Effects of possums and rats on seedling establishment at two forest sites in New Zealand

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Abstract: Introduced rodents and possums in New Zealand eat flowers, fruits, seeds and seedlings, but little is known about their impact on forest regeneration. We investigated seedling establishment in exclosures with mesh of two different sizes to exclude (1) possums and (2) possums and rats, at two mainland forest sites (beech–podocarp–broadleaved and second-growth broadleaved–podocarp) near Dunedin. We recorded all new woody seedlings that established over the next 2 years. The number of seedlings with true leaves differed significantly between treatments after 1.5 years at both sites and after 2 years in beech–podocarp–broadleaved forest. This effect was broadly consistent across all species including pepper tree (*Pseudowintera colorata*), whose adult foliage is unpalatable to possums. Cotyledonous seedlings were relatively ephemeral, but differed significantly in abundance between treatments in second-growth broadleaved–podocarp forest after 1.5 and 2 years. In second-growth broadleaved–podocarp forest, possums were present throughout the study but rats were rare. Numbers of seedlings did not differ significantly between exclosures with different mesh sizes which admitted or excluded rats. In beech–podocarp–broadleaved forest, rats were present periodically throughout the study, but possums may have been scarce during the final 7 months as a result of pest control. At this location, 80 seedlings with true leaves occurred in exclosures that excluded possums and rats, 3.6 times as many as on control plots and 2.1 times as many as in exclosures that deterred only possums. The consequences of these pest impacts on seedling recruitment for forest regeneration must be confirmed in longer-term studies. Exclosures can be effectively used to experimentally separate the impacts of different herbivores on seedling establishment.

Introduction

Introduced ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*) and brushtail possums (*Trichosurus vulpecula*) in New Zealand eat seeds, fruits, foliage and other parts of plants in indigenous forests (Campbell, 1978; Craig *et al*., 1984; Miller and Miller, 1995; Nugent *et al.*, 2000). Where small mammals occur naturally in other parts of the world, they can influence forest succession and the species of trees that survive to canopy dominance through predation on seeds and seedlings (Crawley, 1990; Ostfeld *et al.*, 1997). Little is known about the impacts of possums and rodents on regeneration of trees and shrubs in New Zealand forests, largely because of the difficulty in separating effects of introduced ungulates, particularly deer and goats, from impacts of smaller mammals

(Nugent *et al.*, 2001; Campbell and Atkinson, 2002). Deer, possums and rodents are present throughout mainland New Zealand and on Stewart Island, and feral goats (*Capra hircus*) and pigs (*Sus scrofa*) occur on much of the mainland (King, 1990). As a result, most of our knowledge of the effects of possums and rodents on regeneration comes from studies on islands where ungulates or possums are absent.

Brushtail possums killed seedlings of several tree species on Kapiti Island in the absence of ungulates (Atkinson, 1992). The abundance of seedlings of some tree and shrub species increased after the extermination of Norway rats from Breaksea Island (Allen *et al.*, 1994), and after the removal of kiore or Pacific rats (*R. exulans*) from several offshore islands lacking other herbivorous mammals (Campbell and Atkinson, 1999, 2002). However, it was not possible to separate benefits

to seedling establishment due to removal of Norway rats and kiore from Kapiti Island from natural variation or effects of prior possum eradication (Campbell, 2002). On islands where kiore remained, more seedlings of several woody species established inside rat exclosures than on adjacent control plots (Campbell and Atkinson, 1999, 2002). On the mainland, numbers or average heights of woody seedlings of some species were inversely related to the abundance of possums (Wallis and James, 1972; Nugent *et al.*, 1997). When exclosures were used to keep both possums and deer out of forest plots on Stewart Island, more woody seedlings established than when only deer were excluded, but this difference could not be ascribed with certainty to possums because of problems with replication and with shading due to accumulated litter on the exclosures (Stewart and Burrows, 1988). Finally, possums and rats may disperse germinable seed after eating fruits of native plants (Williams *et al.*, 2000; Dungan *et al.*, 2002).

We tested whether brushtail possums and ship rats or Norway rats inhibited the recruitment of tree and shrub seedlings in two mainland forest sites. We excluded combinations of possums and rats with small exclosures, and counted woody seedlings that established within each treatment during the next 2 years.

Materials and methods

This study took place at two locations near Dunedin, South Island, New Zealand. One site was a 13-ha fenced remnant of native forest on farmland at Pigeon Flat (45° 48' S, 170° 32' E), dominated by low-canopy second-growth *Fuchsia excorticata* (tree fuchsia) and *Melicytus ramiflorus* (māhoe) with scattered *Griselinia littoralis* (broadleaf), and emergent *Prumnopitys ferruginea* (miro), *Dacrydium cupressinum* (rimu), *P. taxifolia* (mataī), and *Podocarpus hallii* (Hall's tōtara). *Pseudowintera colorata* (pepper tree), *Pseudopanax crassifolius* (lancewood), *Raukaua simplex* (haumakōroa) and *Schefflera digitata* (patē) were abundant in the understorey. The second site was protected native forest within the 1322-ha Waipori Falls Scenic Reserve (Allen, 1978), on the north bank of the Waipori River (45° 55' S, 170° 01' E). Here, the dominant trees were *Nothofagus menziesii* (silver beech), with occasional mataī, Hall's tōtara, rimu, broadleaf and *Kunzea ericoides* (kānuka), and an understorey that included lancewood, pepperwood, māhoe, fuchsia, *Myrsine australis* (māpou), *Aristotelia serrata* (wineberry) and *Pittosporum eugenioides* (lemonwood).

At each location, treatments were set out in a randomised block design. Each block (five replicates per site) contained three plots measuring 30cm × 30cm

and marked at the corners with bicycle spokes. Blocks were 26–36 m apart and plots were 1–5 m apart. We chose plots on level ground, under continuous forest cover with similar light levels within each site, but we did not attempt to control for nearby seed sources. Plots at Pigeon Flat were largely covered with leaf litter; at Waipori Falls the plots were on litter and moss, with some small herbaceous plants (*Nertera* spp.). There were no overhanging ferns or herbs.

Each plot was randomly assigned one of three treatments: either a mammal exclosure (50 cm square and 30 cm high) made of galvanised wire woven at one of two mesh sizes, or a control treatment that did not exclude mammals, marked by wire on the ground (50 cm square). Mesh spacing was 40 mm to exclude possums but not rats, and 18 mm to exclude possums and rats. For brevity, these two exclosure treatments are referred to herein as –P+R and –P–R, respectively, and control treatments as +P+R. All treatments admitted house mice (*Mus musculus*). Larger mammals were excluded with electric fences at Pigeon Flat and, although red deer (*Cervus elaphus*) occur in the Waipori Falls Scenic Reserve, we saw no deer sign or evidence of browsing by deer. The edges of the exclosures, made of thick wire, were pressed tightly into the soil or moss and secured with tent pegs and cord. Exclosures were left outdoors for several weeks prior to installation, so that rain would remove any coating that might be toxic to plants.

The experiment was established in December 1999 at Pigeon Flat and in March 2000 at Waipori Falls. All seedlings initially present on the plots were removed. We counted woody seedlings on the plots approximately monthly until November 2000, and then in winter 2001 (June at Pigeon Flat and August at Waipori Falls), and summer 2002 (February). Seedlings were categorised in two groups: those with cotyledons but no true leaves, and those with true leaves. We recorded the species of seedlings with true leaves, and of cotyledonous seedlings when we could identify them. We expected plant litter to accumulate on the exclosures and reduce the supply of nutrients, light and seeds to the plots. Therefore, we tipped litter from the tops of the exclosures onto the plots each time we visited the site to record seedlings or mammal activity (next paragraph), i.e. every 1 or 2 months until winter 2001, and again in February 2002. Very little litter accumulated on top of the exclosures, even during the final 6- or 8-month period; at Pigeon Flat wind tended to blow the litter away, and at Waipori Falls most trees were small-leaved and most litter may have fallen through the mesh.

The presence of possums and rats was assessed when seedlings were counted, and monthly from December 2000 to April 2001, and at Waipori Falls also in June 2001. We did not attempt to quantify the

abundance of the animals. Rats were detected from footprints left in tracking tunnels containing sponges soaked in food colouring and baited at each end with peanut butter (Gillies and Williams, 2002). The species of rats cannot be determined with this method. Possums were detected from bite marks left in orange-scented wax blocks (Thomas *et al.*, 1999). Beginning in October 2000, we smeared the blocks with peanut butter to maximise our chance of detecting possums if they lost interest in the inedible wax (A. McGlinchy and B. Warburton, Landcare Research, Lincoln, N.Z., *pers. comm.*). On each sampling occasion, four tunnels and one wax block were set up within each block of seedling plots, and checked the next day. The tunnels remained at the sites for the duration of the study. We placed tracking tunnels inside the exclosures to test whether rats were excluded successfully, for two consecutive nights in June 2000 at Pigeon Flat and July 2000 at Waipori Falls. Rats were not detected inside rat exclosures (18-mm mesh), but rat tracks occurred in similar numbers of possum exclosures (40-mm mesh) and control plots. Tracks of house mice occurred in all treatments.

Statistical methods

Counts of seedlings were compared between the different treatments at the last two sampling occasions, in winter 2001 and summer 2002. We analysed counts of cotyledonous seedlings and seedlings with true leaves separately, because the former were often ephemeral. We also analysed data from each site separately, because the experiments began at different times and winter measures were made in different months at the two sites. In most instances the data were insufficient for separate analyses by plant species, but we repeated the analysis for true-leaved seedlings of *Pseudowintera colorata* in summer 2002. Generalised linear models with block and treatment factors were fitted, assuming that the counts followed an over- or under-dispersed Poisson distribution (i.e. the variance was not equal to the mean). Function "glm" with quasi-likelihood estimation, in S-PLUS 6 (Insightful Corporation, 2001, pp. 383, 416), was used for these analyses. Counts were not analysed as a function of time because fitting a model to capture the annual peaks in seedling numbers was problematic, due to variation between years and less frequent measurements in the latter part of the study.

To compare pairs of treatments at the end of the study in summer 2002, ratios of counts were calculated from the fitted model's parameters. A ratio of 1 shows that mean counts were identical in two treatments, <1 indicates that the mean count in the first treatment was less than the mean count in the second, and >1 indicates the reverse. Approximate 95% confidence intervals for the ratios were calculated as measures of

the reliability of these comparisons. We considered two mean counts to be significantly different if the upper and lower confidence limits were either both greater than 1 or both less than 1.

Results

Effects of exclosure treatments on seedling establishment

At Pigeon Flat, the number of seedlings with true leaves differed significantly between treatments in winter 2001 ($F_{2,8} = 10.3$, $P = 0.006$) but not in summer 2002 ($F_{2,8} = 3.2$, $P = 0.093$). Only four seedlings with true leaves were found on control (+P+R) plots in summer 2002, and at least 30 in each exclosure treatment, but confidence intervals show that the magnitude of the differences between exclosure and control treatments varied considerably between experimental blocks (Table 1). Numbers of seedlings at the cotyledonous stage differed significantly between treatments at Pigeon Flat in both summer 2002 ($F_{2,8} = 27.0$, $P < 0.001$) and winter 2001 ($F_{2,8} = 60.8$, $P < 0.0001$). Only one cotyledonous seedling was recorded on control plots in summer 2002 at Pigeon Flat, and more than 20 in each exclosure treatment. Again, these differences were very variable between blocks (Table 1). Neither numbers of seedlings with true leaves nor numbers of cotyledonous seedlings differed significantly between –P+R and –P–R treatments (Table 1).

At Waipori Falls, the number of seedlings with true leaves differed significantly between treatments in both summer 2002 ($F_{2,8} = 7.2$, $P = 0.016$) and winter 2001 ($F_{2,8} = 12.2$, $P = 0.004$). In summer 2002, there were 80 true-leaved seedlings on –P–R plots at this site, more than three times the number on control (+P+R) plots and double the number on –P+R plots (Table 1). There were no significant differences between –P+R and +P+R plots. Cotyledonous seedlings did not differ significantly in abundance between treatments at Waipori Falls in either sampling period ($F_{2,8} < 1.8$, $P > 0.23$). Although more cotyledonous seedlings occurred in the exclosure treatments than on control plots, there was considerable variation between plots, and no ratios of counts of cotyledonous seedlings between pairs of treatments differed significantly from 1 at this site (Table 1).

Treatment effects appeared broadly consistent across all species of seedlings at both sites (Table 2). Numbers of true-leaved seedlings of *Pseudowintera colorata* differed significantly between treatments at both sites in summer 2002 (Pigeon Flat: $F_{2,8} = 55.4$, $P < 0.0001$; Waipori Falls: $F_{2,8} = 6.2$, $P = 0.023$). At Pigeon Flat, twice as many seedlings of this species established on –P+R plots than on –P–R plots

Table 1. Ratios of mean seedling counts, and 95% confidence intervals of the ratios, between pairs of treatments at Pigeon Flat and Waipori Falls in summer 2002 (February). Bold type shows ratios that were significantly different from 1, based on C.Is. Blanks show instances with zero denominators, where ratios could not be calculated.

Seedling stage	Site	Treatments compared (numerator / denominator)	Ratio	95% C. I.
Seedlings with true leaves	Pigeon Flat	–P+R / +P+R	7.5	0.8–72.2
		–P–R / +P+R	8.5	0.9–80.6
		–P–R / –P+R	1.1	0.4–3.3
	Waipori Falls	–P+R / +P+R	1.7	0.7–4.0
		–P–R / +P+R	**3.6**	**1.6–7.8**
		–P–R / –P+R	**2.1**	**1.1–3.9**
Cotyledonous seedlings	Pigeon Flat	–P+R / +P+R	**23.0**	**3.9–136.4**
		–P–R / +P+R	**36.0**	**6.2–210.7**
		–P–R / –P+R	1.6	1.0–2.5
	Waipori Falls	–P+R / +P+R	3.4	0.8–14.9
		–P–R / +P+R	1.5	0.3–8.0
		–P–R / –P+R	0.4	0.1–1.6
Pseudowintera colorata[1]	Pigeon Flat	–P+R / +P+R	—	—
		–P–R / +P+R	—	—
		–P–R / –P+R	**0.5**	**0.4–0.8**
	Waipori Falls	–P+R / +P+R	1.0	0.1–10.7
		–P–R / +P+R	**8.0**	**1.4–47.2**
		–P–R / –P+R	**8.0**	**1.4–47.2**

[1] true-leaved seedlings only

Table 2. Numbers of seedlings, by species, present within each of the treatments at the end of the study in February 2002. Both seedlings with true leaves and cotyledonous seedlings are included. All unidentified seedlings were at the cotyledonous stage.

Site	Species	Common names	Treatment +P+R	–P+R	–P–R
Pigeon Flat	*Carpodetus serratus*	putaputawētā, marbleleaf	0	1	6
	Coprosma foetidissima	stinkwood	0	3	2
	C. linariifolia		0	0	1
	C. rotundifolia		0	4	6
	Griselinia littoralis	broadleaf	3	6	5
	Pennantia corymbosa	kaikōmako	2	0	6
	Pseudopanax crassifolius	lancewood	0	0	2
	Pseudowintera colorata	horopito, pepper tree	0	27	16
	Unidentified		0	12	26
	Total		5	53	70
Waipori Falls	*Coprosma linariifolia*		2	2	6
	C. rhamnoides		11	23	45
	Griselinia littoralis	broadleaf	5	2	3
	Myrsine australis	māpou, red matipou	0	0	2
	M. divaricata	weeping māpou	0	0	1
	Nothofagus menziesii	silver beech	3	1	6
	Pittosporum tenuifolium	kōhūhū	0	0	0
	Podocarpus hallii	Hall's tōtara	1	1	0
	Pseudopanax crassifolius	lancewood	2	10	7
	Pseudowintera colorata	horopito, pepper tree	1	1	8
	Raukaua simplex	haumakōroa	1	0	3
	Unidentified		6	32	14
	Total		32	72	95

(Table 1). This result was due to one –P+R plot with 16 seedlings (when that datum was set to zero, the overall comparison between treatments remained significant: $F_{2,8} = 12.4$, $P = 0.004$). Because zero *Pseudowintera* seedlings established on +P+R plots at Pigeon Flat, ratios could not be calculated to compare exclosures with controls. At Waipori Falls, eight seedlings established on –P–R plots but only one in each of the –P+R and +P+R treatments; these differences were statistically significant (Table 1).

Presence of mammals

Possum density was about 15 per hectare at Pigeon Flat when the study began, but dropped to about six per hectare in April 2000 after trapping and removal for another research project (Ramsey *et al.*, 2002). Possum bite marks were found in wax blocks immediately after this cull in April and June 2000 but not again until October 2000 when we began smearing the blocks with peanut butter (Fig. 1a). However, disturbance to rodent tracking tunnels, and bite marks in wax blocks when we tested the peanut butter method in September 2000, showed that possums were present during the entire period. In contrast, rat tracks were found on only three of 18 sampling occasions at Pigeon Flat.

Possums were comparatively scarce at Waipori Falls. Government authorities poisoned possums in summer 1999–2000 at the study site, and each summer in two blocks within 1 km of the site. Some of the poisons—sodium monofluoroacetate (1080), cyanide, brodifacoum and cholecalciferol—almost certainly killed rats also. The residual trap catch (RTC; National Possum Control Agencies, 2000) of possums in both adjacent control blocks fell to less than 3% (considered very low) during the period of the study (A. Win and R. Wilson, Southern Pest Management, Mosgiel, N.Z., *unpubl.*). We detected possums on 12 of the first 15 sampling occasions, but not on the last two occasions in winter 2001 or summer 2002 (Fig. 1b). Rats were detected on seven sampling dates, including the final two (Fig. 1b). The rats present at both sites were probably ship rats, but it is possible that Norway rats occurred instead or in addition.

Discussion

Effects of excluding mammals

Although both exclosure treatments increased seedling numbers in the second-growth broadleaved–podocarp forest at Pigeon Flat, there was considerable variation between plots, and numbers of seedlings with true leaves differed significantly between treatments in winter 2001 but not in the following summer. Rats were rare at this site, and excluding rats did not further increase seedling establishment compared with
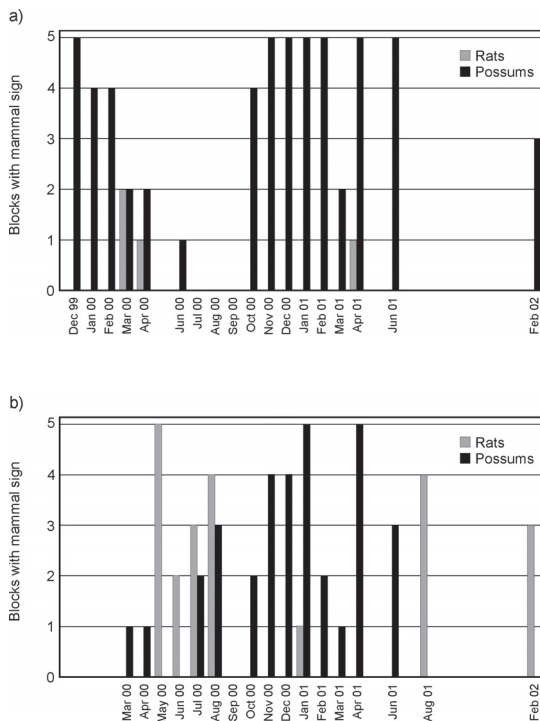

Figure 1. Number of experimental blocks (maximum five at each site) with mammal sign at (a) Pigeon Flat and (b) Waipori Falls, over two years.

excluding only possums. In contrast, in the beech–podocarp–broadleaved forest at Waipori Falls, excluding possums did not significantly elevate seedling numbers, but excluding rats increased the number of seedlings with true leaves, compared with both +P+R and –P+R treatments. Possums were apparently scarce at this location, particularly during the last 7 months of the study, as a result of control efforts. Rats, however, were detected periodically at Waipori Falls throughout the study, and may have taken seeds or seedlings more consistently than possums did.

Introduced chaffinches (*Fringilla coelebs*), blackbirds (*Turdus merula*) and Eastern rosellas (*Platycercus eximius*), which feed on fruits and seeds on or near the ground, were observed in open habitats near both sites, although not in the forest at either location. These relatively large birds were probably excluded from both –P+R and –P–R plots. If so, their effect on seedling establishment on control plots (+P+R) must have been small at Waipori Falls, where –P+R plots did not differ significantly from +P+R plots, but we cannot draw conclusions about the relative

magnitude of possum and bird effects on control plots at Pigeon Flat. Native tomtits (*Petroica macrocephala*) were not seen, but if present they could have entered the –P+R treatments. Although these birds are primarily insectivores (Heather and Robertson, 1996), it is possible that they contributed to the higher seedling numbers in –P–R treatments compared with –P+R treatments at Waipori Falls.

Deer were absent at the fenced Pigeon Flat site, but may have occurred at Waipori Falls. As with large birds, the lack of a significant difference in seedling numbers between –P+R plots and controls (+P+R) at Waipori Falls shows that any effect of deer browsing on control plots was small on average.

Plant parts and species eaten by rats and possums

Norway rats and kiore eat seedlings of several woody plants (Campbell, 1978; Campbell *et al.*, 1984), and possums browse seedlings taller than 10 cm (Atkinson, 1992; McArthur *et al.*, 2000). The consumption of seedlings by ship rats, and of smaller seedlings by possums, has apparently not been investigated. Most diet studies are based on stomach contents, in which seedling tissue is indistinguishable from that of mature plants. However, since possums and ship rats eat buds, leaves and stems (Campbell, 1978; Nugent *et al.*, 2000), it is likely that these mammals remove at least parts of small seedlings.

Possum preference for foliage of different species varies seasonally and geographically, depending on the mix of foods present (Nugent *et al.*, 2000). Of the species that established on our plots, *Raukaua simplex* is usually an important food of possums, but *Carpodetus serratus, Griselinia littoralis, Nothofagus menziesii* and *Pseudowintera colorata* are generally avoided (Owen and Norton, 1995; Nugent *et al.*, 1997, 2000, 2001). Although the adult foliage of *Podocarpus hallii* is usually highly preferred, possums may not significantly affect the growth of its seedlings (Nugent *et al.* 1997, 2001).

Flowers and fruit are important foods for possums, and fleshy fruits may be highly sought after (Nugent *et al.*, 2000). All the species recorded as seedlings on our plots were fleshy-fruited, excepting *Nothofagus menziesii*, and their seeds or those of their congeners have been recorded in possum diets (Gilmore, 1967; Leathwick *et al.*, 1983; Coleman *et al.*, 1985; Cowan, 1990; P.J. Sweetapple, Landcare Research, Lincoln, N.Z., *unpubl.*). Rats also eat the fruits of many New Zealand plants (Campbell, 1978; Williams *et al.*, 2000), and seedlings of both fleshy-fruited and dry-seeded plants increased in numbers after Norway rats were removed from Breaksea Island (Allen *et al.*, 1994). Finally, kiore are known to eat flowers (Campbell, 1978). Ship rats, which are particularly good climbers (King, 1990), probably remove flowers (Ecroyd, 1996)

as well as fruits from trees and shrubs.

We expected numbers of seedlings of *Pseudowintera colorata*, whose adult foliage is unpalatable to possums, to be unaffected by possum exclosures. However, at least 16 seedlings of this species established in each of the exclosure treatments at Pigeon Flat, and none on control plots. This result was probably due to possums eating *Pseudowintera* berries, as recorded by Coleman *et al.* (1985). At Waipori Falls, more *Pseudowintera* seedlings occurred on –P–R plots than in either of the treatments that admitted rats. Ship rats, which ate the fruits (but not the seeds) of the related *Pseudowintera axillaris* in a small feeding trial (Daniel, 1973), may also remove *P. colorata* berries.

Consequences of reduced seedling establishment

Will reduced seedling establishment, caused by a combination of pre-dispersal predation on flowers and seeds, post-dispersal predation on seeds, and predation on seedlings, ultimately alter forest composition? Seed predation affects plant population size if it lowers density below that to which density-dependent mortality (self-thinning) of plants would later reduce the population (Harper, 1977). By analogy, the same is true of predation on seedlings. Seed predation usually limits recruitment only at low seed densities, when reductions in other sources of mortality are insufficient to compensate for losses to predation (Crawley, 2002).

Rates of seed predation can be high (Dijkgraaf, 2002) or low (Moles and Drake, 1999) in New Zealand forests. In some locations, small seedlings of many species are far more numerous than adult trees, despite the presence of possums and rodents, suggesting that predation on seeds or seedlings does not limit regeneration of these species (e.g. Nugent *et al.*, 1997; Bellingham *et al.*, 1999). In contrast, the potential of rats to affect the size of island tree populations by taking seeds and/or seedlings was evident from under-representation in some size classes, which are expected to decrease monotonically in density from small to large (Allen *et al.*, 1994; Campbell and Atkinson, 1999, 2002; Russell *et al.*, 2001). Future reassessment of the population structures would demonstrate whether these depleted size classes endure as the trees mature.

Potential benefits of possums and rats to plant recruitment

Some seeds taken by possums and rats may be dispersed to microsites suitable for germination and survival of seedlings. Possums excrete undamaged, germinable seeds of various sizes, and rats void small germinable seeds (Williams *et al.*, 2000, Dungan *et al.*, 2002). Ship rats and Norway rats cache seeds in their nests (larder-hoarding), which is not predicted to enhance regeneration (Hulme, 2002), but both species may

disperse seeds while carrying them elsewhere for eating (Barnett and Spencer, 1951; Norman, 1970; Ewer, 1971; Williams *et al.*, 2000). Rats and possums may also increase recruitment by killing other seed predators. A decline in the number of seedlings of *Griselinia littoralis* was attributed to herbivory by invertebrates that increased in numbers after Norway rats were removed from Breaksea Island (Allen *et al.*, 1994). However, by reducing the abundance of native frugivorous birds through predation on eggs, chicks and adults (King, 1990; Innes *et al.*, 1999), rats and possums are expected to have detrimental effects on the dispersal of many forest plants (Clout and Hay, 1989).

Experimental herbivore exclosures

Small exclosures are promising tools for researching the impacts of possums and rodents on seedling recruitment. Several modifications can mitigate the problems we experienced in our study. Exclosures can be designed with open tops to minimise shading and admit birds, seeds and fruits, and plant litter (e.g. Campbell, 1978). Ungulates can be excluded with fences, to separate impacts of ungulates and other herbivores. To exclude house mice, 6-mm mesh is recommended (Karori Wildlife Sanctuary, 2002). Study sites and plots within sites should be selected to control or randomise the abundance of herbivores (Russell *et al.*, 2001) and other factors expected to be important, such as substrate and light. Sample sizes may need to be high in forest systems where the distribution of seedlings is patchy. To separate components of seed and seedling predation, known numbers of seeds can be sown (Crawley, 2002) or marked seeds or seedlings monitored (Hulme, 1993; Russell *et al.*, 2001).

Acknowledgements

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