



Neighbourhood analyses of tree seed predation by introduced rodents in a New Zealand temperate rainforest

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House mice *Mus musculus* and other introduced rodents represent a novel source of predation on tree seeds in New Zealand forests. In the northern temperate forests where these rodents are native, spatial and temporal variation in tree seed production can result in dramatic fluctuations in the distribution and abundance of seed predators, with subsequent feedbacks on the distribution and abundance of seedlings. We use neighbourhood models to examine variation in rodent predation on seeds of 4 tree species of the temperate rainforests of New Zealand as a function of 1) spatial variation in local canopy composition and 2) spatial and temporal variation in mouse activity. We placed seeds throughout mapped stands of mixed forests in alluvial valley bottoms and on elevated marine terraces in the Waitutu Forest, South Island. The risk of predation on seeds of 2 dominant canopy trees – rimu *Dacrydium cupressinum* and mountain beech *Nothofagus solandri* var. *cliffortioides* – peaked in neighbourhoods dominated by those species and by silver beech *N. menziesii*, particularly in a year of plentiful seed rain from these species. The risk of predation on rimu and beech seed was also related to measures of local mouse activity. These relationships suggest that the highest local abundance of mice was concentrated in rimu and beech neighbourhoods because of the food provided by seed rain from those trees. Predation on seed of miro *Prumnopitys ferruginea*, which is eaten by rats but not mice, was low in rimu neighbourhoods and where mouse activity was high. These patterns may reflect spatial segregation in the activity of rats versus mice within stands. Our results suggest that the spatial distribution of canopy trees translates into predictable patterns of variation in mouse activity and seed predation. Heterogeneity in rodent activity and seed predation within stands may have important implications for tree population dynamics.

Introduced rodents – house mice *Mus musculus*, ship rats *Rattus rattus*, Norway rats *R. norvegicus* and kiore or Pacific rats *R. exulans* – have become important predators on seeds and fruits of native tree species in New Zealand forests (Campbell 1978, Murphy 1992, Ruscoe et al. 2004, 2005). There are no native rodents in New Zealand forests, and prior to the introduction of rodents by humans, birds and invertebrates were presumably the major tree-seed predators in these ecosystems. Where rodents and other small mammals occur naturally in other parts of the world, their predation on both seeds and seedlings can have strong effects on the dynamics of tree species (Ostfeld et al. 1997, Crawley 2000, Wenny 2000, Andresen and Levey 2004, García et al. 2005). Rats affect seedling establish-

ment on New Zealand's offshore islands (Allen et al. 1994, Campbell and Atkinson 1999) and on the mainland (Wilson et al. 2003). However, most research on the ecological effects of the introduction of rodents, particularly mice, in New Zealand forests has focused primarily on their direct and indirect effects on native bird populations, rather than on their potential long-term effects on forest succession and tree population dynamics.

Mouse densities in New Zealand forests increase as a result of increased reproduction following periodic heavy seed production (masting) by southern beech *Nothofagus* spp. (Nothofagaceae) and rimu trees (Podocarpaceae: *Dacrydium cupressinum*, a conifer) (King 1983, Choquenot and Ruscoe 2000, Ruscoe et al. 2004, 2005).

Ship rats and Pacific rats may also respond numerically to mast crops of beech and rimu (King and Moller 1997, Dilks et al. 2003, Harper 2005). Masting by these trees, which are the dominant canopy species in South Island forests, can also drive the dynamics of granivorous and frugivorous birds (Wardle 1984, Clout and Gaze 1984, Elliott et al. 1996, 2001, Wilson et al. 1998).

Whether a population of mice can consume essentially an entire annual crop of beech seeds before these germinate in the following spring can be predicted from 1) the magnitude of the seedfall and 2) the density of mice when seedfall begins (Ruscoe et al. 2005). This may also be true of rimu seeds, since both beech and rimu seeds are eaten by mice and are of similar size and nutrient content (Ruscoe et al. 2004). However, because of spatial variation in the distribution and density of fallen seed and the activity of rodents, the probability that an individual seed is eaten may vary widely at different locations within a stand. Janzen (1970) and Connell (1971) independently proposed that because most seeds fall near their parent tree, density-dependent responses of seed and seedling predators prevent recruitment near conspecific adults, thereby promoting forest diversity (the Janzen–Connell hypothesis). Density-dependent or distance-dependent mortality of seeds and seedlings has since been documented for many tree species in tropical and temperate forests (Hammond and Brown 1996, Hille Ris Lambers et al. 2002, cf. Hyatt et al. 2003). These patterns appear in relation to predation by invertebrates more often than by mammals, many of which are comparative generalists (Hammond and Brown 1996, Hille Ris Lambers et al. 2002). Recent models predict that the scale of predator movements relative to seed dispersal distances, the degree of predator specialisation, and predator satiation (Janzen 1971) may determine the probability of seed predation as a function of distance from a seed source (Nathan and Casagrandi 2004). Further, because inter-annual differences in seed production may change the spatial distribution of offspring relative to parents, seed predation should be studied in relation to both temporal and spatial variation in seed density (Hammond and Brown 1996).

Seed rain and seedling recruitment of many forest trees is concentrated within tens of metres of a parent (Ribbens et al. 1994, Clark et al. 1998, LePage et al. 2000, Ruscoe et al. unpubl.). The spatial distribution of these seed sources can thus determine the local distribution and abundance of small-mammal seed predators, with consequent effects on the spatial patterns of seed survival and seedling establishment (Schnurr et al. 2002, 2004). These and other fine-scale spatial interactions that regulate tree demography, including shading, competition for light, and soil nutrient dynamics, form the basis of an emerging theory of “neighbourhood” dynamics (Gratzer et al.

2004). Spatially explicit models of forest dynamics based on neighbourhood interactions between individual trees can predict long-term changes in forest structure and composition (Pacala et al. 1996, Law and Dieckmann 2000). Models of this type can be used to forecast outcomes of both ecological processes and forest management decisions, including the consequences of introduced forest herbivores under alternative pest control regimes (Coomes et al. 2003). Seed predation by introduced rodents in different forest neighbourhoods is one of many processes that must be quantified before such management tools can be developed for New Zealand forests.

We investigated rates of seed predation in temperate rainforests in the Waitutu area of the South Island, New Zealand. We tested whether spatial variation in seed predation risk within stands could be predicted from 1) the composition of forest canopy neighbourhoods and 2) local indices of rodent activity. We compared these relationships between 4 tree species, including the dominant conifer (rimu) and one of the dominant angiosperms (mountain beech *Nothofagus solandri* var. *cliffortioides*), between 2 yr with relatively high (2003) and low (2004) rodent abundance, and between forests on 2 different substrates, with many tree species in common but at very different relative frequencies. According to the Janzen–Connell hypothesis, the risk of predation on a seed species should be highest in forest neighbourhoods dominated by that tree species because of the responses of seed predators to high seed density there. However, because the inter-annual change in rodent abundance during our study was associated with variation in rimu and beech seedfall, the distribution, movements, and diet of rodents and hence the spatial pattern of seed predation might be expected to differ between years. Two other mechanisms could also lead to results inconsistent with the Janzen–Connell hypothesis. First, predator satiation (Janzen 1971) near seed sources may lead to a predation rate that increases with distance from parent trees (McCanny 1985), an inversely density-dependent pattern that is predicted to occur when seed predators are highly generalised (mice and rats are omnivorous) or mobile (Nathan and Casagrandi 2004). Second, in mixed forests with generalist predators, seeds may experience high rates of predation near heterospecific seed sources when rodents are actively foraging there (Veech 2000, Kwit et al. 2004, Schnurr et al. 2004).

Methods

Study sites

This research was done in Waitutu Forest, Fiordland National Park, South Island, New Zealand (Ward

1988, Mark et al. 1988). As part of a detailed study of this forest ecosystem, 6 sites were selected in tall (ca 20 m) mixed conifer–angiosperm forests of 2 contrasting substrates: 3 on alluvial terraces (“A” sites) bordering rivers at ca 30 m a.s.l., and 3 on older, uplifted marine terraces (“T” sites) at 80–120 m a.s.l. A map of the study sites is given in Wilson et al. (2006b). Sites were chosen based on the presence of plant species that indicated relatively high fertility of the alluvial soils and lower fertility of the terraces (Coomes et al. 2005). Sites were at least 0.7 km apart, 3 in the catchment of the Crombie Stream (46°14′S, 167°11′E) and 3 in the Waitutu River catchment (46°12′S, 167°04′E). The vegetation and soils at the 6 study sites have been described by Wardle et al. (2004), Coomes et al. (2005), and Williamson et al. (2005).

The spatial position, species, and stem diameter of each canopy tree > 10 cm dbh (stem diameter measured at 1.4 m height), subcanopy trees > 2.5 cm dbh, and tree ferns > 2 m tall were mapped on a plot (100 × 150 m to 150 × 150 m; 1.5–2.25 ha) at each site. Tree positions were measured by triangulation with an Impulse laser rangefinder with digital inclinometer and compass (Laser Technology, Co, USA).

Study species

Seeds of 4 species were used in seed predation trials: rimu, mountain beech, miro (Podocarpaceae: *Prumnopitys ferruginea*, a conifer), and broadleaf (Cornaceae: *Griselinia littoralis*, an angiosperm). These species were chosen because we were interested in the impact of rodents on their regeneration and they are widespread throughout the South Island. Compared with the masting species, rimu and beech, the seed crops of miro and broadleaf are thought to be relatively constant between years. Rimu and mountain beech seeds are eaten by mice and rats (Campbell 1978, Ruscoe et al. 2004). Miro seeds have a thick, hard husk and are eaten by rats (Beveridge 1964, Daniel 1973, Campbell 1978), but were not eaten by mice in laboratory trials (Ruscoe et al. 2004). It was not known whether either rats or mice eat broadleaf seeds, but because the foliage of this tree is a preferred forage of introduced ungulates (Forsyth et al. 2002), whether rodents also affect its regeneration was of interest.

Rimu seeds have a red fleshy aril, miro seeds have a red fleshy coat, and broadleaf seeds, which are one-seeded berries, have a thin black fleshy pericarp; these are adaptations for dispersal by birds (Clout and Hay 1989). Beech nuts, which are not fleshy, have rudimentary wings and are dispersed primarily by wind and gravity. Typical seed lengths (mm) are: rimu 3.2–3.8, mountain beech 4.5–5.5, broadleaf 5.0–6.0, and miro 11–17 (Webb and Simpson 2001). Seeds of a fifth

species of interest, silver beech *Nothofagus menziesii*, were not available, but because silver beech and mountain beech seeds are of similar size and mass (Wardle 1984, Webb and Simpson 2001), we considered that predation rates on the 2 species were probably similar. Seeds were obtained as follows: rimu from Codfish Island, Southland, in 2003; beech from Craigieburn Forest, Canterbury, in 1999; miro from Waitutu Forest in 2003 and 2004; broadleaf from Dunedin in 2003 and 2004.

House mice and ship rats are found in forests throughout New Zealand, whereas Pacific rats now occur only in the south-west and on offshore islands (King 2005). We have never captured Norway rats in Waitutu Forest, although they do occur in forests, usually near water (King 2005). *Mus* and most *Rattus* species seldom store food (Vander Wall 1990). Excavated nests of wild *Mus* spp. in India did not contain hoarded food (Sheikher and Malhi 1983), although in captivity mice, ship rats, and Pacific rats may carry food to a nest box (larder-hoarding; Ewer 1971, Mackintosh 1981, Williams et al. 2000). Ship rats (Norman 1970, Ewer 1971) and Pacific rats (Campbell et al. 1984) may carry food elsewhere for eating, and mice may also do so in captivity (Crowcroft 1966). Scatter-hoarding (i.e. burying food items in widely-spaced caches; Morris 1962) by these species has not been recorded (Vander Wall 1990).

Abundance of rodents

The abundance of mice and rats was estimated by capture-mark-recapture in Elliott live traps, spaced 20 m apart on grids (140 × 140 m) overlaying the mapped plots, in a concurrent study (Ruscoe 2004, Ruscoe et al. 2004, Ruscoe and Wilson unpubl.). Trapping was done every 6 months from May 2001 to November 2002 (Ruscoe et al. 2004), then every 3 months until May 2004, and again in November 2004. Only one mouse and no rats were caught before November 2002, when the populations increased sharply following heavy rimu seedfall the previous (2002) winter (Ruscoe et al. 2004). The estimated density of mice, based on minimum number alive (MNA), rose to 17–28 ha⁻¹ at the different sites and remained high until the next winter (August 2003, Ruscoe et al. 2004, Ruscoe and Wilson unpubl.). In February 2004, mouse density was ca 5–7 ha⁻¹ at 2 sites, with too few captures to estimate density elsewhere, and by May 2004 few animals were caught at any site (Ruscoe and Wilson unpubl.). A small number of Pacific rats and ship rats were caught between November 2002 and February 2004, but too infrequently for rat density to be estimated (Ruscoe 2004, Ruscoe and Wilson unpubl.).

Seed predation trials

We studied rates of seed predation during late autumn seedfall, both when rodent density was high in June 2003 and when it was low in May 2004. The arils of rimu seeds and fleshy coats of miro seeds were removed by soaking in water so that seeds were similar within species and did not rot, but the thin pericarps of broadleaf seeds were retained. All seeds were then air-dried and refrigerated until used. Seeds were presented in Petri dishes because 3 of the 4 species were too small to tether or to find among forest litter if placed directly on the ground (based on preliminary trials). Each dish had drainage holes and was fixed to the ground with a nail, with a rectangular A-frame plastic cover ($20 \times 14 \times 10$ cm high) to protect it from rain and from ground-feeding birds, although these were uncommon. Four dishes, each containing 5 seeds of a single species, were placed ca 1 m apart at each rodent trap station on the mapped parts of the rodent trapping grids (20-m spacing; 48–64 stations per grid; 319 stations total). Dishes and seeds were handled with surgical gloves and/or forceps (Wenny 2002, Duncan et al. 2002), although seeds had been touched when first collected. Entire seeds remaining in each Petri dish were counted after 2, 4, and 7 nights. Seeds at site T3 in 2004 were counted after 2 and 5 nights but not after 7 nights, because of flooding. The presence or absence of husks or partially eaten seeds remaining in the dishes was recorded by one of 5 observers in 2003 and by all observers in 2004.

Seedfall

We measured natural seed rain to assess this component of the food available to rodents during the experiments. Fifteen 0.28-m^2 seed traps, each consisting of a cone of fibreglass insect screening (mesh size ca 1.5 mm) suspended from a circle of thick wire (Wardle 1970) and supported 1 m above the ground on 3 wooden posts, were spaced evenly across each trapping grid. Although these seed traps were accessible to rodents and birds, rodent droppings were never found in them, seed-eating birds, which are scarce in these forests, were not observed foraging in them, and the accumulated litter became tightly packed. We therefore assumed that seed predation inside the seedfall traps was negligible. Seeds that accumulated in the seed traps were collected when rodents were trapped (see above), and were sorted and counted by species.

Analytical methods

The experimental unit for statistical analysis was a dish of seeds, with predation on the seeds within a dish treated as a categorical response (predation vs no

predation). A dish was considered to have escaped predation for 7 d if 3 or more seeds remained, to allow for accidental loss of one or 2 seeds and for seed predators avoiding sterile seeds (Kollmann et al. 1998). We used 5-d removal rates for site T3 in 2004. Dishes that were flooded or moved (probably by brushtail possums *Trichosurus vulpecula*) were excluded from analyses.

We defined the neighbourhood of each station (consisting of 4 seed dishes and a rodent trap) to be the area within a 15-m radius. This radius was based on our studies of seed dispersal patterns of beech and rimu trees (Ruscoe et al. unpubl.). The vast majority of rimu seed fell within 10 m of the trunk of a parent tree in a 2-yr study at Waitutu Forest (Ruscoe et al. unpubl.). Most mountain beech and silver beech nuts, which have rudimentary wings for wind dispersal, fell within 15 m of the trunk when measured perpendicular to the prevailing wind direction, and within 25 m of the trunk in a downwind direction (Fig. 1 in Ruscoe et al. unpubl.). The distribution of seedlings relative to adult trees was consistent with these conclusions (Wright et al. unpubl.).

For stations located on the edge of the mapped plot, the neighbourhood included only trees within the plot. The relative basal area of each tree species (i.e. basal area of the species divided by total basal area) within the 15-m-radius neighbourhood for each station was used in principal components analyses (PCA) to describe the variation in tree neighbourhoods at alluvial sites ($n = 160$) and terrace sites ($n = 159$). These ordinations were done separately for the 2 forest types so that differences between neighbourhoods within each forest type, and not differences between forest types, would dominate the results.

We calculated a mouse capture index for each trap station in May 2003 and May 2004. We used simulation and inverse prediction in program Density (Efford 2004) to fit spatial detection models to the trapping data. A function $g(x)$ was used to estimate the decline in daily capture probability with distance x between a trap and the centre of a mouse's area of activity (Efford 2004) (this function could not be fitted to the sparse rat-capture data). The function was fitted as a half-normal distribution with mean 0 m and standard deviation σ m. The radius of a mouse's area of activity was approximated as 2.45σ , based on a 95% activity contour and assuming that utilisation of the area of activity has a circular bivariate normal distribution; this area is analogous to the "home range" of Jennrich and Turner (1969), but because few animals have circular bivariate normal home ranges we have not called it a home range estimate.

We used this same function $g(d)$ to model the decline in probability of seed predation with distance d between the seed dish station and the location of each

recent mouse capture. An index of mouse density at each station was then calculated as

$$\text{Mouse capture index} = 10 \times \sum_{\text{mice } i} g(d_i)$$

for all mice i caught within 73 m ($d_i < 73$ m). More distant captures were ignored because $g(73)$ was $< 1\%$ of $g(0)$. The factor 10 scales the index so that most values are between 0.1 and 2.0 in order to facilitate numerical analysis (below). Although the units of this scaled sum of daily capture probabilities are day^{-1} , for simplicity we treat it as a unit-less index.

To identify relationships between predation risk and the independent variables we followed the general approach of Schnurr et al. (2004). The independent variables used were 1) principal components scores describing variation in tree neighbourhoods in each forest type and 2) spatial mouse capture indices in both forest types combined. Since the dependent variable, survival of a dish of seeds for 7 d, was binary, we used non-linear regression to fit an equation of the form (Schnurr et al. 2004)

$$Y = A \times B^{(X-C)^2}$$

In this function, the parameter A determines the maximum predicted rate of predation (ranging from 0 to 1), B determines the shape of the function, and C determines the value of the independent variable where the peak (A) occurs (Schnurr et al. 2004). Separate models were estimated for the sets of 3 alluvial sites and 3 terrace sites, because separate ordinations were done for each forest type (above). We used simulated annealing, a global optimisation procedure, to find estimates of A , B , and C that maximised the likelihood of observing the data. The optimisation procedure was performed using software written in the Delphi programming environment (Delphi 6, Borland Software 2001). Asymptotic 2-unit support intervals (analogous to 95% confidence intervals) were calculated for each maximum likelihood parameter estimate.

We used Akaike's information criterion corrected for small sample size (AICc; Akaike 1974, Hurvich and Tsai 1989) to compare the fit of alternative models to the data of survival of each seed species in a given forest type (alluvial vs terrace) in 2003 and 2004 as a function of each independent variable. Five models were compared to test for effects of neighbourhood and for differences in predation rate between the 3 sites within each forest type (number of parameters in parentheses):

$$\text{Full: } Y = A_s \times B_s^{(X-C_s)^2}$$

The subscripts $s = 1, 2, 3$ indicate that the parameters A , B and C are estimated separately for each of the 3 sites s within a forest type (9).

$$\text{Neighbourhood + Sites: } Y = A_s \times B^{(X-C)^2}$$

A is estimated separately for each site s , B and C are common to all sites within a forest type (5).

$$\text{Neighbourhood: } Y = A \times B^{(X-C)^2}$$

A , B and C are estimated across all observations at all 3 sites within a forest type (3).

$$\text{Sites: } Y = A_s$$

Y is a different constant for each site s within a forest type, equal to the mean of all the observations at that site; $B = 1$ (3).

$$\text{Null: } Y = A$$

Y is a single constant equal to the mean of all the observations at all sites within a forest type; $B = 1$ (1).

Estimates of mean predation risk on each seed species at each site, obtained from the Sites models, were compared between years with paired t-tests.

Results

Seed removal events were frequent at most sites only for rimu and mountain beech seeds (Fig. 1), and seeds of these species were removed more often in 2003 than in 2004 ($t_4 > 7.2$, $p < 0.001$) (this comparison remained statistically significant if site T3, where 5-d predation rates were used in 2004, was omitted: $t_3 > 6.4$, $p < 0.003$). Rates of removal of broadleaf and miro seeds were low except at site T3 in 2003 (Fig. 1), and rates of removal of these species did not differ significantly between years ($t_4 < 2.2$, $p > 0.15$). Predation on rimu and mountain beech seeds was usually characterised by seed husks remaining in the dish [91% ($n = 79$) and 77% ($n = 94$) of predation events on the 2 species, respectively, for which the presence or absence of husks were recorded], and sometimes by the presence of mouse droppings. Seed remains were noted in only 5% of broadleaf seed predation events and 6% of miro seed predation events ($n = 55$ and $n = 31$, respectively).

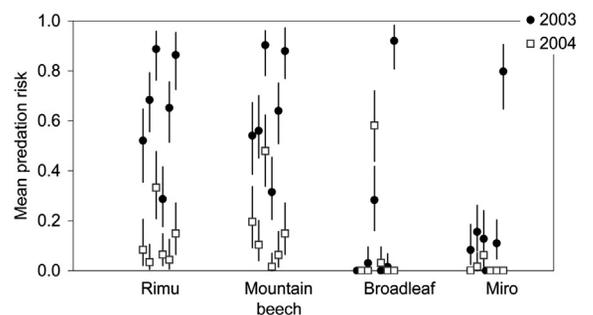


Fig. 1. Mean risk of predation after 7 d at each site on experimental dishes containing seeds of one of 4 species, in 2003 and 2004. Sites are plotted in order A1, A2, A3, T1, T2, T3. Error bars show 2-unit support intervals.

While most birds are unlikely to have removed seeds from dishes under plastic covers, New Zealand robins *Petroica australis*, which are omnivorous, were seen foraging on the ground near experimental seed dishes at site A3 in 2004, and may have been responsible for some seed predation. Large invertebrates [probably ground beetles (Coleoptera: Carabidae) or weta (Orthoptera: Stenopelmatidae)] may also have taken some of the smaller seeds.

Principal components analysis of canopy tree neighbourhoods

A single principal components axis was identified that explained 62% of the variation in the canopy tree neighbourhoods at the alluvial sites, and the first 2 axes explained 63% of variation at the terrace sites (Fig. 2). We confined our analyses to these components because they explained the majority of variation in canopy neighbourhood composition.

At alluvial sites, the first principal component discriminated between neighbourhoods dominated by silver beech (negative end of the axis) and by the angiosperm tree kamahi (Cunoniaceae: *Weinmannia racemosa*) (positive end of the axis; Fig. 2a). Silver beech and kamahi were the only common large trees at the alluvial sites.

At terrace sites, the first principal component discriminated between neighbourhoods dominated by silver beech and those dominated by rimu (Fig. 2b). The second component at these sites separated neighbourhoods dominated by the conifer Hall's totara (Podocarpaceae: *Podocarpus hallii*) and those dominated by rimu, with a mixture of species including silver and mountain beech at intermediate values (Fig. 2c) (mountain beech was absent from site T2).

Seedfall

In autumn and winter 2003 (February–August, 6 months), ca 1400–1700 seeds m^{-2} (all tree species combined) were collected at alluvial sites and 750–1000 seeds m^{-2} at terrace sites (Table 1). Seedfall was much lighter in 2004, with <250 seeds m^{-2} collected from February to November (9 months, Table 1). Most seedfall at alluvial sites was of silver beech, rimu, and understorey angiosperms in the genus *Pseudopanax* (Araliaceae). Much of the variation between alluvial sites reflected differences in forest composition: sites A1 and A3 each had only 2 rimu trees and no mountain beech. At terrace sites, most seedfall was of rimu and either silver beech or mountain beech (absent from site T2).

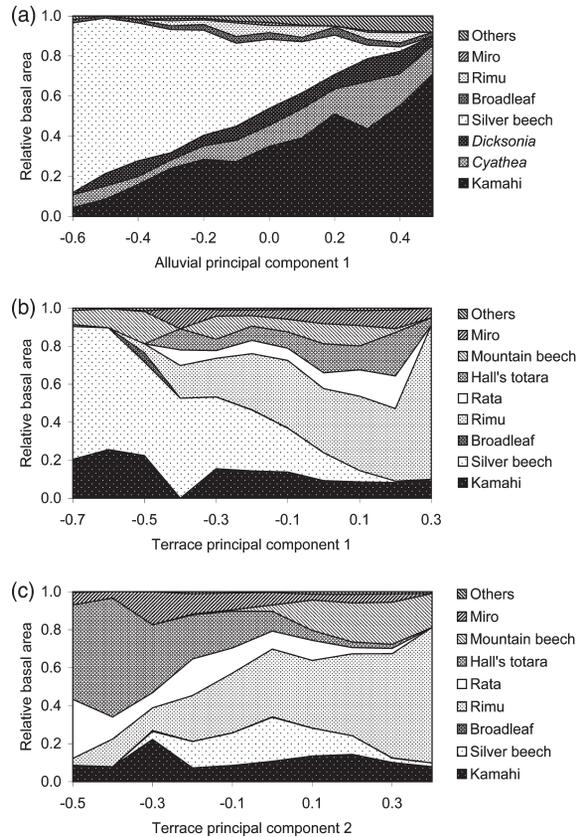


Fig. 2. Relative basal area of tree species at (a) alluvial sites, plotted against the first principal component identified at alluvial sites, (b) terrace sites, plotted against the first principal component identified at terrace sites and (c) terrace sites, plotted against the second principal component identified at terrace sites. Mean basal areas were calculated and plotted at 0.1-unit increments of each component. Species names not given in the text are the tree ferns *Dicksonia squarrosa* (Dicksoniaceae) and *Cyathea smithii* (Cyatheaceae), and southern rata (Myrtaceae: *Metrosideros umbellata*).

Variation in seed predation as a function of canopy tree neighbourhoods

At alluvial sites the probability of predation on rimu seed was higher in silver beech neighbourhoods than in kamahi neighbourhoods in both years (i.e. was negatively related to the first principal component; Fig. 3). The Neighbourhood + Sites model was the most parsimonious model in both years (Table 2). Predation on mountain beech, miro, and broadleaf seed did not vary significantly as a function of neighbourhood at the alluvial sites in either year (i.e. either the Sites or Null models were best for these species; Table 2).

At terrace sites in 2003 (the year of high seed rain), the risk of predation on rimu, miro, and mountain beech seed varied between rimu neighbourhoods and Hall's totara neighbourhoods (i.e. was related to the

Table 1. Seedfall per square metre at sites in Waitutu Forest, New Zealand, in February–August 2003 and February–November 2004.

Year	Forest type	Site	Seed species					Total
			Rimu	Silver beech	Mountain beech	<i>Pseudopanax</i>	Other	
2003	Alluvial	A1	34	868	0	398	88	1388
		A2	575	355	109	607	48	1694
		A3	8	1581	0	1	31	1621
	Terrace	T1	469	17	283	11	17	796
		T2	355	374	0	1	22	752
		T3	602	70	294	0	26	993
2004	Alluvial	A1	3	18	0	38	27	85
		A2	180	3	3	21	35	242
		A3	1	37	0	0	6	45
	Terrace	T1	80	1	113	2	22	219
		T2	57	19	1	0	30	107
		T3	64	4	9	0	38	116

second principal component; Fig. 4a–c). Predation on rimu seed was higher in rimu neighbourhoods than in

totara neighbourhoods, and predation on miro seed showed the reverse pattern (Neighbourhood + Sites models). Predation on mountain beech seed peaked in neighbourhoods with different mixtures of rimu and mountain beech or silver beech at different terrace sites (Full model; Fig. 2c and 4c). This site difference can be attributed to the absence of mountain beech at T2. Predation did not vary significantly between neighbourhoods for any of the 4 seed species at terrace sites in 2004 (Fig. 4d).

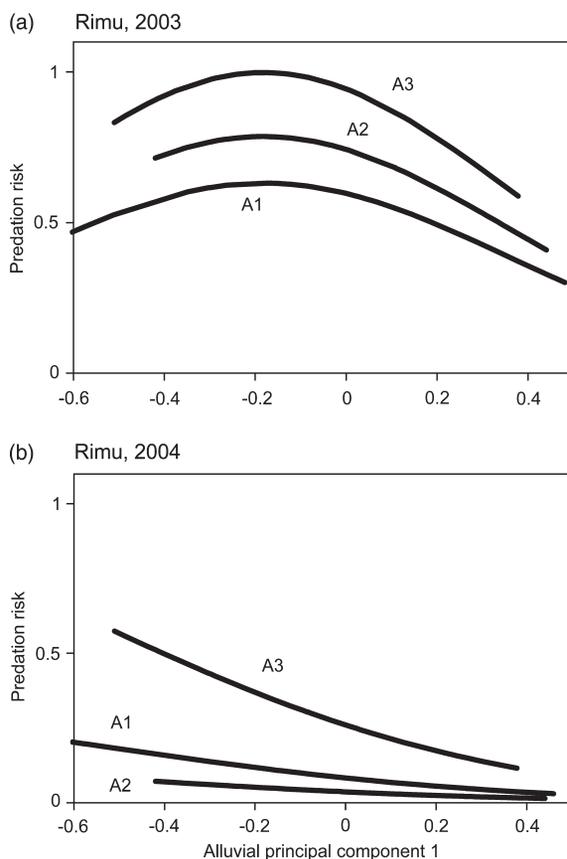


Fig. 3. Estimated risk of predation after 7 d on experimental dishes of rimu seed at alluvial sites (A1, A2 and A3) as a function of the first principal component in (a) 2003 and (b) 2004.

Relationship between seed predation and mouse capture indices

The estimated values of σ for mice (14.2 m in May 2003 and 23.6 m in May 2004) gave areas of activity of 0.4 ha (radius 35 m) in 2003 and 1.1 ha (radius 58 m) in 2004. Mouse capture indices at each station ranged between 0 and 2.6 in 2003 and 0 and 1.0 in 2004 (Fig. 5). Predation on rimu seed in both years and on mountain beech seed in 2004 were positively related to the mouse capture index (Fig. 5; Table 2). Predation on miro seed was also related to the mouse capture index in 2004, peaking at a low value of the index (Fig. 5; Table 2), although there were only 4 predation events that year and the index accounted for only 2% of the variation in miro predation. The most parsimonious models were Neighbourhood + Sites for rimu in 2003 and Neighbourhood models for rimu, mountain beech, and miro in 2004. Predation on mountain beech and miro seeds in 2003 and on broadleaf seeds in both years was not significantly related to the mouse capture index (Table 2). Site differences did not indicate consistent differences between alluvial and terrace forests (Fig. 5a).

Table 2. $\Delta AICc$ (the increment in $AICc$ compared with the best-fitting model, which has $\Delta AICc = 0$) for each of 5 models relating the risk of predation on different seed species to 4 different dependent variables in 2003 and 2004. R^2 values of the best-fitting models are given in parentheses.

Independent variable	Model	2003				2004			
		Rimu	Mountain beech	Broadleaf	Miro	Rimu	Mountain beech	Broadleaf	Miro
Alluvial principal component 1	Full	6.7	5.5	10.0	13.8	9.3	7.3	12.7	9.5
	Neighbourhood+Sites	0 (0.17)	2.7	4.0	6.4	0 (0.20)	1.2	3.8	3.9
	Neighbourhood	9.9	13.3	23.7	3.5	10.9	14.2	75.5	4.2
	Sites	9.3	0 (0.11)	0 (0.17)	2.7	1.0	0 (0.14)	0 (0.49)	0 (0.03)
Terrace principal component 1	Null	21.4	14.8	22.0	0 (0.00)	16.4	16.2	74.7	0.1
	Full	7.1	6.4	8.1	10.9	11.6	10.4	13.2	17.2
	Neighbourhood+Sites	3.9	3.9	1.5	4.1	4.3	2.6	4.3	8.4
	Neighbourhood	33.5	35.1	140.4	91.1	3.7	6.0	3.7	4.1
Terrace principal component 2	Sites	0 (0.21)	0 (0.21)	0 (0.87)	0 (0.56)	0.4	0 (0.05)	0.5	4.1
	Null	30.8	31.1	136.9	87.0	0 (0.00)	3.4	0 (0.00)	0 (0.00)
	Full	4.1	0 (0.25)	12.8	5.7	11.1	9.2	13.3	17.2
	Neighbourhood+Sites	0 (0.23)	2.5	4.2	0 (0.60)	3.9	3.5	4.5	8.4
Mouse capture index	Neighbourhood	25.0	20.8	132.2	76.3	3.2	3.2	1.5	4.1
	Sites	0.1	0.4	0 (0.87)	0.8	0.4	0 (0.05)	0.5	4.1
	Null	30.9	31.5	136.9	87.8	0 (0.00)	3.4	0 (0.00)	0 (0.00)
	Full	12.9	12.1	15	16.7	26.3	19.3	26.0	25.5
Neighbourhood+Sites	Neighbourhood+Sites	0 (0.18)	3.2	4	0.5	6.1	2.2	4.2	4.6
	Neighbourhood	44.1	48.2	162	90.0	0 (0.16)	0 (0.24)	33.0	0 (0.02)
	Sites	2.5	0 (0.16)	0 (0.65)	0 (0.37)	10.1	14.2	0 (0.65)	0.7
	Null	47.8	45.3	168	89.3	26.1	51.7	103.4	0.5

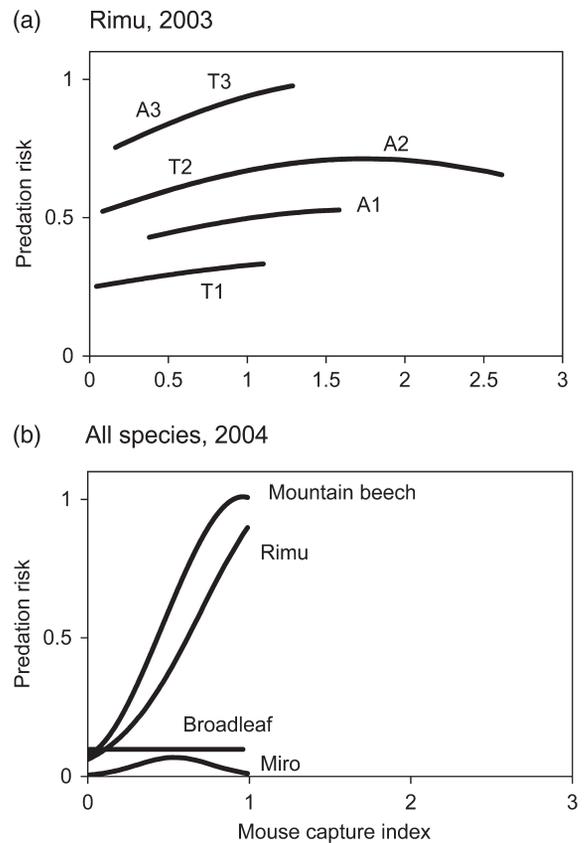
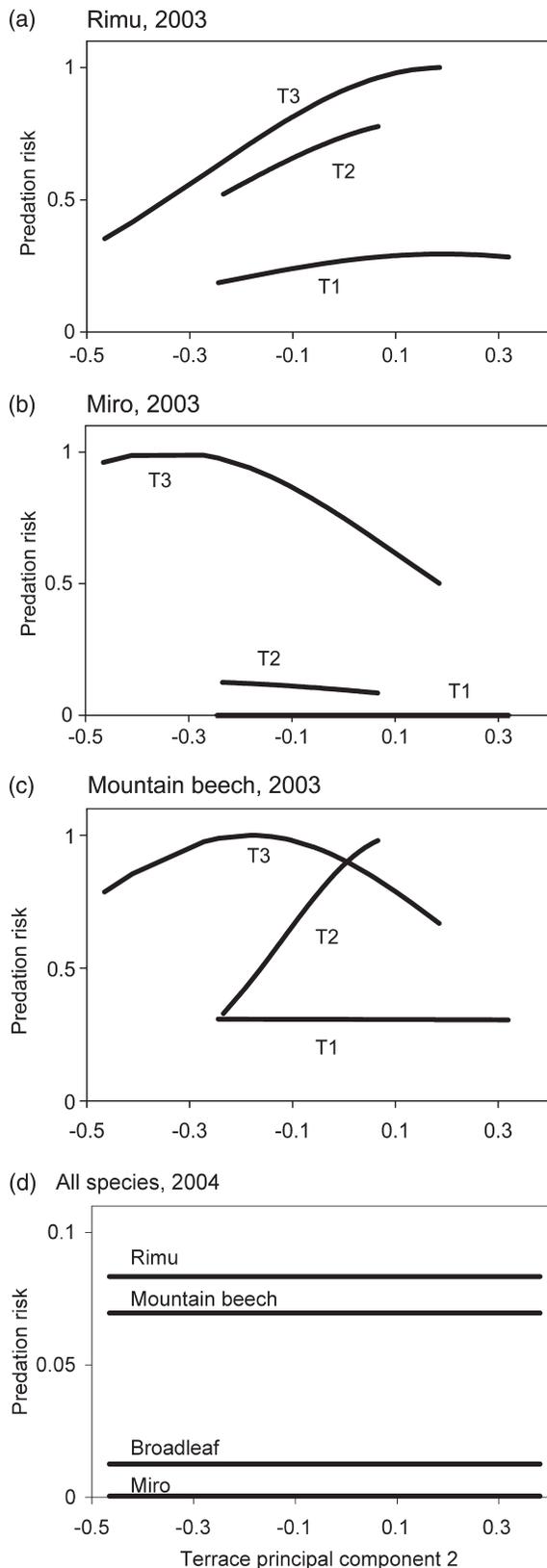


Fig. 5. Estimated risk of predation on experimental dishes of (a) rimu seed in 2003 and (b) all species trialled in 2004, as a function of the mouse capture index at alluvial and terrace sites combined.

Discussion

Vander Wall et al. (2005) cautioned that in many studies reporting seed predation, the seeds were likely to have instead been hoarded by rodents, ants (Formicidae), or dung beetles (Scarabaeidae: Aphodiinae), and were therefore dispersed rather than depredated. We are convinced that most of the seed removal we observed was seed predation, for 4 reasons. First, the rodents present at our study site were not scatter-hoarders (see Study species) and the larder-hoarding that they may practise to a small degree does not usually favour seed germination (Vander Wall 1990, Hulme 2002). Second, the ant fauna of New Zealand is depauperate, and the few species that are relatively abundant in forests are not primarily seed-hoarders

Fig. 4. Estimated risk of predation at terrace sites (T1, T2 and T3) on experimental dishes of (a) rimu seed in 2003, (b) miro seed in 2003, (c) mountain beech seed in 2003, (d) all seed species trialled in 2004, as a function of the second principal component. Note different scale of y-axis in (d).

(Don and Harris 2005a, b). Third, New Zealand's dung beetles are not coprophages but "soft saprophages", which consume liquid or semi-liquid components of decomposing plant matter (Stebnicka 2001), and therefore are unlikely to remove seeds. Finally, husks of rimu and beech seeds usually remained in our seed dishes, indicating that the seeds had been eaten (Results).

Seed predation in relation to canopy neighbourhood and rodent activity

The risk of predation on rimu, mountain beech, and miro seeds could be predicted both from the composition of the forest canopy in neighbourhoods equivalent to the seed shadows of individual trees (15-m diameter; ca 700 m²) and from captures of house mice adjusted for distance from the experimental seeds. Our results suggest that the local abundance of mice was concentrated in rimu and beech neighbourhoods, since mice eat seeds of both species (Ruscoe et al. 2004, 2005) and rodent activity often is highest in neighbourhoods where the seed rain comprises species that they preferentially consume (Schnurr et al. 2004). Predation risk on rimu and beech seed was highest in neighbourhoods dominated by rimu and beech trees, which produced most of the seed rain in both years of this study. Predation risk on rimu and beech seed was also higher at stations with high mouse capture indices.

The spatial pattern of seed predation on rimu seed was more complex than that predicted by the Janzen–Connell model. Predation risk on rimu seed, which varied with neighbourhood in both forest types and with mouse activity in both years, was high not only near conspecific trees but also near heterospecific trees (silver beech) with copious seed rain. Few studies have considered the effects of shared enemies on alternative prey ("apparent competition", Holt 1977) in relation to the Janzen–Connell hypothesis (Kwit et al. 2004). However, elevated risk to seeds in forest neighbourhoods where seed predators were foraging for heterospecific seeds has been documented recently (Kwit et al. 2004, Schnurr et al. 2004), and even less-preferred seeds may suffer high predation risk when associated with preferred species (Veech 2000, Schnurr et al. 2004). The peak in predation on rimu seed at alluvial sites in 2003, which occurred not where silver beech dominated most strongly but where there was also an intermediate component of kamahi (compare Fig. 2a and 3a), suggests that mice were satiated (Janzen 1971) close to beech trees. Declining predation risk with distance from a seed source due to predator satiation (McCanny 1985) accords with the predictions of Nathan and Casagrandi (2004) for mobile, generalist seed predators, since mice are omnivorous and their

areas of activity (35-m diameter) exceeded the typical maximum dispersion of silver beech seeds (15–25 m; Ruscoe et al. unpubl.). In contrast, in 2004 when beech seedfall was lighter, predation on rimu seed peaked in the most silver-beech-dominated neighbourhoods (Fig. 2a and 3b).

Satiation of mice in neighbourhoods where natural silver beech seed rain was most plentiful (i.e. at alluvial sites in 2003) may also have reduced the chance of mice preying on experimental mountain beech seeds there. Reduced predation risk due to predator satiation in these locations may have flattened the curves relating predation on beech seed to both alluvial canopy composition and mouse capture index. These effects may explain why we detected variation in predation on mountain beech seeds between terrace neighbourhoods but not between alluvial neighbourhoods, and in relation to mouse activity in 2004 but not in 2003.

Miro seeds experienced a low risk of predation in rimu-dominated neighbourhoods in terrace forests in 2003, and where mouse capture indices were high in 2004. Because miro seed is eaten by rats but not mice (Beveridge 1964, Daniel 1973, Campbell 1978, Ruscoe et al. 2004), this result suggests differential habitat use by these rodents. Others have observed inverse relationships between indices of abundance of rats and mice, and have suggested that rats may suppress the local abundance or activity of mice (Brown et al. 1996, Sweetapple and Nugent 2005). Predation on broadleaf seeds was uniformly low, did not vary significantly between neighbourhoods, and was not related to the mouse capture index. Our results suggest that these seeds may be avoided by mice and, because the relationships between miro seed predation and either terrace forest canopy neighbourhood or mouse capture index were not apparent for broadleaf seeds, possibly also by rats.

Between-year variation in spatial patterns of predation risk

Temporal variation in the spatial pattern of seed predation may result from temporal changes in both animal abundance and seed rain (Schnurr et al. 2004). We found that most relationships between predation risk and canopy neighbourhood were apparent only in 2003, when both seedfall and mouse abundance were relatively high. In 2004, when seedfall was low in all neighbourhoods, the distribution of rodents may have been determined by factors other than seed rain. For example, when seeds of preferred species are scarce, mice may forage primarily for invertebrates, which are often prominent in their diet (Fitzgerald et al. 1996, Ruscoe and Murphy 2005, Wilson et al. 2006a). The microhabitat preferences of mice in New Zealand have

not been analysed, but rats' habitat choices may be influenced by the presence of related individuals (Dowding and Murphy 1994) and the availability of cover (Harper et al. 2005). In the north-eastern USA, rodent activity was segregated by forest understorey characteristics at low rodent density but by canopy characteristics at high density (Schnurr et al. 2004).

Our results also demonstrate temporal variation in the degree of spatial variability in risk to seeds, related to the abundance of rodents and the locations of their foraging ranges. Most relationships between predation risk and mouse activity were apparent only in 2004, when seedfall and mouse abundance were low. Some experimental seed dishes may have been placed in locations free of mammalian seed predators in 2004, whereas the risk to experimental seeds within the foraging range of even one mouse may have been great because food from the seed rain was scarce. These factors would tend to create the steep curves of seed predation risk as a function of mouse capture index observed in 2004 (Fig. 5b). In contrast, at the relatively high mouse density in 2003 (17–28 ha⁻¹), most seed dishes were probably within the foraging range of several mice because the estimated area of activity of one mouse (radius 35 m) would have encompassed multiple seed dishes (20 m apart). Therefore, predation risk would have been high even where the capture index was low. On the other hand, predator satiation by the plentiful food in the seed rain in 2003 may have lessened the risk of predation on the experimental seeds, even where the mouse capture index was high. Combined, these factors would flatten the curves relating predation risk to mouse capture index.

We can predict relatively safe sites for rimu and mountain beech seeds based on the spatial distribution of canopy trees whose seeds are eaten by mice, in years of plentiful seed production and abundant mice (Schnurr et al. 2004). However, temporal heterogeneity in the spatial patterns of rodent activity and seed predation within stands may have important implications for tree population dynamics. To predict safe sites when seed rain is sparse or mice are scarce, we need to know more about the factors affecting spatial movements of mice in such conditions. Since forest litter-feeding lepidopteran larvae can be important foods for mice (Fitzgerald et al. 1996), understorey or substrate characteristics may be useful predictors of mouse activity when suitable seeds are scarce. Almost nothing is known of the species of forest seeds other than rimu and beech that are consumed by house mice in New Zealand. The Janzen–Connell hypothesis was insufficient to describe the spatial pattern of predation by mice on rimu seed, in part because of the influence of heterospecific seed sources. The spatial and temporal distribution of predation “safe sites” for seeds of other tree species also are likely to be defined by multivariate

relationships; that is, dependent on seed production by several tree species or on multiple characteristics of the forest understorey.

Implications of spatial patterns in seed predation

The neighbourhood patterns we observed show that the rimu and beech seeds most likely to escape predation were those that fell >15 m from parent trees of both taxa. Seed predation may therefore promote stand diversity in these forests (Janzen 1970, Connell 1971). However, most seeds of these species do not fall more than 15 m from their parent, although some rimu seeds are dispersed farther by birds and some beech seeds by wind (Ruscoe et al. unpubl.). Restricting seed survival to sites distant from mother trees of both of these common taxa may therefore strongly limit the locations where seedling recruitment can occur. Seedling establishment is further limited by the availability of suitable microsites, particularly in the alluvial forests, where the dense canopy and ferns create deep shade (Coomes et al. 2005). For example, silver beech seedlings were more likely to establish on elevated surfaces than on the forest floor of both forest types (Coomes et al. 2005); seed predators could reduce the suitability of raised microsites that are located close to beech or rimu trees. Seed predation by introduced mice may therefore both lower the rates of establishment of beech and rimu seedlings, and in time alter the spatial composition of these forests by displacing new generations of beech and rimu trees away from existing trees of both species. The relationships that we have quantified between forest canopy composition and seed predation can be used to parameterise spatially explicit simulation models that predict long-term changes to the forest with and without introduced rodents.

Ruscoe et al. (2005) used simulation modelling to predict whether a population of mice could consume an annual crop of beech seed before spring germination, in a pure beech forest system. At the mouse densities observed in February 2003 (17–28 ha⁻¹; Ruscoe et al. 2004), no beech seed would survive unless annual seedfall exceeded ca 1000–1200 m⁻² (Ruscoe et al. 2005). Combining annual seedfall of beech and rimu seeds (Table 1 in Ruscoe et al. unpubl.), and assuming silver beech and mountain beech seeds are of similar size (Wardle 1984, Webb and Simpson 2001) but adjusting for the lower seed mass of rimu compared with mountain beech (ca 76%; Ruscoe et al. 2004), this calculation suggests that some seeds of these species may have survived in 2003 at alluvial sites and at site T3 (975–1800 beech-seed equivalents m⁻²) but possibly not at the other 2 terrace sites (850–940 beech-seed equivalents m⁻²). Few seeds may have survived in 2004 either, with seedfall below 200 beech-seed

equivalents m^{-2} and mouse density as high as ca 5–7 ha^{-1} at 2 alluvial sites in February 2004, but lower elsewhere (Ruscoe and Wilson unpubl.). No rimu or beech seeds would have survived unless mouse density was well below 1 ha^{-1} , based on the isocline in Ruscoe et al. (2005).

Although these calculations suggest that in some years few seeds of species eaten by mice will escape predation at this location, some seeds of masting species such as rimu and beech should survive in years of high seed production. Enhanced seed survival in mast years may be typical of many masting species because of predator satiation (Janzen 1971, Crawley and Long 1995, Kelly and Sork 2002). Even when seeds are cached by scatter-hoarding rodents, the survival of cached seeds may be higher in mast years relative to non-mast years, leading to enhanced seed dispersal and germination in mast years (Vander Wall 2002, Jansen et al. 2004). We do not know whether fewer seeds survive in mast years in New Zealand now that rodents have replaced the depleted avian and invertebrate fauna (Holdaway 1989, Clout and Hay 1989) as the primary seed predators in New Zealand's forests. However, the ultimate effects of seed predators on tree populations can be predicted with simulations that incorporate the rates of seed production and loss that we have measured, in addition to rates of seedling and sapling growth and mortality (Pacala et al. 1996, Law and Dieckmann 2000).

Seed predation may lead to evolutionary selection for dispersal of seeds far from the parent tree (the "escape hypothesis", Howe and Smallwood 1982). However, rimu and beech trees in New Zealand forests evolved without rodents, and since most seeds may not disperse far enough to avoid them, birds and wind as agents of seed dispersal may be critical to seed survival in some years. New Zealand has a depleted number of seed-dispersing birds compared with pre-human times, because of the introduction of predators such as rats and stoats *Mustela erminea* (Clout and Hay 1989). Introduced birds, primarily blackbirds *Turdus merula*, and mammals, primarily possums, disperse some forest seeds (Beveridge 1964, Cowan 1990, Lord 1991, Burrows 1994, Williams et al. 2000, Dungan et al. 2002) but are unlikely to duplicate this function of the lost avian community because the introduced and native animals differ in abundance, movements, and the sizes of seeds eaten (Clout and Hay 1989, Williams 2003, 2006). The interactive effects of birds (both native and introduced) and rodents on seed predation may be complex, particularly in years of abundant seed production. For example, "contagious" (Schupp et al. 2002) (i.e. patchy) seed dispersal by birds beneath heterospecific fruiting trees where seed predators are also abundant may negate the advantage to the seed of escaping from its parent tree (Kwit et al. 2004).

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