata*		*Pseudopanax arboreus*		*Pennantia corymbosa*	
	D.f.	F	P	D.f.	Chisq	P	F	P	Chisq	P
EU	4	**2.66**	**0.045**	4	0.81	0.938	0.56	0.689	0.32	0.988
H	1	**26.32**	**<0.001**	1	1.99	0.158	1.00	0.322	1.2	0.274
E	1	**27.27**	**<0.001**	1	0.36	0.548	1.00	0.322	2.74	0.098
S	2	1.49	0.237	2	0.21	0.899	**5.49**	**0.007**	0.05	0.977
S × E	2	0.45	0.638							
E × H	1	1.12	0.295							
S × H	2	1.52	0.231							
S × H × E	2	0.18	0.839							

4.4 Discussion

4.4.1 Determination of recruitment limitations at Peel Forest

The question of whether or not plant species are experiencing recruitment limitations is crucial in determining the importance of mammalian post-dispersal seed predators to plant population dynamics. Though this preliminary study resulted in low numbers of seedlings, my experiment using a combination of seed addition, plot manipulations and predator exclusion still highlighted that at Peel Forest, several tree species are experiencing a range of recruitment limitations and exotic mammalian post-dispersal seed predators are capable of further reducing seedling establishment of tree species which are seed limited.

I had limited success germinating *Pennantia corymbosa* in the laboratory; the majority of seeds rotting within a short period. I also observed poor seedling establishment in the field experiment. A previous study on the germination of *Pennantia corymbosa* reported an average 82% of seeds germinated within 6 months (Burrows 1995). Burrows noted that *Pennantia corymbosa* germination was "slow to begin" compared to other tree species, but unlike my experiment, he made no observations of seeds rotting. In Chapter Three I reported considerable numbers of *Pennantia corymbosa* seedlings were observed at Peel Forest. This previous personal observation combined with Burrow's findings, suggests that the lack of germination in this current experiment is atypical and that the seed used may not have been viable. Therefore it would be inappropriate to draw conclusions for this species so further discussion of *Pennantia corymbosa* is limited.

Although my field experiment resulted in low numbers of seedlings, I did find some support for my hypothesis that seed limitation at Peel Forest is positively correlated with seed size. While the largest-seeded species studied, *Pennantia corymbosa* did not provide usable results, the smallest seeded species, *S. digitata*, is clearly microsite limited. *Schefflera digitata* had only a small increase with the addition of seed and when reviewed with respect to the amount of seed added to achieve this increase in seedling establishment (i.e. 3600 seeds per square metre for the 10× natural seed density treatment) *S. digitata* appears to be experiencing substantial microsite limitation at Peel Forest. My findings for this small-seeded species are similar to many overseas studies. Both Seiwa & Kikuzawa (1996) and Dalling & Hubbell (2002) concluded that small-seeded species are regularly microsite limited.

Both *C. rotundifolia* and *Pseudopanax arboreus* have seeds of a similar size and both species showed an increase in seedling establishment with the addition of seed. By adding seed, more available germination sites were potentially being occupied indicating these species are experiencing some level of seed limitation. Though *Pseudopanax arboreus* experienced statistical seed limitation, only the addition of *C. rotundifolia* seed resulted in seedling establishment sufficient to change the population recruitment at Peel Forest of this species (i.e. biological seed limitation). Variation in the level of seed limitation experienced by tree species with similar seed sizes is not unusual. Eriksson and Ehrlén (1992) and Eriksson and Fröborg (1996) report a similar variation in levels of seed limitation in several populations of boreal forest species overseas. Although *C. rotundifolia* appears seed limited, canopy cover also appears to influence seed germination. Disruptions of the canopy such as isolated single tree fall (as in this study) or loss of large tracts of forest resulting in canopy gaps provide a stark contrast to the forest understorey (Schupp 1988; Gillman et al. 2004), and are considered important for successful seed germination of many New Zealand tree species (McAlpine and Drake 2002; Stewart 2002), but the importance of habitat characteristics may change over time and further research is required. Edwards and Crawley (1999) suggested the differences they observed between seasons on seedling recruitment arose because the study plant species was seed limited in autumn but microsite limited in spring.

4.4.2 Influence of mammalian post-dispersal seed predators

By combining a seed addition experiment with seed predator exclosures, I was interested to investigate if the impact of mammalian post-dispersal seed predators on early plant recruitment was dependent on the type of recruitment limitation the plant species was experiencing. *Coprosma rotundifolia* is known to be a food source of exotic mammals (see Chapter Two), and in the current experiment I found the presence of mammals combined with the seed limitation experienced by *C. rotundifolia* to further reduce early seedling establishment, particularly at higher seed densities (Figure 4.1). This interaction highlights the importance of simultaneously focusing on several factors known to be influential in plant recruitment. If mammalian post-dispersal seed predation was not considered then in presence of mammals (i.e. the norm) a simpler seed addition experiment would have under-estimated the relative importance of seed limitation for *C. rotundifolia*.

Previously, I have observed that *S. digitata* was preyed upon by mammalian post-dispersal seed predators (see Chapter Two) but the lack of a significant response in the number of seedlings observed with respect to the exclusion of mammals in this experiment does not mean that exotic mammals did not prey upon this plant species. As *S. digitata* was determined to be microsite limited, the lack of a noticeable effect to the exclusion of mammals is not unexpected. Mammals may have killed a proportion of the seeds sown, but as germination and subsequent seedling establishment of *S. digitata* is controlled by other external factors, the seeds preyed upon by mammals were unlikely to have germinated, resulting in the mammals having a limited impact.

4.4.3 Consequences to forest tree recruitment at Peel Forest

The combination of the recruitment limitations experienced by a plant species and differential seed predation by exotic mammals may have two main effects to the plant community at Peel Forest. First, if recruitment is seed-limited then further reductions in seed survival may result in a shift in plant regeneration at the community level. This would not be dramatic but over several generations of a plant species, changes in relative seedling recruitment may lead to a reduction in adult density and/or a shift in a species' relative abundance within the community. Campbell and Atkinson (2002) hypothesised that this type of slow change to plant community structure has occurred on several islands of New Zealand since the arrival of mammals approximately 800 years ago and a similar situation can be predicted for mainland New Zealand. Second, at the population level, small inter-individual differences in seed survival may have a large influence on future generations of a plant species, especially if seed predators select certain traits which lead to an increase, decrease or exclusion of certain genes from the population (Anderson 1989; Chapman and Chapman 2002). However, as discussed in Chapter Three, the impact of mammalian post-dispersal seed predation at the seedling establishment stage may disappear by the time of plant maturation. For annual plants, post-dispersal seed predators have the same effect as a lower seed output from the parent plant and act at a critical stage of regeneration (i.e. the only link between parent and offspring), hence post-dispersal seed predators have a direct affect on the next generation (Hulme 1996). But is it possible to make generalisations regarding the interactions between recruitment limitations and mammalian post-dispersal seed predators on regeneration of long-lived species? Though providing a insight to the dynamics of early seedling establishment, short-term studies (such as this one) are unlikely to identify the extent to which recruitment limitations and

mammalian post-dispersal seed predators influence past or future patterns in regeneration of long-lived plants. This has been experimentally highlighted in Cummings and Alexander's (2002) study of sunflowers. In their study, Cummings and Alexander reported that though there was an initial increase in seedlings after seed density manipulation, there was no difference in the number of breeding adults. To fully understand the impact of post-dispersal seed predation on individual plant species recruitment and overall plant community structure, the shifts in species composition and relative seedling densities need to be followed through each stage of plant recruitment until maturity. Unfortunately this has yet to be attempted in any New Zealand landscapes affected by the introduction of mammals.

To conclude, though only a preliminary study of four tree species, I found some support that seed limitation is positively related to increasing seed size and though exotic mammalian post-dispersal seed predators can further decrease plant recruitment of plant species experiencing seed limitation, the influence of mammals on determining plant recruitment is minimal for plant species experiencing microsite limitation. I have previously discussed that rates of mammalian post-dispersal seed predation differs among plant species in the same community (see Chapter Two), and seed predation can lead to differences in seedling richness and density at a community level (see Chapter Three). When combined with my observations from this preliminary experiment, it is evident that mammalian post-dispersal seed predators play an important role in determining landscape abundance and distribution of many plants species at Peel Forest.

Chapter Five: Synthesis

Despite extensive international acceptance of the critical role played by mammalian post-dispersal seed predation in many plant communities, in New Zealand we have limited knowledge of these predators' influence on plant recruitment in our forests. The effect of small mammals on early plant establishment is often overlooked as it is hard to separate their effects from the impacts of large ungulates (Veblen and Stewart 1982). Despite this the consequence of multiple mammals need to be incorporated as they impact on different phases of the plant lifecycle. The principal objective of my thesis was to determine the relative importance of exotic mammals as post-dispersal seed predators in New Zealand conifer-broadleaf forests. To achieve this I conducted five main experiments and in this chapter I will summarise the findings of my experiments with respect to the four specific objectives discussed in Chapter One, discuss limitations and possible improvements to my research as well as discussing additional questions that have arisen from this research.

5.1 Exotic mammalians as post-dispersal seed predators

My first specific objective was to determine the overall level of post-dispersal seed predation in a conifer-broadleaf forest and determine the relative proportion of seed lost to exotic mammalian predators. The time-lapse video and cafeteria experiments provided clear evidence that exotic mammals are not only post-dispersal seed predators at Peel Forest but are responsible for the majority of predation events observed in these experiments. This confirms previous speculation that exotic mammals are post-dispersal seed predators in New Zealand (e.g. Campbell 1978; Fitzgerald et al. 1996). Ship rats (*Rattus rattus*) were the dominant exotic mammalian post-dispersal seed predators observed in all experiments conducted as part of my thesis. Brushtail possums (*Trichosurus vulpecula*) and house mice (*Mus musculus*) were also found to be important post-dispersal seed predators for the several tree species.

5.2 Factors influencing mammalian seed predation rates

My second and third objectives were to determine how variations in habitat and seed characteristics affect the level of mammalian post-dispersal seed predation. In the cafeteria experiment, I found that exotic mammals and remnant native invertebrates foraged in similar habitats. My results indicate that while habitat structure appeared to have little influence on encounter rates of depots for all mammalian seed predators observed, the vegetation structure

did affect seed exploitation (i.e. the proportion of seed preyed upon once a depot had been encountered). Overall the amount of seed exploited was positively related to the ground-layer vegetation and the amount of leaf litter present.

As part of the cafeteria experiment I found evidence indicating that exotic mammals target larger-seeded species than remnant native seed predators. Native invertebrates were found to be primarily post-dispersal predators of the smallest seeded plant species studied, but the divergence between the 'Invertebrates access only' exclosure treatment and the two exclosure treatments allowing mammals access indicate that post-dispersal seed predation by mammalian species were positively related to seed size. Variation in mammalian seed exploitation between seeds of a similar size was also observed suggesting that seed size is only one of a number of variables underlying mammalian seed preferences. Other physical characteristics and secondary compounds may influence seed exploitation levels. Though discussed further in Chapter Two, seeds often receive a greater investment in anti-herbivore defence than vegetative tissue (Janzen 1971). Seeds may be poisonous or have a large amount of secondary compounds that either impair digestibility or just make them unpalatable (Campbell 1978; Kollmann et al. 1998; Hulme and Benkman 2002). How effective these defences are against exotic mammalian post-dispersal seed predators is unknown and further research is required to fully answer their importance in determining rates of post-dispersal seed predation. But it is unlikely there has been sufficient time for plants to have adapted their seed defences to become effective against any new seed predation pressure from exotic mammals (Ruscoe et al. 2005).

Both exotic mammals and remnant native invertebrate post-dispersal seed predators appear to respond in similar ways to changes in seed density. In Chapter Two I discuss evidence that for both types of predators, the probability of a seed encounter was positively related to seed density. But there was no apparent increase in the proportion of seed preyed upon was observed for any exclosure treatments. This lack of significant relationships between the proportion of seed preyed upon and the initial seed density suggests that all predator types (both native and exotic) consumed a constant proportion of seeds irrespective of the seed density, a density-independent response and were treating each depot as a single prey clump regardless of initial seed density.

5.3 Importance of exotic mammalian post-dispersal seed predation to early seedling establishment

The final objective of my thesis was to determine the flow-on effects of mammalian post-dispersal seed predation on early seedling establishment. I have demonstrated that exotic mammals are not only post-dispersal seed predators but are responsible for the majority of predation events observed. The differences observed between plant species and variation in predator behaviour implies selection, which may have important ecological flow on effects. However, a major obstacle in assessing the role of post-dispersal seed predation in plant recruitment is demonstrating the impact of a predator on plant population demography or community structure (Crawley 1989). The potential impact of post-dispersal seed predation on plant recruitment is determined in part by whether or not the predator is capable of affecting functional or numerical changes in plant abundance (Hulme and Benkman 2002; Ruscoe et al. 2005). So even though I discussed evidence of differential seed predation by exotic mammals, this predation may have little affect on the overall seedling diversity and plant abundance at Peel Forest.

Herbivory often effects plant species richness with herbivores regularly associated with increased species diversity (Olff and Ritchie 1998). But if mammalian post-dispersal seed predators are to promote plant diversity they must target the dominant plant species, since predation of competitively inferior species will tend to decrease diversity. The role of mammalian post-dispersal seed predators in regulating species richness at Peel Forest remains unclear, as my findings reported in Chapter Three gave conflicting results. Over three years, I observed significantly higher seed germination at Peel Forest in the absence of mammalian seed predators, but I found no evidence to support my hypothesis that the presence of mammals significantly altered the overall species richness suggesting that exotic mammals are not a major factor in controlling species richness at Peel Forest. Though at a broad community level, post-dispersal seed predation by exotic mammals may not be a significant factor in determining overall community structure at Peel Forest, mammalian post-dispersal seed predators appear to play critical roles in determining early plant recruitment of individual plant species. Mammalian post-dispersal seed predators may either act alone as the dominant factor, or they may either counteract or exacerbate other factors influencing seedling recruitment of individual plant species. Campbell et al. (2002) believed that kiore depressed recruitment of 11 out of 17 plant species studied, whilst Allen et al. (1994) also found several

plant species increased once Norway rats were eradicated from Breaksea Island. At Peel forest, though several tree species were observed benefiting from the presence of mammals, most plant species showed either no or a negative response to the presence of exotic mammals (see Chapter Three).

Mammalian post-dispersal seed predation may contribute to the maintenance of species diversity if the spatial distribution of establishment sites is uncorrelated across plant species (Rey et al. 2002). In habitats with high variation in seed predation intensity, establishment sites may allow the survival of preferred species (Schupp 1988; Meiners and Stiles 1997). Within New Zealand conifer-broadleaf forests, the importance of canopy gaps in tree species regeneration is also well accepted (Ogden 1985; McDonald and Norton 1992; Smale and Kimberley 1993; Stewart 2002). However, although canopy gaps and the resulting light regime is important to plant regeneration, it may be over-estimated, as the interaction between mammalian post-dispersal seed predators and abiotic factors are not generally considered by researchers. I found that the interaction between canopy cover and exotic mammalian seed predation is complex. Although I did not find evidence of an interaction between the presence of mammals and habitat type with respect to the overall community structure, I found indications that mammals interacted with habitat to influence seedling establishment for several individual plant species. Under a continuous canopy cover, many plant species studied showed a negative response in seedling numbers to the presence of exotic mammals. The less favourable microsite conditions for germination under an intact continuous canopy allow mammals the opportunity to exacerbate habitat-related patterns of seed mortality and have a noticeable effect on seedling establishment in the natural recruitment experiment. Thus increasing the apparent variation in seedling establishment between canopy habitats that are commonly accredited to the influence of light alone.

To fully gauge the impact that mammalian post-dispersal seed predators have on plant recruitment, the conditions of seed abundance and habitat disturbance, under which plant populations experience recruitment limitations needs to be considered in relation to post-dispersal seed predators (Anderson 1989). My seed addition experiment found some support for the hypothesis that seed limitation at Peel Forest is positively correlated with seed size. The smallest seeded species, *S. digitata*, is clearly microsite limited, while the two larger seeded species (*Coprosma rotundifolia* and *Pseudopanax arboreus*) were found to be experiencing variable levels of seed limitation at Peel Forest. I also found evidence that while

exotic mammalian post-dispersal seed predators can further reduce recruitment of plant species experiencing seed limitation, the impact of mammalian post-dispersal seed predators on plant species experiencing microsite limitation is minimal.

5.4 How similar are exotic mammals to extinct native avian seed predators?

Exotic mammals are now the only post-dispersal seed predators for many plant species at Peel forest, but are mammals exerting a new pressure or have they simply replaced pre-existing avian seed predators? In pre-human New Zealand forests it is unlikely that a valuable food source such as seeds would not have been fully utilized by native fauna including many avian species now extinct at Peel Forest. Red crown parakeet (*Cyanoramphus novaezelandiae novaezelandiae*), weka (*Gallirallus australis*), New Zealand quail (*Coturnix novaezealandiae*) and kiwi (*Apteryx* spp.) all foraged on the forest floor similar to the exotic mammals in this study (Reid et al. 1982; Clout and Hay 1989; Heather and Robertson 1996). While other avian species (such as Finch's duck (*Euroyanas finchsi*) and moa (*Dinornis* spp.)) may have also been post-dispersal seed predators (Duncan and Holdaway 1989; Worthy and Holdaway 2002). See Chapter Two for a full summary of avian species that may have been post-dispersal seed predators. Though differences with respect to population densities, breeding strategies and foraging behaviour would exist, the biggest difference between extinct avian seed predators and the newer exotic mammals is their digestion systems. Avian seed predators have no teeth and simpler stomachs (often incorporating gizzard stones) compared to mammals which have a more complex digestive system (Cooper et al. 1993). Mammals possess a prehensile tongue and teeth as well as grasping digits, which improves the ability of mammals to effectively grasp and process dispersed seeds located on the forest floor as a food source than avian species.

With large quantities of fallen fruit and seeds removed from the forest floor, moa and other ground foraging avian species may have been important secondary dispersal agents in pre-human New Zealand forest ecosystems. Though not strictly post-dispersal seed predation, the process of secondary seed dispersal is often a result of an attempted predation event. Due to their simpler digestion system, a proportion of seeds eaten would have survived digestion and be further dispersed (Burrows 1980). Exotic mammals may also play a role in New Zealand as secondary dispersal agents. While house mice have been shown to destroy all seed eaten (Williams et al. 2000), a percentage of seeds swallowed whole by larger rodents and brushtail

possums remain viable (Howe and Smallwood 1982; Dungan et al. 2002). Seeds may also be secondary dispersed by mammals while being transported to shelter before being consumed (Campbell et al. 1984).

Previous researchers have speculated that exotic mammals have simply replaced extinct avian post-dispersal seed predators (e.g. Campbell 1978; Ramsay 1978), and though exotic mammals potentially share many traits with extinct avian species, no two seed feeding species will have the same effect on plant recruitment. Any major lasting change in the distribution and diversity of predators will usually have profound effects on all other organisms in the surrounding ecosystem (Caughley 1988).

5.5 Implication for the maintenance of tree species communities

Post-dispersal seed predation by exotic mammals is only one factor of many affecting plant recruitment in New Zealand forests. Nevertheless, the generalist feeding habits of mammals and the limited ability of plants either to compensate for or to respond to post-dispersal seed losses suggests that post-dispersal seed predation can have a considerable impact on plant populations (Hulme 1998; Blaney and Kotanen 2001).

Apart from the immediate changes in seedling composition, as part of my thesis I have demonstrated that exotic mammals have the potential to affect plant evolution if differential predation results in variation to some heritable plant traits (Anderson 1989; Chapman and Chapman 2002). Seed size, seed chemistry and fruit structure are commonly heritable traits and may be affected by differential seed predation (Hulme and Benkman 2002). While any changes in the gene flow within the tree species populations of New Zealand may have been minimal, it is likely that changes in the type of predators and their selection of seed would have resulted in changes in the seedling composition at Peel Forest.

My study has proven that exotic mammals are now the dominant post-dispersal seed predators at Peel Forest, the amount of seed preyed upon varies among plant species, and post-dispersal seed predation by mammalian species can lead to differences in seedling richness and abundance. I have also proved that the influence of exotic mammals on seedling establishment is linked to habitat structure and recruitment limitations. When combined these observations suggest that exotic mammalian post-dispersal seed predators play an important

role in determining landscape abundance and distribution of many plant species at Peel Forest.

5.5 Limitations and improvements to thesis

As with all research, the power of hindsight allows clear assessment of the limitations of the work. Many limitations have already been discussed in the previous chapters but I would like to discuss several additional limitations of my research that should be acknowledged.

One major limitation is the lack of knowledge of the actual predator population densities. The predator density may possibly affect the probability of an encounter and possibly the level of seed exploitation. The original objective of my thesis was to investigate all potential post-dispersal seed predators at Peel Forest. But as the initial field-season ended, the focus shifted to the specific role played by exotic mammals only. Though tracking tunnels indicated mammals were present throughout the study, exact population densities of these mammals were not determined. Rodent numbers are known to vary seasonally and annually, so I performed all experiments between late Summer and Autumn, during the time rodents have been reported to be most abundant (Choquenot and Ruscoe 2000; Blackwell et al. 2002).

All field-based experiments used wire exclosures to exclude specific mammalian species. While this method is commonly used overseas, it is itself a major limitation. The size of wire mesh used is based on the minimum size needed to exclude a target predator. However, as many mammals overlap in body size, while the wire prevents the smallest of the target species, it also may prevent the largest individual of a smaller non-target species. Apart from acknowledging that this limitation occurs, it is a major restraint in this type of experiment that cannot be easily corrected.

The use of petri dishes in the density and cafeteria experiments allowed seeds to be easily re-located, however, the use of dishes may have resulted in over-estimating the foraging success of the predators. Naturally dispersed seeds may escape post-dispersal seed predation in two ways. First, the seed predator needs to be able to differentiate between seeds and other objects on the forest floor; therefore seeds may escape by being hidden amongst the vegetation, litter or soil particles surrounding the seed (Price and Heinz 1984). And second, overseas studies found that the amount of seed preyed upon was substantially lower for buried

seeds than for seeds exposed on the surface (Hulme 1994) and that larger seeds have a higher risk of predation as they take longer to be incorporated into the soil (Bekker et al. 1998).

Each replicate in the cafeteria experiment ran for 15 days, but the threat of post-dispersal seed predation lasts until the seed either dies from other causes or germinates. As a result, any time period used would underestimate post-dispersal seed predation. Previous studies have used 14 days (Willson and Whelan 1990), 15 days (Moles and Drake 1999), 28 days (Osunkoya 1994), up to 56 days (Kollmann et al. 1998). In the first field-season, I performed a series of replicates where seed depots were monitored daily for 21 days. Though post-dispersal seed predation occurred throughout the whole 21 day period, over 80 % of seed losses were observed in the first 15 days. Consequently due to logistic restrictions, 15 day replicates were considered acceptable and were used in subsequent field-seasons.

Although the focus in my study is mammalian post-dispersal seed predators, these same mammals are also known to consume seedlings of many of the studied plant species (Campbell 1978; Sweetapple and Nugent 1998). While my results highlight the influence of exotic mammals on seedling recruitment, they do not necessarily reflect post-dispersal seed predation events only. Further specifically designed experiments to investigate these indirect effects of mammals are needed before a full understanding of the influence of exotic mammals on early plant recruitment can be achieved. Also competition between seedlings may have affected seedling survival between measurements of the natural recruitment experiment. Moles et al. (2003) concluded their observations of a relative increase in the establishment of large-seeded species following the addition of predator-proof cages (such as used in my thesis) was a result of increased inter-specific competition following the removal of predators, rather than a relative increase in the number of large seeds as suggested by Brown & Heske (1990). This is because large-seeded species, with more resources initially, will do better than small seeds in a highly competitive environment (Turnbull et al. 1999).

5.6 Recommendations for future research

Since the initiation of this study in 1999, progress has been made towards filling some of the gaps in the knowledge of the role that exotic mammals play as post-dispersal seed predators in New Zealand forests. Wilson et al. (2003) and Wilson et al. (2006) have investigated the effect of rodents, brushtail possums and deer on seed and seedling survival in South Island

forests, while Ruscoe et al. (2004) and Ruscoe et al. (2005) have studied the population dynamics of the house mouse with respect to seedfall in beech forests. However, more research is required before a full understanding of the importance of small mammals to forest ecosystems will be obtained. There are several potential areas of research into mammal behaviour that have arisen as a result of the current study.

The seed sizes used in the manipulative experiments are relatively small compared to the range of seed sizes of native tree species in New Zealand. As I found evidence that mammalian post-dispersal seed predation was positively related to seed size, larger-seeded species (e.g. *Beilschmiedia tawa* and *Corynocarpus laevigatus*) may be at greater risk than those studied. Unfortunately, these species do not naturally occur at Peel Forest but the role of exotic mammals as predators for these larger-seeded species should be investigated.

I considered the removal of seed from the depot and immediate area as a successful post-dispersal predation event. Although, small mammals commonly destroy seeds during ingestion, some seeds swallowed whole maybe passed still viable in the faeces (Williams et al. 2000; Dungan et al. 2002). Mammals may also secondarily disperse seeds in the process of carrying them to shelter to eat them (Campbell et al. 1984). Studying this aspect of mammalian behaviour was outside the scope of my thesis but is worth pursuing.

Finally, while wire exclosures were used to allow the relative importance of specific mammalian species when compared to other species, ideally experiments that compare many different densities of the same predator are needed to fully determine the influence of the predator species on plant dynamics. Unfortunately, the resources required to manipulate mammalian population densities on the scale required to affect seedling recruitment is beyond that of a PhD thesis.

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Appendix One: Summary results of the cafeteria experiment

A1.1 Overall predation levels (mean proportion removed ± 1 standard error)

Species	Melicytus ramiflorus	Schefflera digitata	Coprosma rotundifolia	Coprosma robusta	Coprosma lucida	Griselinia littoralis	Pseudopanax arboreus	Hedycarya arborea	Pennantia corymbosa
Seed size (mg)	0.7	0.6	8	5.6	17	26	9	171	17
Replicates (per exclosure per canopy type)	16	22	22	22	22	18	14	16	16

Open Canopy

	Melicytus ramiflorus	Schefflera digitata	Coprosma rotundifolia	Coprosma robusta	Coprosma lucida	Griselinia littoralis	Pseudopanax arboreus	Hedycarya arborea	Pennantia corymbosa
Control	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Invertebrates only	0.34 ± 0.06	0.17 ± 0.03	0.01 ± 0.01	0.05 ± 0.02	0.01 ± 0.01	0.02 ± 0.01	0.04 ± 0.03	0.00 ± 0.00	0.01 ± 0.01
Rodents and invertebrates access only	0.43 ± 0.09	0.19 ± 0.04	0.06 ± 0.02	0.12 ± 0.04	0.09 ± 0.02	0.01 ± 0.01	0.10 ± 0.04	0.21 ± 0.10	0.31 ± 0.09
Possums, rodents and invertebrates access	0.63 ± 0.07	0.42 ± 0.06	0.24 ± 0.06	0.27 ± 0.05	0.24 ± 0.05	0.06 ± 0.01	0.28 ± 0.07	0.61 ± 0.12	0.41 ± 0.09

Edge Canopy

	Melicytus ramiflorus	Schefflera digitata	Coprosma rotundifolia	Coprosma robusta	Coprosma lucida	Griselinia littoralis	Pseudopanax arboreus	Hedycarya arborea	Pennantia corymbosa
Control	0.01 ± 0.01	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Invertebrates only	0.32 ± 0.05	0.17 ± 0.03	0.07 ± 0.03	0.02 ± 0.01	0.01 ± 0.01	0.00 ± 0.00	0.03 ± 0.01	0.00 ± 0.00	0.04 ± 0.02
Rodents and invertebrates access only	0.45 ± 0.06	0.25 ± 0.05	0.10 ± 0.03	0.12 ± 0.03	0.08 ± 0.02	0.03 ± 0.01	0.06 ± 0.03	0.17 ± 0.09	0.23 ± 0.07
Possums, rodents and invertebrates access	0.53 ± 0.06	0.39 ± 0.05	0.31 ± 0.06	0.24 ± 0.05	0.20 ± 0.04	0.07 ± 0.02	0.29 ± 0.07	0.57 ± 0.11	0.43 ± 0.09

Continuous Canopy

	Melicytus ramiflorus	Schefflera digitata	Coprosma rotundifolia	Coprosma robusta	Coprosma lucida	Griselinia littoralis	Pseudopanax arboreus	Hedycarya arborea	Pennantia corymbosa
Control	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Invertebrates only	0.31 ± 0.05	0.27 ± 0.04	0.04 ± 0.01	0.02 ± 0.01	0.01 ± 0.01	0.02 ± 0.02	0.05 ± 0.03	0.00 ± 0.00	0.01 ± 0.01
Rodents and invertebrates access only	0.36 ± 0.06	0.21 ± 0.04	0.05 ± 0.02	0.11 ± 0.04	0.13 ± 0.04	0.05 ± 0.03	0.13 ± 0.06	0.10 ± 0.06	0.21 ± 0.10
Possums, rodents and invertebrates access	0.56 ± 0.09	0.42 ± 0.06	0.36 ± 0.07	0.35 ± 0.07	0.30 ± 0.07	0.14 ± 0.04	0.39 ± 0.10	0.55 ± 0.11	0.41 ± 0.10

Appendix One - Continued

A1.2 Encounter rate (proportion of replicates with at least one seed removed)

Species	Melicytus ramiflorus	Schefflera digitata	Coprosma rotundifolia	Coprosma robusta	Coprosma lucida	Griselinia littoralis	Pseudopanax arboreus	Hedycarya arborea	Pennantia corymbosa
Open Canopy									
Control	0.00	0.05	0.00	0.05	0.00	0.00	0.00	0.00	0.00
Invertebrates only	0.88	0.73	0.09	0.27	0.05	0.22	0.21	0.00	0.06
Rodents and invertebrates access only	0.92	0.73	0.32	0.55	0.59	0.11	0.50	0.31	0.75
Possums, rodents and invertebrates access	1.00	0.95	0.64	0.82	0.91	0.56	0.86	0.69	0.88
Edge Canopy									
Control	0.06	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Invertebrates only	0.94	0.86	0.33	0.14	0.09	0.00	0.29	0.00	0.19
Rodents and invertebrates access only	1.00	0.86	0.55	0.59	0.45	0.28	0.36	0.19	0.63
Possums, rodents and invertebrates access	1.00	0.95	0.77	0.82	0.82	0.56	0.93	0.69	0.81
Continuous Canopy									
Control	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Invertebrates only	0.88	0.86	0.36	0.18	0.14	0.11	0.29	0.00	0.07
Rodents and invertebrates access only	0.93	0.81	0.32	0.45	0.48	0.28	0.50	0.25	0.31
Possums, rodents and invertebrates access	0.93	0.90	0.86	0.81	0.68	0.61	0.86	0.75	0.75

Appendix One – Continued

A1.3 Exploitation levels once encountered (mean proportion exploited ± 1 standard error)

Species	*Melicytus ramiflorus*	*Schefflera digitata*	*Coprosma rotundifolia*	*Coprosma robusta*	*Coprosma lucida*	*Griselinia littoralis*	*Pseudopanax arboreus*	*Hedycarya arborea*	*Pennantia corymbosa*
Open Canopy									
Control	0.00 ± 0.00	0.10 ± 0.00	0.10 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Invertebrates only	0.39 ± 0.06	0.23 ± 0.03	0.15 ± 0.05	0.20 ± 0.05	0.10 ± 0.00	0.10 ± 0.00	0.20 ± 0.06	0.00 ± 0.00	0.10 ± 0.00
Rodents and invertebrates access only	0.47 ± 0.10	0.28 ± 0.04	0.20 ± 0.03	0.23 ± 0.06	0.15 ± 0.01	0.10 ± 0.00	0.20 ± 0.05	0.68 ± 0.18	0.41 ± 0.10
Possums, rodents and invertebrates access	0.63 ± 0.8	0.44 ± 0.06	0.38 ± 0.07	0.33 ± 0.05	0.27 ± 0.05	0.11 ± 0.01	0.33 ± 0.07	0.89 ± 0.07	0.47 ± 0.09
Edge Canopy									
Control	0.10 ± 0.00	0.10 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Invertebrates only	0.34 ± 0.05	0.19 ± 0.02	0.20 ± 0.05	0.13 ± 0.03	0.10 ± 0.00	0.00 ± 0.00	0.10 ± 0.00	0.00 ± 0.00	0.23 ± 0.03
Rodents and invertebrates access only	0.45 ± 0.07	0.29 ± 0.05	0.18 ± 0.04	0.21 ± 0.03	0.17 ± 0.03	0.10 ± 0.00	0.16 ± 0.06	0.90 ± 0.10	0.36 ± 0.09
Possums, rodents and invertebrates access	0.53 ± 0.06	0.41 ± 0.05	0.41 ± 0.06	0.29 ± 0.05	0.25 ± 0.04	0.12 ± 0.01	0.31 ± 0.07	0.83 ± 0.08	0.53 ± 0.08
Continuous Canopy									
Control	0.10 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Invertebrates only	0.36 ± 0.05	0.32 ± 0.04	0.10 ± 0.00	0.13 ± 0.03	0.10 ± 0.00	0.20 ± 0.10	0.18 ± 0.05	0.00 ± 0.00	0.10 ± 0.00
Rodents and invertebrates access only	0.38 ± 0.07	0.26 ± 0.04	0.14 ± 0.03	0.24 ± 0.07	0.27 ± 0.06	0.18 ± 0.08	0.29 ± 0.09	0.40 ± 0.20	0.68 ± 0.18
Possums, rodents and invertebrates access	0.60 ± 0.09	0.47 ± 0.06	0.42 ± 0.07	0.43 ± 0.07	0.45 ± 0.07	0.23 ± 0.05	0.46 ± 0.11	0.73 ± 0.11	0.55 ± 0.11

Appendix Two: Summary results of the density experiment

Species	Seed Encounter (proportion of replicates with at least one seed removed)			Overall Seed Predation (mean proportion removed ± 1 std error)		
	Schefflera digitata	*Coprosma robusta*	*Griselinia littoralis*	*Schefflera digitata*	*Coprosma robusta*	*Griselinia littoralis*
Replicates	6	6	6	6	6	6

Initial Density: 1 seeds

Open Canopy

Invertebrates only	0.00	0.00	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Rodents and invertebrates access only	0.00	0.00	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Possums, rodents and invertebrates access	0.00	0.00	0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

Continuous Canopy

Invertebrates only	0.00	0.00	0.17	0.00 ± 0.00	0.00 ± 0.00	0.17 ± 0.17
Rodents and invertebrates access only	0.00	0.00	0.17	0.00 ± 0.00	0.00 ± 0.00	0.17 ± 0.17
Possums, rodents and invertebrates access	0.17	0.17	0.00	0.17 ± 0.17	0.17 ± 0.17	0.00 ± 0.00

Initial Density: 5 seeds

Open Canopy

Invertebrates only	0.33	0.17	0.00	0.33 ± 0.21	0.17 ± 0.17	0.00 ± 0.00
Rodents and invertebrates access only	0.33	0.33	0.17	0.33 ± 0.21	0.50 ± 0.34	0.83 ± 0.83
Possums, rodents and invertebrates access	0.83	0.17	0.66	1.67 ± 0.71	0.67 ± 0.67	0.83 ± 0.31

Continuous Canopy

Invertebrates only	0.17	0.17	0.00	0.17 ± 0.17	0.17 ± 0.17	0.00 ± 0.00
Rodents and invertebrates access only	0.50	0.00	0.33	0.83 ± 0.48	0.00 ± 0.00	0.33 ± 0.21
Possums, rodents and invertebrates access	0.33	0.17	0.17	0.67 ± 0.49	0.17 ± 0.17	0.50 ± 0.50

Species	Seed Encounter (proportion of replicates with at least one seed removed)			Overall Seed Predation (mean proportion removed ± 1 std error)		
	Schefflera digitata	*Coprosma robusta*	*Griselinia littoralis*	*Schefflera digitata*	*Coprosma robusta*	*Griselinia littoralis*
Replicates	6	6	6	6	6	6

Initial Density: 10 seeds

Open Canopy

Invertebrates only	0.50	0.00	0.17	0.83 ± 0.40	0.00 ± 0.00	0.33 ± 0.33
Rodents and invertebrates access only	0.50	0.33	0.00	1.00 ± 0.45	0.50 ± 0.34	0.00 ± 0.00
Possums, rodents and invertebrates access	1.00	0.50	0.17	2.67 ± 0.61	1.00 ± 0.52	0.83 ± 0.83

Continuous Canopy

Invertebrates only	0.50	0.17	0.17	0.83 ± 0.40	0.17 ± 0.17	0.33 ± 0.33
Rodents and invertebrates access only	0.83	0.33	0.33	1.17 ± 0.31	0.33 ± 0.21	1.33 ± 1.15
Possums, rodents and invertebrates access	0.50	0.66	0.17	1.00 ± 0.52	1.33 ± 0.61	1.17 ± 1.17

Initial Density: 15 seeds

Open Canopy

Invertebrates only	0.66	0.33	0.00	1.17 ± 0.40	0.33 ± 0.21	0.00 ± 0.00
Rodents and invertebrates access only	0.66	0.17	0.17	1.33 ± 0.49	0.50 ± 0.50	0.17 ± 0.17
Possums, rodents and invertebrates access	0.83	0.50	0.33	3.33 ± 1.58	1.17 ± 0.54	2.17 ± 1.64

Continuous Canopy

Invertebrates only	0.83	0.17	0.00	1.50 ± 0.43	0.17 ± 0.17	0.00 ± 0.00
Rodents and invertebrates access only	0.50	0.17	0.33	0.67 ± 0.33	1.50 ± 1.50	0.33 ± 0.21
Possums, rodents and invertebrates access	0.66	0.66	0.33	2.17 ± 1.22	3.33 ± 1.52	1.50 ± 1.31

Appendix Three: Summary results of the natural recruitment experiment

Habitat type (canopy cover)	Open canopy			Continuous canopy		
Exclosure treatment	'Possums, rodents and invertebrates access'	'Rodents and invertebrates access'	'Invertebrates access only'	'Possums, rodents and invertebrates access'	'Rodents and invertebrates access'	'Invertebrates access only'
Aristotelia serrata	36.14 ± 9.10	25.14 ± 5.27	69.00 ± 26.45	2.86 ± 1.04	21.14 ± 6.83	25.14 ± 6.22
Carpodetus serratus	2.43 ± 1.68	0.00 ± 0.00	0.43 ± 0.19	0.00 ± 0.00	0.14 ± 0.13	0.00 ± 0.00
Coprosma rotundifolia	9.57 ± 3.48	14.14 ± 4.88	17.86 ± 5.89	2.86 ± 0.77	2.57 ± 0.78	4.86 ± 1.00
Coprosma spp.	2.43 ± 1.50	2.00 ± 0.90	3.00 ± 1.31	0.14 ± 0.13	0.43 ± 0.28	0.43 ± 0.40
Dacrycarpus dacrydioides	3.86 ± 2.67	3.29 ± 2.29	3.57 ± 3.15	1.00 ± 0.64	0.14 ± 0.13	0.00 ± 0.00
Fuchsia excorticata	10.14 ± 4.01	11.43 ± 4.73	11.29 ± 4.49	0.71 ± 0.39	4.29 ± 2.15	10.86 ± 6.00
Griselinia littoralis	19.57 ± 5.36	12.29 ± 5.52	8.43 ± 1.99	7.29 ± 2.80	4.71 ± 1.66	6.00 ± 2.34
Hoheria angustifolia	1.57 ± 0.94	1.00 ± 0.67	1.43 ± 1.32	0.29 ± 0.17	0.71 ± 0.44	1.86 ± 1.57
Melicytus ramiflorus	4.00 ± 1.53	7.00 ± 3.56	6.57 ± 2.29	0.71 ± 0.39	1.29 ± 0.56	3.00 ± 0.76
Pennantia corymbosa	1.29 ± 0.39	5.29 ± 2.78	3.14 ± 0.68	0.43 ± 0.28	11.00 ± 7.91	1.43 ± 0.70
Pittosporum eugenioides	1.57 ± 0.45	1.71 ± 0.75	0.71 ± 0.39	1.43 ± 0.80	1.43 ± 0.49	1.00 ± 0.78
Plagianthus regius	1.71 ± 1.44	1.57 ± 0.92	1.29 ± 0.63	0.29 ± 0.17	1.14 ± 0.62	1.57 ± 0.85
Pseudopanax arboreus	3.00 ± 1.77	2.43 ± 0.97	2.00 ± 1.09	1.43 ± 1.18	1.43 ± 1.18	2.43 ± 0.78
Pseudowintera colorata	5.14 ± 1.96	8.29 ± 3.07	13.43 ± 4.43	0.43 ± 0.28	1.57 ± 0.60	1.43 ± 0.49
Schefflera digitata	4.71 ± 1.84	5.43 ± 2.91	4.14 ± 1.33	1.14 ± 0.91	0.86 ± 0.37	1.00 ± 0.61
Total seedlings	107.14 ± 13.35	101.00 ± 16.26	146.29 ± 24.43	21.00 ± 4.49	52.86 ± 7.64	61.00 ± 10.60

Summary results are the mean number of seedlings observed per seedling plot ± 1 standard error. Number of replicates per treatment = 7. Each seedling plot was 1 × 0.75m

Appendix Four: Summary results of the seed addition experiment

Plant species	*Schefflera digitata*	*Coprosma rotundifolia*	*Pseudopanax arboreus*	*Pennantia corymbosa*
Natural density				
Open Canopy				
Mammals present	0.40 ± 0.24	1.00 ± 0.32	0.60 ± 0.24	0.00 ± 0.00
Mammals excluded	0.00 ± 0.00	1.00 ± 0.00	0.20 ± 0.20	0.20 ± 0.20
Continuous Canopy				
Mammals present	0.00 ± 0.00	0.60 ± 0.40	0.00 ± 0.00	0.00 ± 0.00
Mammals excluded	0.00 ± 0.00	1.40 ± 0.24	0.80 ± 0.37	0.00 ± 0.00
5 x natural density				
Open Canopy				
Mammals present	0.20 ± 0.20	7.80 ± 1.16	0.80 ± 0.37	0.20 ± 0.20
Mammals excluded	0.80 ± 0.37	12.20 ± 1.11	0.60 ± 0.24	0.40 ± 0.24
Continuous Canopy				
Mammals present	0.40 ± 0.24	2.80 ± 0.97	0.20 ± 0.20	0.00 ± 0.00
Mammals excluded	0.00 ± 0.00	7.20 ± 0.66	0.80 ± 0.20	0.20 ± 0.20
10 x natural density				
Open Canopy				
Mammals present	1.20 ± 0.58	13.80 ± 3.06	1.00 ± 0.32	0.20 ± 0.20
Mammals excluded	0.60 ± 0.24	19.80 ± 3.14	1.00 ± 0.45	0.80 ± 0.37
Continuous Canopy				
Mammals present	0.60 ± 0.24	7.20 ± 1.83	0.40 ± 0.40	0.40 ± 0.24
Mammals excluded	0.80 ± 0.37	14.00 ± 1.76	0.80 ± 0.37	0.40 ± 0.24

Summary results are the mean number of seedlings observed per seedling plot ± 1 standard error. Number of replicates per treatment = 5. Each seedling plot was 0.3 × 0.3m