

An experimental study of the impacts of understorey forest vegetation and herbivory by red deer and rodents on seedling establishment and species composition in Waitutu Forest, New Zealand

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Abstract: Introduced mammalian herbivores are changing the structure and composition of New Zealand's forest ecosystems and may modify forest succession after natural disturbances. We studied how introduced ungulates (red deer and feral pigs) and rodents (rats and house mice) affected the rate of recovery (i.e. the engineering resilience) of the forest understorey following artificial disturbance. We imposed disturbances by clearing understorey vegetation dominated by *Blechnum* ferns in forests on relatively fertile alluvium and elevated infertile marine terraces, and recorded recovery of vegetation (seedling establishment, species composition, cover and volume) in herbivore exclosures and controls. Seedlings quickly established on cleared plots: after 2 years, numbers of woody seedlings and ground cover of vascular plants relative to initial values were similar on cleared and uncleared treatments. Volume of plant biomass <2 m remained low on cleared subplots. Ungulates significantly reduced the re-establishment of woody seedlings ≥ 10 cm tall: only one seedling reached this height outside exclosures, compared with 29 seedlings inside. The number of seedlings <10 cm tall, expressed relative to numbers present pre-clearing, was not significantly affected by ungulates. The species composition of regenerating vegetation was more similar (Jaccard index) to pre-clearing understorey vegetation inside ungulate exclosures than outside. No consistent effect of rodents (primarily house mice) on seedling establishment or species composition was detected after 2 years, and rodent exclosures did not significantly affect survival of seedlings (*Griselinia littoralis* and *Aristotelia serrata*) planted as an index of rodent herbivory pressure. No significant differences in vegetation recovery were apparent between forest types. Rapid seedling recruitment in the absence of understorey vegetation and the presence of herbivores provided evidence that understorey vegetation competes with seedlings for light. Ungulate effects were consistent with other experiments that showed herbivores reduced the rate and altered the trajectory of vegetation regrowth after disturbance.

Keywords: deer; disturbance; feral pig; forest; herbivory; recovery rate; resilience; rodent; seed predation; seedling recruitment.

Introduction

Introduced mammalian herbivores are changing the structure and composition of New Zealand's forest ecosystems (e.g. Allen *et al.*, 1984, 1994; Cowan *et al.*, 1997; Wardle *et al.*, 2001). Deer (most notably red deer, *Cervus elaphus*) may interfere with succession in New Zealand forests re-establishing after disturbances such as fire and windthrow, by browsing seedlings of shrubs and trees and retarding their growth (McKelvey, 1973; Payton *et al.*, 1984; Wardle, 1984, p. 224). The rate of recovery of an ecosystem after a disturbance is known as resilience (Pimm, 1982) or engineering resilience (Holling, 1996). Holling (1996) coined the

latter term to distinguish it from ecological resilience, which he defined as the amount of disturbance that can be absorbed by a system before it shifts to a new state (Holling, 1973). Both terms quantify aspects of ecosystem stability (recently reviewed by Hooper *et al.*, 2005). How mammals other than possums (*Trichosurus vulpecula*) (*cf.* Wallis and James, 1972) affect the rate of recovery of New Zealand forests after disturbance has not been studied.

Mathematical and simulation models have predicted that the relative rates of recovery of hypothetical ecosystems with and without herbivores depend on the supply of limiting and non-limiting nutrients (DeAngelis *et al.*, 1989a, b). Recent

experimental tests have demonstrated that it may not be possible to generalise the impacts of adding herbivores or predators on recovery rates (Carpenter and Cottingham, 1997; Wardle *et al.*, 2000); instead the effect of adding a trophic level may be idiosyncratic (*sensu* Lawton, 1994), i.e. determined by interactive effects of the component species. For instance, insect herbivores and predators had no strong or consistent effects on the rate that experimental plant communities, in pots in a glasshouse, recovered from drought (Wardle *et al.*, 2000), and adding predatory fish to an experimental lake increased the recovery rate of phytoplankton after phosphorus addition because it changed the composition of the grazer community to organisms that could respond more rapidly to perturbation (Carpenter and Cottingham, 1997).

Most field tests of how herbivores affect the recovery of plant communities after perturbations have focused on post-fire dynamics, with mammalian herbivores either present or excluded by fences. Elk, marsupials, rabbits and rodents all slowed the re-establishment of post-fire vegetation or changed its species composition, by altering seedling survival and the growth of young and resprouting plants (Mills, 1986; studies reviewed by Quinn, 1986; Bailey and Whitham, 2002), although where herbivores were at low density or avoided burned areas their effects were not detected (Tyler, 1996; Hill and French, 2004). For example, low forest grew back inside quokka (the macropod *Setonix brachyurus*) exclosures in Australia after fire, but was replaced by heath outside (reviewed by Quinn, 1986), and in Central Otago, New Zealand, sheep grazing substantially slowed the post-fire regeneration of snow tussock grasses (*Chionochloa rigida*) (Gitay *et al.*, 1992). Insect herbivores also altered the growth rate and species composition of seedlings establishing after fire (Mills 1986). Changes to species composition mediated by herbivory following disturbance illustrate mechanisms by which these processes may combine to alter diversity (Caswell, 1978; Connell, 1978; Huston, 1979).

We tested the hypothesis that rodents and ungulates slow recovery after disturbance (i.e. lower the engineering resilience) of the New Zealand forest understorey by reducing the rate of seedling establishment and altering the species composition of regenerating vegetation through preferential feeding. Experimental clearing of patches of forest understorey was used as a model of disturbance. We compared the structure and composition of the recovering understorey vegetation to its pre-treatment state, which had probably developed in the presence of rodents and ungulates, of which most species arrived in New Zealand in the last 200 years (King, 2005). The forest has therefore been modified by these mammals in unknown ways compared to the mammal-free state (Caughley, 1989).

Seed of species palatable to mammals continues to be supplied by trees that pre-date the introduction of the herbivores and by epiphytes of these species growing above the reach of deer (e.g. Stewart, 1986; Stewart and Burrows, 1989; Wardle, 1991, pp. 573–576). After ungulates are excluded, therefore, the recruitment rate of preferred species rises and species composition diverges from that of the pre-exclosure vegetation (Jane and Pracy, 1974; Stewart and Burrows, 1989; Smale *et al.*, 1995; Nugent *et al.*, 1997).

The seedlings and vegetatively regenerating plants that colonise experimental plots after older plants have been removed are vulnerable to herbivory because (1) young tissue is often relatively nutrient-rich (Vesey-Fitzgerald, 1960; Arnold, 1964), (2) a single bite can kill a seedling (Quinn, 1986), (3) ungulates preferentially use clearings (Wardle, 1984, p. 224), (4) preferred forage plants may be easier for herbivores to find on cleared sites, and (5) non-trophic effects of herbivores such as digging and trampling (Tilman, 1983; McNaughton, 1983; Duncan and Holdaway, 1989) are likely to affect seedlings more than larger plants. Therefore, the relative mortality rates of plants of preferred and less preferred species may change after clearing, with fewer palatable species able to survive in the presence of herbivores on clearings compared with surrounding areas. The species composition on cleared plots may therefore diverge from its pre-clearing state in both the presence and absence of herbivores, but in different directions. Which effect is greater will depend on levels of herbivore pressure and relative recruitment rates of different species in the absence of herbivores. Vegetation regenerating on burned plots resembled the pre-treatment vegetation more within than outside herbivore exclosures (Mills, 1986; studies reviewed by Quinn, 1986).

Our hypothesis therefore leads to the predictions that (1) after experimental clearing, seedlings will establish more rapidly inside than outside ungulate exclosures and rodent exclosures and (2) the species composition of recovering vegetation will diverge from that of the original understorey vegetation both within exclosures and outside. We also predicted that (3) the difference in recovery rates with and without herbivores will be greater at more fertile sites, because abundant soil nutrients will increase both plant growth rates and the palatability of regenerating tissue.

Methods

Study sites

This research was done in Waitutu Forest, Fiordland National Park, South Island, New Zealand (Mark *et al.*, 1988; Ward, 1988). Six study sites were established

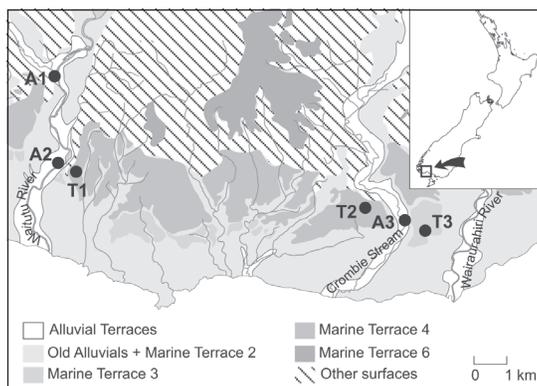


Figure 1. Map of the study area in Waitutu Forest showing its position on the western south coast of New Zealand (inset), and alluvial (A1–A3) and terrace (T1–T3) study sites. Numbering of marine terraces follows Ward *et al.* (1988).

in tall (~20 m) mixed forests of two vegetation types, with three sites on alluvial terraces bordering rivers at ~30 m a.s.l. ('A' in Fig. 1) and three on older, uplifted marine terraces 3 and 4 ['T' in Fig. 1; terrace numbers follow Ward (1988)] at 80 to 120 m a.s.l. Sites were chosen based on the presence of representative plant species indicating relatively high fertility of the alluvial soils and lower fertility of the terraces. The ground layer in these forests was dominated by the ferns *Blechnum discolor* (crown fern) at alluvial sites and *B. procerum* at terrace sites (Coomes *et al.*, 2005). Sites were at least 0.7 km apart and separated by steep cliffs at terrace edges, three in the catchment of the Crombie Stream (46° 14' S, 167° 11' E) and three in the Waitutu River catchment (46° 12' S, 167° 04' E). The vegetation and soils at the six study sites have been described by Wardle *et al.* (2004), Coomes *et al.* (2005), and Williamson *et al.* (2005).

Abundance of deer, rodents and possums

The density of deer faecal pellet groups along transects at each site was measured as an index of red deer abundance (Forsyth, D.A.; Scroggie, M.P.; Reddiex, B. 2003. unpubl. data). Mean pellet group density (PGD) ranged from 88 to 202 per hectare at the different sites. PGD was 62% higher at site T1 than the average at the other two terrace sites, based on 95% confidence intervals, but did not otherwise differ significantly between sites (Forsyth, D.A.; Scroggie, M.P.; Reddiex, B. 2003. unpubl. data). Deer densities cannot be calculated from these abundance indices, as defecation rates and pellet decay rates are unknown.

The abundance of mice (*Mus musculus*) and rats (*Rattus* spp.) was estimated by capture-mark-recapture in Elliott live traps, on 1.4-ha trapping grids surrounding

each study site, every 6 months from May 2001 to November 2002 (Ruscoe, 2004; Ruscoe *et al.*, 2004), and every 3 months thereafter. Only one mouse and no rats were caught before November 2002, when the populations increased sharply following a heavy *Dacrydium cupressinum* (rimu) seedfall the previous (2002) winter (Ruscoe *et al.*, 2004). The minimum density of mice, estimated based on minimum number alive (MNA; Krebs, 1966), rose to 17–28 per hectare at the different sites, remained high until the next winter (August 2003), then declined to low levels by autumn (May) 2004 (Ruscoe *et al.*, 2004; Ruscoe and Wilson, unpubl. data). Kiore (Polynesian rats, *Rattus exulans*) and ship rats (*R. rattus*) were caught beginning in November 2002, but too infrequently for rat density to be estimated (Ruscoe, 2004; Ruscoe and Wilson, unpubl. data). Kiore were caught at all sites but A2, most in the Crombie Stream catchment. Ship rats were caught at all sites but T3.

Brush-tail possums are a relatively recent arrival in Waitutu Forest (since the 1970s; Cowan, 2005) and were intensively poisoned throughout the Waitutu River valley in 1997 (C. J. West, Department of Conservation, N.Z., pers. comm.). The mean residual trap catch (RTC; NPCA, 2004) of possums near the Waitutu River in March 2001 was 2.5% (0.9–4.1 95% CI) in the valley and 1.8% (0.6–2.9) on terraces above the river (M. Mawhinney, Department of Conservation, N.Z., pers. comm.), which is below the 5% RTC threshold commonly used as a possum management goal. Because of these low possum abundance indices in an area which includes two alluvial sites and one terrace site in the western part of our study area, we did not design this study to test for effects of possums. However, RTC was 21.2% (13.9–28.5) in April 2002 in a 3-km-square area centred on the Crombie Stream and including the alluvial site and two terrace sites in the eastern part of our study area (M. Mawhinney, Department of Conservation, N.Z., pers. comm.). The data collectively suggest that possum density decreases from east to west in our study area, with three sites having relatively high possum density, and three having relatively low density. Feral pigs (*Sus scrofa*) were also present in these forests, particularly at the alluvial sites, at unknown density.

Ungulate enclosures

One ungulate enclosure (23 m × 23 m) was built at each site in February 2001, where canopy cover was intermediate and the plant species used to choose study sites (above) were present. Enclosures were constructed of wire deer fencing, 1.8 m high with 15-cm mesh, supported by wooden posts, with barbed wire around the lower edge to exclude feral pigs.

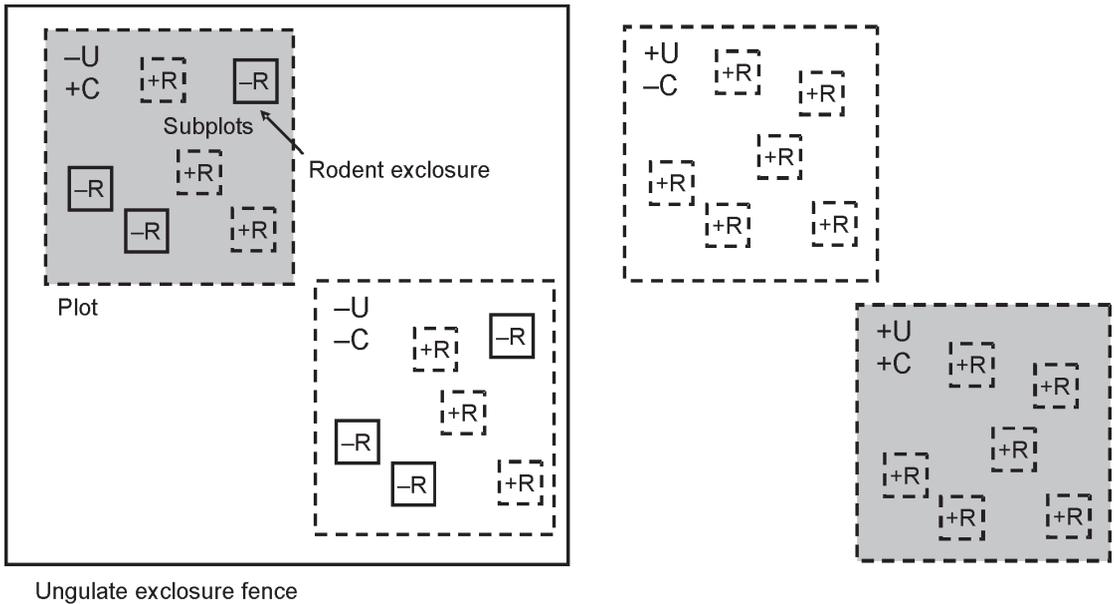


Figure 2. Experimental design, repeated at each of the three alluvial and three terrace sites, showing plots (5 m × 5 m) and subplots (0.5 × 0.5 m). +/- U and +/- R indicate treatments with and without ungulates and rodents respectively; rodent exclusion fences were 1 m square. Shading indicates cleared (+C) plots. Drawing is not to scale.

Study plots

In October and December 2001, two 5 m × 5 m plots were established within each ungulate exclusion (-U treatments), and two outside each exclusion (+U, Fig. 2). Plots were chosen with moderate cover of *Blechnum discolor* at alluvial sites or *B. procerum* at terrace sites, and without large trees or tree ferns. We recorded vegetation composition and structure on each 5 m × 5 m plot according to the RECCE method (Allen, 1992).

Within each plot, six terrestrial subplots (0.5 m × 0.5 m) were marked at the corners with bicycle spokes. Subplots were located away from mounds and logs, with similar fern cover on each. At alluvial sites, each subplot was positioned with a large *Blechnum discolor* (0.55–1.55 m high) just outside its western edge. Although no large *Blechnum discolor* plants were present on plots, overhanging fronds of nearby plants of this species covered 25–100% of each plot. On terrace sites, subplots were chosen with similar cover (15–60%) of *Blechnum procerum*.

Vegetation was measured when the experiment was established in 2001 and remeasured in November 2002 and November 2003, in the ground-level layer (0–0.1 m) and above this in the browse layer (0.1–2 m). On each subplot we recorded by species: number of woody seedlings < 10 cm tall, heights of seedlings and saplings ≥ 10 cm and ≤ 2 m tall, and percentage cover in each layer, estimated based on a 50-cm-square

quadrat frame divided into squares 10 cm × 10 cm. The top and bottom heights of foliage in the tier 0.1–2 m were also recorded for each species. Volume of plant biomass 0.1–2 m above the subplot was calculated for each species as the product of the vertical distance between these top and bottom heights and the area of the subplot covered (i.e. 0.25 m² × percentage cover in this layer ÷ 100). Finally, total percentage cover of all species between 0.1 and 2 m was recorded. Plants that resprouted after experimental clearing (see below) were not counted as seedlings but were included in calculations of cover, volume and species composition.

Experimental clearing

After measuring vegetation for the first time (in 2001), we cleared understorey plants from one plot (5 m × 5 m; including the six subplots within the plot) inside and one outside each ungulate exclusion, chosen at random (+C treatments, Fig. 2). All vascular plants of height ≤ 2 m or dbh (stem diameter measured at breast height, 1.4 m) < 5 cm were removed by clipping or sawing at ground level. Moss, litter and duff were disturbed as little as possible. Plants rooted outside the plot or growing as epiphytes above the plot surface were not removed.

In November 2003, we additionally recorded the species and height of all seedlings ≥ 10 cm tall that had established on each cleared 5 m × 5 m plot. Parts of

plots within rodent exclosures, or disturbed by the construction of rodent exclosures, were excluded from these whole-plot counts.

Rodent exclosures

Once clearing of ground vegetation was completed, rodent exclosures (1 m square and 1 m high) were built around three of the six subplots, chosen at random, on the cleared and uncleared plots inside ungulate exclosures (-U-R treatments, Fig. 2). Subplots outside ungulate exclosures (+U+R) did not receive rodent exclosures because these would effectively exclude ungulates in addition to rodents, duplicating the -U-R treatments. Rodent exclosures were made of 6-mm galvanised wire mesh, 120 cm wide, stapled to wooden posts at each corner. The lower 20 cm of the mesh was folded outwards to form a skirt, which was stapled to the ground with wire and covered with soil. Prior to use, the mesh was left outdoors for several weeks or rinsed in river water to remove any coating that might be toxic to plants. Aluminium sheeting was folded over the top edge of the mesh so that it covered the top 40 cm of mesh outside and the top 20 cm inside the structure, to prevent rodents from climbing up the mesh and into the exclosure. It is difficult to completely exclude mice, because although 6-mm mesh excludes even juveniles (Day, T. and MacGibbon, R., Xcluder™ Pest Proof Fencing Company, 2002. unpubl. data), mice are so light-weight that they can climb all but very smooth surfaces. The vertical cut edge of the aluminium was therefore covered with smooth plastic tape so that mice could not climb along it. Overhanging or leaning vegetation that would enable rodents to enter the exclosure was removed at the beginning of the study and twice yearly thereafter.

We tested whether rodents entered the exclosures by placing baited tracking tunnels inside for three nights in February 2003 when rodent density was high. No rodent tracks were found inside the rodent exclosures. At the same time, mouse tracks were recorded in five to eight of nine tunnels spaced across each rodent trapping grid, although rat tracks were found in only one tunnel on each of two grids (at A2 and T3). Possums could enter the ungulate exclosures but may have been deterred by the rodent exclosures, and no sign of faecal pellets or browse attributable to possums was recorded in rodent exclosures. Rodent exclosures did not significantly reduce light availability on the subplots, based on nine quantum sensor (LI-190SA, LI-COR Corporation, Nebraska) light readings near the surface of each +R and -R subplot at four of the six sites, standardised relative to the average of continuous light readings taken nearby (t -tests on data from each of four sites, $t_{11} < 1.4$, $P > 0.23$).

Survival of planted seedlings as an index of rodent herbivory

As an index of rodent herbivory pressure, four seedlings, about 10 cm tall, of each of two tree species, *Griselinia littoralis* (broadleaf) and *Aristotelia serrata* (wineberry), were planted adjacent to each uncleared -R and +R subplot. These species were chosen because they were readily available and are preferred forage plants of ungulates (Forsyth *et al.*, 2002), although their palatability to rodents is not known. Broadleaf is common on both alluvial and terrace sites, and wineberry is uncommon but occurs in the Waitutu River valley. Seedlings were supplied bare-rooted by Ribbonwood Nurseries, Dunedin, grown from seed obtained near Dunedin (45° 53' S, 170° 30' E). In June 2002, seedlings were planted at four of our six sites, one alluvial and one terrace site within each of the Crombie and Waitutu catchments (96 seedlings per species in total). The seedlings were planted just outside the subplots (but inside rodent exclosures at -R subplots), one of each species on each side of the square. Survivors were counted in November 2002 and counted and removed in June 2003 (368 days total). In June 2003, fresh seedlings were planted at all six sites (144 seedlings per species), counted in November 2003, and counted and removed in late May 2004 (349 days).

Variables indicating rate of recovery of vegetation after clearing

For testing effects of ungulates on recovery of vegetation after clearing, and for comparing cleared and uncleared treatments, variables were calculated for each plot (the experimental unit for these tests) by combining data from the subplots without rodent exclosures within each plot (+U+R and -U+R subplots). For testing effects of rodents, variables were calculated for each subplot (the experimental unit for these tests) inside ungulate exclosures only (-U+R and -U-R subplots). The -R subplots were used only to test for rodent effects and were not used in tests of effects of ungulates or clearing.

Seedling establishment and cover and volume of vegetation

The number of woody seedlings <10 cm tall 1 or 2 years after clearing, relative to numbers before clearing in 2001, was calculated as

$$\frac{\text{Total number of seedlings in 2003 (or 2002)}}{\text{Total number of seedlings before clearing in 2001}}$$

However, when this calculation was made for each subplot for testing rodent effects, the denominator was often zero because many subplots had no seedlings in

2001. Therefore, an alternative calculation was made for testing rodent effects:

$$\frac{\text{Total number of seedlings in 2003 (or 2002)}}{\text{Mean number of seedlings in 2003 (or 2002) and before clearing in 2001}}$$

When the numerator and denominator of this ratio were both zero (six instances in 2002 and six in 2003), the result was set to 1 to indicate no change.

Similarly, percentage ground cover and the volume of vegetation 0.1–2 m above subplots 1 and 2 years after clearing were expressed relative to the value of these variables before clearing, as

$$\frac{\text{Ground cover or volume in 2003 (or 2002)}}{\text{Ground cover or volume before clearing in 2001}}$$

Numbers of seedlings ≥ 10 cm on the cleared 5 m \times 5 m plots could not be expressed relative to initial values because they were counted in 2003 only, and were left as counts.

Species composition

Jaccard similarity coefficients (Krebs, 1989, p. 293), were used to compare the species composition on subplots 1 and 2 years after clearing with the species composition on the same subplots prior to clearing in 2001. Jaccard similarities, which take account of the presence but not the abundance of species, were chosen so that abundant ferns did not dominate the comparisons. For each subplot, the Jaccard similarity coefficient was calculated as:

$$\frac{a}{a + b + c}$$

where a represents the number of species present both after clearing in 2003 (or 2002) and before clearing in 2001, b the number of species present before but not after clearing, and c the number of species present after but not before clearing. For testing ungulate effects, similarities were calculated for all subplots in a treatment combined. Because there were twice as many +U+R subplots as –U+R subplots, +U+R subplots within a treatment were randomly separated into two groups of three and the similarity scores for each group were averaged to obtain a single score.

Similarity coefficients were also calculated to compare the species composition on each 5 m \times 5 m plot 1 and 2 years after clearing with the species composition on the same plot before clearing in 2001.

When treatment effects were statistically significant, we tested whether these effects were consistent for species preferred and avoided by deer, by calculating similarity scores based only on these species. Preferences of red deer were based on Forsyth *et al.* (2002), substituting preferences of other deer or other ungulates where data were unavailable.

Statistical methods

Linear mixed models were fitted, using residual (or restricted) maximum likelihood estimation [REML procedure in GenStat (GenStat Committee, 2002)], to the relative seedling number, ground cover and volume data from 2002 and 2003 (following \log_e transformation), and to similarity data from 2002 and 2003 (following arcsine square-root transformation). The REML method avoids the biased estimates of variance components generated by ordinary maximum likelihood estimation in models with both random and fixed effects. Vegetation type (alluvial or terrace) was considered a random factor because it represented two of many possible fertility regimes that were of little individual interest. Site was also a random factor, nested within Vegetation type. The treatments Clearing, Ungulates and Rodents were considered fixed factors. These models were used to calculate means and standard errors of the data from both years, but statistical tests were done only on the results from 2003, 2 years after clearing.

Because of the unbalanced experimental design, effects of ungulates and rodents were tested separately, with plot and subplot, respectively, used as experimental units. Experimental units were considered to be independent for the purposes of these tests, although subplots within a plot may have been affected by the same population of rodents. Variation between vegetation types or sites was considered unimportant unless the estimated variance component due to the factor was large relative to its standard error, but these random factors were always left in the model. Wald χ^2 tests were used to test for statistically significant ($P < 0.05$) treatment effects. These tests tend to give significant results too frequently when sample sizes are small. Therefore, results that were marginally significant and based on small samples (12 plots or fewer) were confirmed by means of likelihood-ratio (LR) tests comparing the mixed model to a nested submodel; in mixed models these tests tend to be slightly conservative (GenStat Committee, 2002). When a significant interaction between treatments occurred ($P < 0.05$), the effects of ungulates or rodents were tested separately for cleared and uncleared plots.

Seedling counts on cleared 5 m \times 5 m plots in 2003 were compared between ungulate treatments with a generalised linear mixed model [GLMM procedure in GenStat (GenStat Committee, 2002)], assuming that the counts followed an over- or under-dispersed Poisson distribution (i.e. with the variance unequal to the mean). As above, Vegetation type and Site were considered random factors, Ungulates was considered a fixed factor, and a Wald χ^2 test was used to test for a statistically significant treatment effect.

The probability of survival of planted seedlings was estimated with the Known Fates model in program

Table 1. Characteristics of vegetation on subplots (24 per site, 0.5 × 0.5 m), < 10 cm and 0.1–2 m above the ground (excluding epiphytes), prior to clearing in 2001.

	Ground cover < 10 cm (%) Mean ± SE	Volume of plant biomass 0.1–2 m (m ³) Mean ± SE	Number of seedlings < 10 cm. Mean and range	Number of seedlings 0.1–2 m. Mean and range	Number of species Mean and range	Species per site
Alluvial sites						
A1	5 ± 1	0.10 ± 0.01	1.8 (0–10)	0.04 (0–1)	1.8 (0–5)	29
A2	10 ± 1	0.08 ± 0.01	3.1 (0–21)	0.04 (0–1)	3.7 (1–8)	37
A3	7 ± 2	0.11 ± 0.01	1.4 (0–7)	0.00 (0–0)	2.8 (0–7)	35
Terrace sites						
T1	24 ± 3	0.01 ± 0.00	9.1 (0–36)	0.38 (0–3)	4.3 (2–9)	36
T2	13 ± 2	0.01 ± 0.00	5.1 (0–15)	0.71 (0–3)	3.7 (1–8)	36
T3	18 ± 2	0.01 ± 0.00	8.4 (0–21)	1.75 (0–12)	7.7 (5–13)	29

MARK (White and Burnham, 1999). The experimental unit for this analysis was the seedling, although four seedlings of each species were planted at each subplot. Survival parameters were estimated separately for the two seedling species, the two years, the four or six sites used in the different years, and inside and outside rodent exclosures. Simpler models were then fitted, with survival set equal between species, vegetation types (alluvial or terrace), sites within each vegetation type, years, or rodent treatments. The best of these models was selected based on minimising Akaike's Information Criterion corrected for small sample sizes (AICc; Akaike, 1974; Hurvich and Tsai, 1989).

Results

Vegetation characteristics prior to clearing

At the beginning of the study, alluvial sites had lower ground cover, fewer seedlings per subplot, and much higher volume of plant biomass between 10 cm and 2 m, compared with terrace sites (Table 1). The number of vascular species present, excluding epiphytes, was similar at all sites (Table 1). *Blechnum* ferns accounted for a large percentage of the total ground cover <10 cm on terrace sites (66 ± 7% SE; alluvial sites 11 ± 4%) and the total volume of plant biomass 0.1–2 m above subplots on all sites (98 ± 1%).

Recovery of vegetation after clearing

Most regeneration of woody species occurred through the establishment of new seedlings (Tables 2, 3), but a few individuals of *Metrosideros umbellata* (southern rātā), *Weinmannia racemosa* (kāmahī) and *Neomyrtus pedunculata* (rōhutu) resprouted where they had been clipped. Ferns, a liane (*Metrosideros diffusa* or white climbing rātā) and herbaceous plants including *Libertia pulchella*, *Nertera* spp., and several orchid species regenerated from rhizomes or bulbs.

In all our mixed models of recovery of vegetation after clearing, the estimated variance components due to Vegetation type (alluvial or terrace) and Site were of a magnitude similar to that of their standard errors. We therefore concluded that there was no significant variation in any of our dependent variables measuring recovery of vegetation that could be ascribed to differences between vegetation types or sites. Means presented below were calculated across all sites.

Seedling establishment

Seedlings quickly established on cleared plots, so that 2 years after clearing the number of seedlings <10 cm tall relative to initial numbers was close to one and was similar between cleared and uncleared subplots (Fig. 3a; $\chi^2_1 = 0.3$, $P = 0.60$). At alluvial sites more than four times as many seedlings <10 cm tall of woody species known to be preferred by deer established per cleared subplot, on average, in –U+R compared with +U+R treatments (Table 2). At terrace sites, however, the number of preferred seedlings establishing was similar in the two treatments (Table 2). When numbers of these small seedlings were expressed relative to their pre-clearing numbers, they were not significantly affected by ungulates, either when all species were combined or when statistical tests were done separately for species preferred by deer and for other species (Fig. 3a; $\chi^2_1 \leq 1.7$, $P > 0.19$). Rodents did not significantly affect the establishment of seedlings < 10 cm (Fig. 3b; $\chi^2_1 = 0.01$, $P = 0.92$).

Only one seedling ≥10 cm occurred on our cleared subplots in 2003 (a *Schefflera digitata*, patē, seedling on an alluvial –R–R subplot). On the cleared 5 m × 5 m +U plots one seedling (a *Prumnopitys ferruginea* or miro) reached a height ≥10 cm by 2003, whereas 29 seedlings did so on cleared 5 m × 5 m –U plots outside rodent exclosures (Table 3). Most of these seedlings were <20 cm tall. The difference between ungulate treatments was significant ($\chi^2_1 = 8.1$, $P = 0.004$). There was no significant variation in numbers of these

Table 2. Mean numbers of seedlings < 10 cm tall on cleared subplots (0.5 × 0.5 m) at alluvial and terrace sites in November 2003, 2 years after clearing. Preferences of red deer were based on Forsyth *et al.* (2002), substituting preferences of other deer or other ungulates where data were unavailable. Blank entries represent zeroes.

Species	Alluvial sites			Terrace sites		
	+U+R	-U+R	-U-R	+U+R	-U+R	-U-R
Species preferred by deer						
<i>Aristotelia serrata</i>			0.1			
<i>Coprosma foetidissima</i>	0.1	1.2	0.7	0.1	0.3	
<i>Elaeocarpus hookerianus</i>				0.1		0.1
<i>Griselinia littoralis</i>	0.2	1.6	0.6	0.1		
<i>Pennantia corymbosa</i>	0.2	0.4	0.3			
<i>Pseudopanax</i> spp.*	0.1				0.3	0.3
<i>Ripogonum scandens</i>	0.2	0.1				0.1
<i>Schefflera digitata</i>		0.4	0.4			
<i>Weinmannia racemosa</i>	0.2		0.1		0.6	
Mean seedlings per subplot	0.8	3.8	2.2	1.0	0.7	0.2
Species neither preferred nor avoided						
<i>Carpodetus serratus</i>	0.2	0.1	0.4			
<i>Clematis paniculata</i>	0.1	0.1				
<i>Myrsine australis</i>		0.3	0.1			
Unidentified cotyledons	1.2	0.1	0.6	0.2	0.1	
Mean seedlings per subplot	1.4	0.7	1.1	0.2	0.1	0.0
Species avoided by deer						
<i>Coprosma</i> spp. **	1.3	2.2	1.2	0.3	0.1	
<i>Dacrydium cupressinum</i>					0.2	0.1
<i>Myrsine divaricata</i>	0.3		0.2			
<i>Neomyrtus pedunculata</i>				0.1	0.1	0.3
<i>Nothofagus solandri</i> var. <i>cliffortioides</i>					0.7	0.4
<i>Nothofagus menziesii</i>	0.3	0.2		0.5	0.3	1.0
<i>Podocarpus hallii</i>				0.2	0.1	0.1
<i>Prumnopitys ferruginea</i>				1.0	1.6	0.3
<i>Pseudowintera colorata</i>	0.1	0.1	0.1			
<i>Rubus australis</i>		0.1				0.1
Mean seedlings per subplot	2.0	2.7	1.6	3.2	3.0	2.3
Grand mean seedlings per subplot	4.2	7.1	4.9	4.4	3.8	2.9

* includes *Raukawa simplex*

** small-leaved species including unidentified individuals of *C. foetidissima*

seedlings attributable to differences between terraces or sites, although 22 of the 29 tall seedlings occurred at site A1 (the ungulate effect remained significant if this outlier was eliminated, $\chi^2_1 = 6.4$, $P = 0.012$).

Species composition

After 2 years, species assemblages were less similar to their initial state on cleared subplots than on uncleared subplots (Fig. 4; $\chi^2_1 = 5.5$, $P = 0.019$). Mean similarity to initial species assemblages was higher on -U treatments (0.53) than on +U treatments (0.42) on cleared subplots only (Fig. 4; Wald test $\chi^2_1 = 5.2$, $P = 0.022$; LR test $\chi^2_1 = 3.6$, $P = 0.058$). On uncleared subplots the effect of ungulates was not significant (+U 0.63, -U 0.64; $\chi^2_1 = 1.3$, $P = 0.25$; interaction

between Clearing and Ungulates $\chi^2_1 = 4.1$, $P = 0.042$). Rodents did not significantly affect the similarity of the species composition 2 years after clearing to the initial species composition ($\chi^2_1 = 0.5$, $P = 0.50$).

On the 5 m × 5 m plots, the similarity of species assemblages to their initial state after 2 years was lower on cleared than on uncleared plots (Fig. 5; $\chi^2_1 = 15.4$, $P < 0.001$), consistent with the results on subplots, but did not differ significantly between -U and +U treatments ($\chi^2_1 = 0.08$, $P = 0.78$).

When similarity was calculated based on species preferred or avoided by deer (done where effects above were significant), neither the effect of ungulates (preferred: $\chi^2_1 = 1.2$, $P = 0.27$; avoided: $\chi^2_1 = 0.0$, $P = 0.96$) nor the effect of clearing (preferred: $\chi^2_1 = 1.1$, P

Table 3. Seedlings ≥ 10 cm tall that established on $5\text{ m} \times 5\text{ m}$ cleared plots, outside rodent exclosures. Deer preference categories as in Table 2. Blank entries represent zeroes.

Species	Alluvial sites		Terrace sites	
	+U+R	-U+R	+U+R	-U+R
Species preferred by deer				
<i>Coprosma foetidissima</i>		1		
<i>Fuchsia excorticata</i>		1		
<i>Pennantia corymbosa</i>		14		
<i>Raukaua simplex</i>				1
<i>Schefflera digitata</i> *		3		
Total	0	19	0	1
Species avoided by deer				
<i>Coprosma ciliata</i>		1		
<i>Coprosma rotundifolia</i>		3		
<i>Nothofagus solandri</i> var. <i>cliffortioides</i>				1
<i>Podocarpus hallii</i>				1
<i>Prumnopitys ferruginea</i>			1	2
<i>Pseudowintera colorata</i>		1		
Total	0	5	1	4

* One additional *Schefflera digitata* seedling > 10 cm tall established on an alluvial -U-R plot.

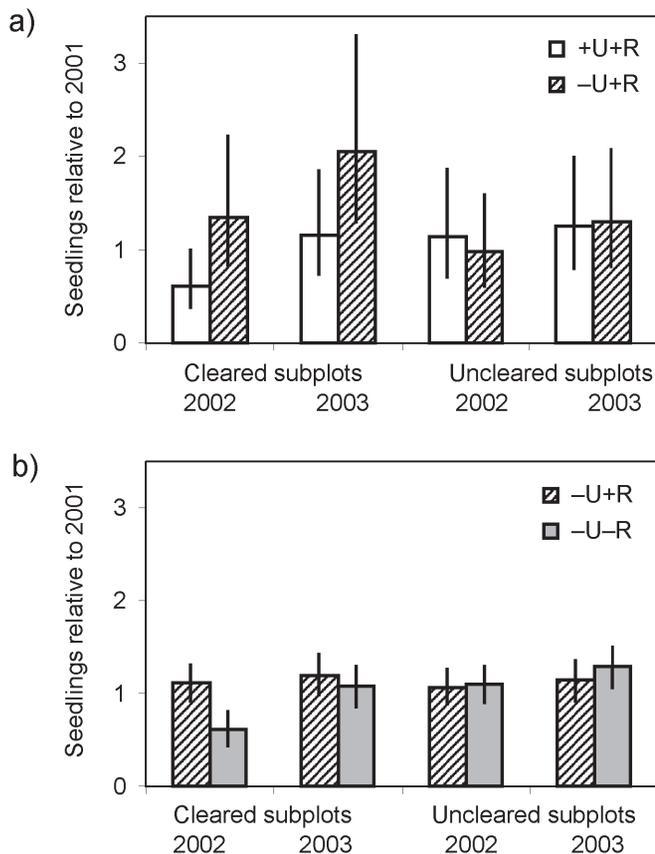


Figure 3. a) Number of seedlings < 10 cm tall in 2002 and 2003 relative to number of seedlings in 2001, on cleared and uncleared subplots with rodents and with (+U+R) and without ungulates (-U+R). b) Number of seedlings < 10 cm tall, in 2002 or 2003 relative to the average of the numbers in that year and in 2001, on cleared and uncleared subplots without ungulates and with (-U+R) and without rodents (-U-R). Data from all alluvial and terrace sites are combined. Since estimates in (a) were calculated at the plot level (combining three or six +R subplots per plot) and estimates in (b) were calculated at the subplot level, estimates and error bars for -U+R treatments differ between (a) and (b). Error bars denote standard errors.

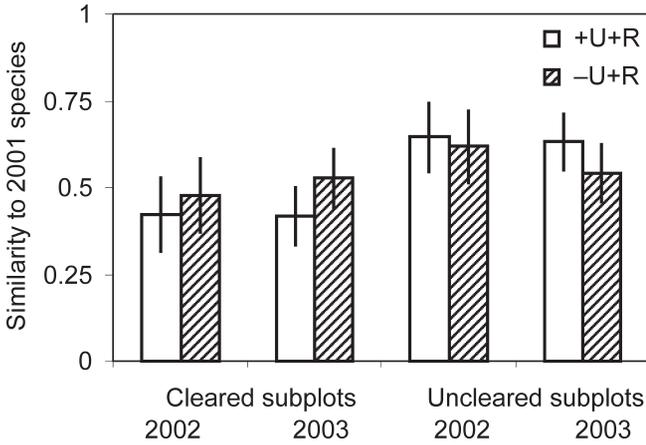


Figure 4. Jaccard similarities comparing species assemblages on subplots in 2002 and 2003 with the species initially present on subplots in 2001, on cleared and uncleared subplots with rodents and with (+U+R) and without ungulates (-U+R). Error bars denote standard errors.

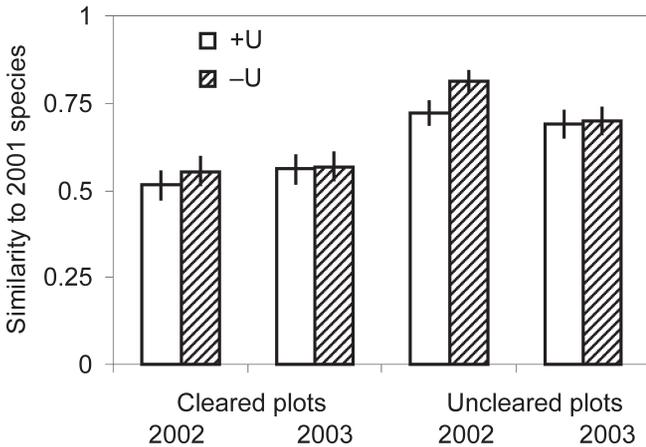


Figure 5. Jaccard similarities comparing species assemblages from RECCEs on 5 m x 5 m plots in 2002 and 2003 with the species initially present in 2001. Cleared and uncleared plots with (+U) and without ungulates (-U) are shown. Error bars denote standard errors.

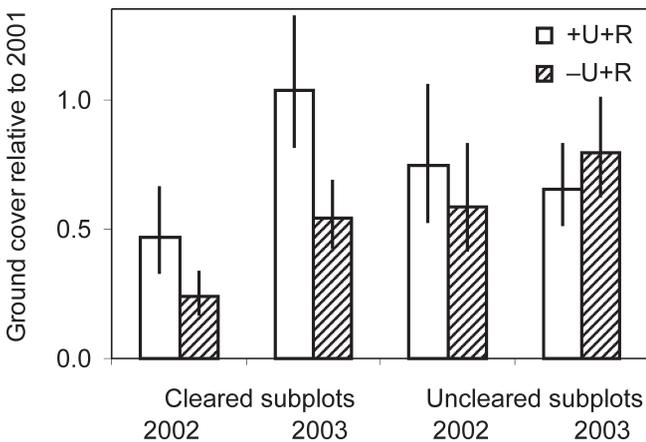


Figure 6. Percentage ground cover in 2002 and 2003 relative to percentage ground cover before clearing in 2001, on cleared and uncleared subplots with rodents and with (+U+R) and without ungulates (-U+R). Error bars denote standard errors.

= 0.30; avoided: $\chi^2_1 = 2.8$, $P = 0.10$) were significant on subplots. Deer-avoided species assemblages were less similar to their initial state on cleared 5 m × 5 m plots than on uncleared 5 m × 5 m plots after 2 years ($\chi^2_1 = 44.4$, $P < 0.001$), but the effect of clearing on deer-preferred assemblages was not significant on 5 m × 5 m plots ($\chi^2_1 = 0.9$, $P = 0.77$).

Cover and volume of vegetation

The ground cover (<10 cm) and volume (0.1–2 m) of plant biomass on recovering cleared subplots were dominated by *Blechnum discolor* and *B. procerum* (proportion of total ground cover: 0.56 ± 0.14 on alluvial and 0.86 ± 0.05 on terrace sites; proportion of total volume: 0.87 ± 0.13 on alluvial and 1.0 ± 0.00 on terrace sites, 2 years after clearing in 2003). Two years after clearing, the ground cover of vascular plants relative to 2001 did not differ significantly between +C and –C treatments (Fig. 6; $\chi^2_1 = 0.4$, $P = 0.85$), but the volume of plant biomass 0.1–2 m above cleared subplots remained below 4% of its initial value ($\chi^2_1 = 157$, $P < 0.001$).

After 2 years, +U treatments had higher ground cover relative to initial cover compared with –U treatments, on cleared subplots (Fig. 6; Wald $\chi^2_1 = 5.2$, $P = 0.022$; LR $\chi^2_1 = 3.6$, $P = 0.058$) but not on uncleared subplots ($\chi^2_1 = 1.1$, $P = 0.29$), and there was some evidence of an interaction between Clearing and Ungulates (Wald $\chi^2_1 = 3.7$, $P = 0.054$; LR $\chi^2_1 = 3.3$, $P = 0.069$). However, the high relative ground cover on cleared +U treatments was the result of regrowth of *Blechnum discolor* and *B. procerum* ferns in the < 10 cm tier at site A3, where before clearing they had been present only ≥ 10 cm. Although the –U subplots at this site had only a slightly higher pre-clearing ground cover (<10 cm) of these ferns (<2%), this difference between the ungulate treatments had a large effect on the calculations of relative change in cover after 2 years. There was no significant effect of ungulates on volume of plant biomass relative to initial volume ($\chi^2_1 = 0.0$, $P = 0.99$, cleared and uncleared subplots combined). Effects of rodents on ground cover ($\chi^2_1 < 0.03$, $P = 0.86$) and volume of plant biomass ($\chi^2_1 = 0.7$, $P = 0.40$) relative to their initial values were also not significant.

Survival of planted seedlings as an index of rodent herbivory

The best model of seedling survival assumed equal survival inside and outside rodent exclosures, and separate survival parameters for each seedling species, each site and each year (40 parameters, relative AICc = 0). Estimates of annual survival ranged from 0.04–0.32 (95% CI) to 0.76–0.95, with so much variation between species, sites and years that conclusions could

not be drawn about the effects of any of these factors. The next best model assumed equal survival in +R and –R treatments for wineberry but not for broadleaf (60 parameters, relative AICc = 5.0). All other models tested had much higher values of relative AICc (≥ 27.5).

Discussion

Seedling establishment

Disturbances that remove understorey vegetation may improve conditions for the recruitment and growth of seedlings by increasing irradiance of the forest floor and reducing competition for nutrients. The rapid establishment of seedlings after experimental removal of above-ground understorey vegetation suggests that competition for light by understorey plants reduces the rate of seedling establishment in this forest. In systematic samples of 1.5 ha of the forest surrounding our study sites, the ground fern *Blechnum discolor* (crown fern) intercepted 61% on average of incoming photosynthetically active radiation (PAR) at the alluvial sites, and *B. procerum* intercepted 20% of PAR at the terrace sites (Coomes *et al.*, 2005). These values are probably typical of our plots, which were selected to have intermediate cover of *Blechnum* and where these ferns made up 98% of the volume of plant biomass 0.1–2 m above the plot. Dense cover of ferns including *Blechnum discolor* inhibits the establishment of beech seedlings (June and Ogden, 1978; Wardle, 1980; Wardle, 1984, pp. 266–267) and our results suggest that both *B. discolor* and *B. procerum* inhibit other woody species also. These results provide evidence that these unpalatable ferns, which may have increased in abundance as the result of selective browsing by deer (McKelvey, 1973; Wardle, 1984, p. 227; Wardle *et al.*, 2001; Bellingham and Allan, 2003), might hinder forest recovery after deer control (Coomes *et al.*, 2003). These ideas could be tested further by comparing recruitment on plots with ferns present and experimentally removed, in deer exclosures or following intensive culling of deer.

Effects of ungulates

The effect of excluding ungulates on seedling establishment was most apparent on angiosperms ≥ 10 cm tall on cleared plots. Although 29 seedlings (26 angiosperms and three gymnosperms, *Podocarpus hallii* and *Prumnopitys ferruginea*) grew to 10 cm on our 5 m × 5 m cleared plots in ungulate exclosures after 2 years, only one gymnosperm seedling (*P. ferruginea*) did so outside the exclosures. Of the 29 seedlings that reached 10 cm on cleared plots in ungulate exclosures, 20 were of species preferred by ungulates in New Zealand (i.e. proportionately more is eaten than

expected based on availability, Forsyth *et al.*, 2002) and the remainder, including the gymnosperms, were of species avoided by ungulates (i.e. although they are eaten by ungulates in New Zealand, proportionately less is consumed than expected based on availability, Forsyth *et al.*, 2002). These results suggest that ungulates restricted the regeneration not only of highly palatable species but also of relatively unpalatable species although the number of the latter was small (nine seedlings). That so few seedlings in total grew to 10 cm in 2 years is not surprising, as woody plants in New Zealand respond slowly to deer exclusion, and enclosure plots are usually remeasured 10 years or more after fencing (e.g. Jane and Pracy, 1974; Allen *et al.*, 1984; Stewart and Burrows, 1989; Husheer *et al.*, 2003). For example, seedlings of deer-preferred species establishing in enclosures were only 5–10 cm tall after 2 years in the Waihaha catchment, Pureora Forest Park, (Nugent *et al.*, 1997) and woody seedlings grew at an average rate of only 5 mm per year at Huapai Scientific Reserve (Gillman and Ogden, 2003) (both locations are in the North Island, New Zealand). At some locations, effects of excluding deer on plant species richness or vegetation density were undetectable after more than 10 years (Allen *et al.*, 1984; Wardle *et al.*, 2001). Changes in our enclosures may have been particularly slow since they were not placed in canopy gaps (Allen *et al.*, 1984; Stewart and Burrows, 1989), which are important for regeneration of many of the tree species in these forests (Veblen and Stewart, 1980; Wardle, 1984, p. 274).

Impacts of deer on seedlings < 10 cm tall may be difficult to detect, since seedlings below 3 cm may escape browsing by red deer (Nugent *et al.*, 1997; and see Sweetapple and Nugent, 2004) and small plants may benefit from increased availability of light after taller plants are browsed (Suominen *et al.*, 1999). In the Waihaha catchment, the mean height of deer-preferred seedlings was about 3 cm and unrelated to deer density, whereas numbers of seedlings 3–15 cm tall of these species doubled after only 2 years in deer enclosures (Nugent *et al.*, 1997). After 10 years or more, woody seedlings \geq 15 cm occurred more frequently inside than outside deer enclosures in the Urewera forests, North Island, New Zealand, but the frequency of seedlings < 15 cm did not differ significantly between the treatments (Allen *et al.*, 1984). Our finding that numbers of seedlings < 10 cm tall were not significantly affected by ungulates is consistent with these earlier results.

Whereas red deer are primarily browsers, feral pigs are omnivores that not only browse but also forage on the ground for fruits and carrion, and turn over soil and vegetation to find invertebrates and underground plant parts (Nugent, G.; Parkes, J.P.; Dawson, N.; Caley, P. unpubl. data; McIlroy, 2001).

The impacts of pigs on New Zealand forest vegetation are not well understood although they may affect plant species composition by consuming fruits, eating, uprooting and barking plants, and also by clearing new substrate for seedling establishment (Wardle, 1984, p. 232; Nugent, G.; Parkes, J.P.; Dawson, N.; Caley, P. unpubl. data). We consider that most of the ungulate effects observed in this study were due to deer, but pigs may have contributed, although they disturbed the soil of only one subplot during the 2 years of the project.

Effects of rodents

In other studies, excluding rats led to increased seedling establishment (Campbell and Atkinson, 1999, 2002; Wilson *et al.*, 2003). Seedling establishment also increased after *Rattus norvegicus* (Norway rats) were exterminated from Breaksea Island (Allen *et al.*, 1994), and after *R. exulans* (kiore) were removed from other offshore islands (Campbell and Atkinson, 1999, 2002). Although house mice (*Mus musculus*) were abundant in Waitutu Forest from November 2002 to May 2003, rats seem to have been comparatively scarce. Our results suggest that effects of mice on seedling establishment may be negligible or difficult to detect after only 2 years. Mice eat seeds of *Dacrydium cupressinum* (rimu) and *Nothofagus* spp. (beech) but not *Prumnopitys ferruginea* (miro) (Ruscoe *et al.*, 2004), and possibly do not eat many of the other species of seeds or fruits that fell onto our plots. In a seed predation experiment at the same study sites in June 2003 when mice were abundant, we found high rates of predation on *Dacrydium cupressinum* and *Nothofagus solandri* var. *cliffortioides* (mountain beech) seeds but low rates of predation on *Griselinia littoralis* (broadleaf) and *Prumnopitys ferruginea* seeds (Wilson, D.J., Wright, E.F., Canham, C.D., Ruscoe, W.A., unpubl. data). In contrast, in May 2004 when mice were scarce, the rates of predation on all four species of seeds were low. *Dacrydium cupressinum* and *Nothofagus* seedlings established on our plots at numbers too low to test for effects of mice on these species (Table 2). Finally, seeds that fell when rodents were scarce may have become buried in the duff or soil (Ogden, 1985) and thereby been protected from predation after rodent density increased. After rodent enclosures were built, germination of these seeds (discussed further under Species composition) would mask any effect of the enclosures on survival of newly fallen seeds.

Rattus norvegicus and *R. exulans* eat seedlings of several woody plants (Campbell, 1978; Campbell *et al.*, 1984), but as far as we know the consumption of seedlings by *R. rattus* (ship rats) and mice has not been investigated. Most diet studies are based on stomach contents, in which seedling tissue is often indistinguishable from that of mature plants. Since

Rattus rattus eat buds, leaves and stems (Campbell, 1978), it is probable that they remove at least parts of small seedlings. House mice also eat leaves and roots (Cockburn, 1980; Miller and Webb, 2001), although the bulk of their diet is invertebrates and seeds (Ruscoe and Murphy, 2005) and it seems unlikely that they would routinely kill seedlings as large as the planted seedlings (10 cm). Our nursery-grown seedlings may initially have been artificially high in nutrients, leading to a higher level of predation than occurs on natural seedlings (Arnold, 1964; Mattson, 1980). However, the large improvements in AICc from setting survival of the two planted species equal between rodent treatments (-5.0 and -22.5) is evidence that the effect of rodents on survival of the planted seedlings was relatively small. This result is particularly strong because the sample size for testing rodent effects was inflated by modelling survival at the seedling level although four seedlings were planted at each +R and -R subplot (Hurlbert, 1984). Therefore, although the preference of rodents for *Griselinia littoralis* and *Aristotelia serrata* (wineberry) tissue is unknown, this result suggests a low impact of rodents on the survival of similar-sized seedlings of these species during this study.

Species composition

The composition of New Zealand mixed forests is never static, as natural disturbances and other changes alter circumstances that favour the establishment and growth of different species (Wardle, 1984, p. 303). Because many New Zealand tree species vary in the amount of seed produced in different years (Wardle, 1984; Schauber *et al.*, 2002), the probability of re-establishment of a seedling of a particular species on a small plot within only 2 years may be low. Although it is thought that few seeds of most indigenous tree species remain viable on the forest floor longer than 18 months (Wardle, 1991, p. 64), some seeds persist for many years in duff and soil (Ogden, 1985). It is not known what fraction of annual germination originates from this buried seed bank, although small seeds that are buried too deeply will not germinate successfully (Wardle, 1984, p. 267). We found that species assemblages remained less similar to initial assemblages on cleared plots compared with uncleared plots after 2 years, although numbers of seedlings and ground cover of ferns recovered quickly on all treatments. Regeneration from rhizomes, bulbs and sprouts ensured that on most recovering cleared plots some species matched those present before clearing. However, seedlings establishing on cleared plots may never duplicate the pre-clearing species assemblage that had developed as the result of past conditions and chance events.

Nutrient-rich seedlings (Vesey-Fitzgerald, 1960;

Arnold, 1964) of preferred forage species may be particularly susceptible to ungulates on cleared plots, because (1) preferred forage plants may be easier for ungulates to find on cleared sites and (2) ungulates may preferentially use the cleared spaces (Wardle, 1984, p. 224). In the presence of ungulates, therefore, the dominance of unpalatable species in vegetation establishing on cleared sites may increase relative to its composition prior to clearing, as noted by Wardle (1984, p. 227). We found that species assemblages diverged from their initial pre-clearing state to a greater degree where ungulates were present than where they were excluded, consistent with Mills (1986) and the studies reviewed by Quinn (1986). However, in the present study this effect could not be explained by differential changes in deer-preferred or deer-avoided assemblages. This is not surprising since so few palatable seedlings reached ≥ 10 cm on the regenerating cleared plots, and most palatable species were present only as small seedlings (< 10 cm), which, as discussed above, often escape deer browsing, or as small orchids and ferns. The effects of ungulates on the species composition of regenerating vegetation, and the mechanisms by which these occur, may become more apparent as these plants grow into a more browse-susceptible tier.

Effect of soil fertility

With herbivores and shading ferns removed, plants should grow more quickly where soil nutrients are more plentiful—i.e. at the alluvial sites, where the soils were richer in nutrients compared with the terrace sites (Coomes *et al.*, 2005). We found no statistically significant differences in recovery rates between vegetation types (although this experiment was designed to detect only quite large effects of vegetation type, with only three sites in each). Of the 29 seedlings ≥ 10 cm tall that established on cleared plots inside ungulate exclosures, only four were at terrace sites. However, because most of the remainder (22) were at a single alluvial site, this difference between the vegetation types cannot be explained by soil fertility alone.

Herbivory and engineering resilience of the forest understorey

Ungulates significantly delayed the recovery of vegetation within 2 years after disturbance by experimental clearing of the forest understorey. They slowed the establishment of seedlings ≥ 10 cm tall and reduced the similarity of re-establishing vegetation to its prior species composition. These results are consistent with other demonstrations that herbivores reduced rates of recovery or altered successional trajectories after perturbations (Mills, 1986; Quinn, 1986; Gitay *et al.*, 1992; Bailey and Whitham, 2002).

The definition of engineering resilience assumes an ecosystem that is at equilibrium prior to disturbance, and describes the rate of return to that equilibrium state (May, 1973). Prior to our experiment, the structure and composition of the forest understorey had probably developed in the presence of mammalian herbivores. Because we excluded herbivores at the same time as the disturbance (clearing) was imposed, vegetation inside exclosures was not expected to return to its pre-treatment state. This problem may be alleviated by adjusting for the different trajectories of change of uncleared plots with and without ungulates. However, as little divergence between treatments had occurred on uncleared plots after only 2 years, such an adjustment was not needed in the present analysis.

Changes wrought by herbivores to the composition and structure of this ecosystem may have idiosyncratic (*sensu* Lawton, 1994) consequences for its ability to recover from a perturbation, in addition to effects of herbivory on recruitment, growth or mortality of plants. For example, unpalatable plants may grow more slowly than palatable species because of the additional resources that must be allocated to chemical or structural defences (Mooney, 1986, pp. 364–367). Conversely, an understorey biomass depleted by herbivory may regenerate more quickly than will a dense understorey because fewer nutrients are required to replace the removed tissue (DeAngelis *et al.*, 1989b). Therefore, if the species and density of plants in ungulate exclosures diverge from those outside, the ability of this vegetation to recover from disturbance may change, and the results of a future clearing experiment in the exclosures may be very different.

Our results show that introduced ungulates have the potential to change the rate and trajectory of recovery of patches of forest that have been damaged by natural and human-induced disturbances including windthrow, flooding, land slips, pig rooting, fire, disease and human activities. Although our experimental clearing treatment does not precisely mimic these processes, these disturbances can create small or large areas of reduced or absent vegetation. In the presence of ungulates, vegetation will re-establish on these patches more slowly and with a different species composition than in the absence of ungulates. Disturbance events may increase the forest's vulnerability to the impacts of ungulates and accelerate the changes they inflict. It is too early to conclude from this study whether mice and rats exacerbate these effects or are unimportant, and we have not addressed impacts of possums, which can also reduce seedling establishment (Nugent *et al.*, 1997; Wilson *et al.*, 2003) and alter the species composition of plant communities establishing on patches of bare soil created by erosion (Wallis and James, 1972).

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References

- Akaike, H. 1974. A new look at statistical model identification. *IEEE transactions on automatic control AU-19*: 716-722.
- Allen, R.B. 1992. *RECCE: an inventory method for describing New Zealand vegetation*. Forest Research Institute Bulletin 176. Forest Research Institute, Christchurch, N.Z.
- Allen, R.B.; Lee, W.G.; Rance, B.D. 1994. Regeneration in indigenous forest after eradication of Norway rats, Breaksea Island, New Zealand. *New Zealand Journal of Botany* 32: 429-439.
- Allen, R.B.; Payton, I.J.; Knowlton, J.E. 1984. Effects of ungulates on structure and species composition in the Urewera forests as shown by exclosures. *New Zealand Journal of Ecology* 7: 119-130.
- Arnold, G.W. 1964. Factors within plant associations affecting the behaviour and performance of grazing animals. In: Crisp, D.J. (Editor), *Grazing in terrestrial and marine environments*, pp. 133-154. Blackwell, Oxford, U.K.
- Bailey, J.K.; Whitham, T.G. 2002. Interactions among fire, aspen, and elk affect insect diversity: reversal of a community response. *Ecology* 83: 1701-1712.
- Bellingham, P.J.; Allan, C.N. 2003. Forest regeneration and the influences of white-tailed deer (*Odocoileus virginianus*) in cool temperate New Zealand rain forests. *Forest Ecology & Management* 175: 71-86.

- Campbell, D.J. 1978. The effects of rats on vegetation. In: Dingwall, P.R.; Atkinson I.A.E.; Hay C. (Editors), *The ecology and control of rodents in New Zealand nature reserves*, pp. 99-120. New Zealand Department of Lands and Survey, Wellington, N. Z.
- Campbell, D.J.; Atkinson, I.A.E. 1999. Effects of kiore (*Rattus exulans* Peale) on recruitment of indigenous coastal trees on northern offshore islands of New Zealand. *Journal of the Royal Society of New Zealand* 29: 265-290.
- Campbell, D.J.; Atkinson, I.A.E. 2002. Depression of tree recruitment by the Pacific rat (*Rattus exulans* Peale) on New Zealand's northern offshore islands. *Biological Conservation* 107: 19-35.
- Campbell, D.J.; Moller, H.; Ramsay, G.W.; Watt, J.C. 1984. Observations on the foods of kiore (*Rattus exulans*) found in husking stations on northern islands of New Zealand. *New Zealand Journal of Ecology* 7: 131-138.
- Carpenter, S.R.; Cottingham, K.L. 1997. Resilience and restoration of lakes. *Conservation Ecology* 1: 2. URL: <http://www.consecol.org/vol1/iss1/art2>. Accessed 22/12/1999.
- Caswell, H. 1978. Predator-mediated coexistence: a nonequilibrium model. *American Naturalist* 112: 127-154.
- Caughley, G. 1989. New Zealand plant-herbivore systems - past and present. *New Zealand Journal of Ecology* 12 (Supplement): 3-10.
- Cockburn, A. 1980. The diet of the New Holland mouse (*Pseudomys novaehollandiae*) and the house mouse (*Mus musculus*) in a Victorian coastal heathland. *Australian Mammalogy* 3: 31-34.
- Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199: 1302-1310.
- Coomes, D.A.; Allen, R.B.; Bentley, W.A.; Burrows, L.E.; Canham, C.D.; Fagan, L.; Forsyth, D.M.; Gaxiola-Alcantar, A.; Parfitt, R.L.; Ruscoe, W.A.; Wardle, D.A.; Wilson, D.J.; Wright, E.F. 2005. The hare, the tortoise, and the crocodile: the ecology of angiosperm dominance, conifer persistence, and fern filtering. *Journal of Ecology* 93: 918-935.
- Coomes, D.A.; Allen, R.B.; Forsyth, D.M.; Lee, W.G. 2003. Factors preventing the recovery of New Zealand forests following control of invasive deer. *Conservation Biology* 17: 450-459.
- Cowan, P.E. 2005. Brushtail possum. In: King, C.M. (Editor), *The handbook of New Zealand mammals*, Second edition, pp. 56-80. Oxford University Press, Melbourne, Australia.
- Cowan, P.E.; Chilvers, B.L.; Efford, M.G.; McElrea, G.J. 1997. Effects of possum browsing on northern rata, Orongorongo Valley, Wellington, New Zealand. *Journal of the Royal Society of New Zealand* 27: 173-179.
- DeAngelis, D.L.; Bartell, S.M.; Brenkert, A.L. 1989a. Effects of nutrient recycling and food chain length on resilience. *American Naturalist* 134: 778-805.
- DeAngelis, D.L.; Mulholland, P.J.; Palumbo, A.V.; Steinman, A.D.; Huston, M.A.; Elwood, J.W. 1989b. Nutrient dynamics and food-web stability. *Annual Review of Ecology and Systematics* 20: 71-95.
- Duncan, K.; Holdaway, R. 1989. Footprint pressures and locomotion of moas and ungulates and their effects on the New Zealand indigenous biota through trampling. *New Zealand Journal of Ecology* 12 (Supplement): 97-101.
- Forsyth, D.M.; Coomes, D.A.; Nugent, G.; Hall, G.M.J. 2002. Diet and diet preferences of introduced ungulates (Order: Artiodactyla) in New Zealand. *New Zealand Journal of Zoology* 29: 323-343.
- GenStat Committee, 2002. *The guide to GenStat® release 6.1. Part 2: Statistics*. VSN International, Oxford, U.K.
- Gillman, L.N.; Ogdin, J. 2003. Seedling mortality and damage due to non-trophic animal interactions in a northern New Zealand forest. *Austral Ecology* 28: 48-52.
- Gitay, H.; Lee, W.G.; Allen, R.B.; Wilson, J.B. 1992. Recovery of *Chionochloa rigida* tussocks from fires in South Island, New Zealand. *Journal of Environmental Management* 35: 249-259.
- Hill, S.J.; French, K. 2004. Potential impacts of fire and grazing in an endangered ecological community: plant composition and shrub and eucalypt regeneration in Cumberland Plain Woodland. *Australian Journal of Botany* 52: 23-29.
- Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4: 1-23.
- Holling, C.S. 1996. Engineering resilience vs. ecological resilience. In: Schulze, P.C. (Editor), *Engineering within ecological constraints*, pp. 31-43. National Academy Press, Washington, DC, U.S.A.
- Hooper, D.U.; Chapin, F.S.; Ewel, J.J.; Hector, A.; Inchausti, P.; Lavorel, S.; Lawton, J.H.; Lodge, D.M.; Loreau, M.; Naeem, S.; Schmid, B.; Setälä, H.; Symstad, A.J.; Vandermeer, J.; Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75: 3-35.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187-211.
- Hurvich, C. M.; Tsai, C. 1989. Regression and time series model selection in small samples. *Biometrika* 76: 297-307.

- Husheer, S.W.; Coomes, D.A.; Robertson, A.W. 2003. Long-term influences of introduced deer on the composition and structure of New Zealand *Nothofagus* forests. *Forest Ecology and Management* 181: 99-117.
- Huston, M.A. 1979. A general model of species diversity. *American Naturalist* 113: 81-101.
- Jane, G.T.; Pracy, L.T. 1974. Observations on two animal enclosures in Hikurangi forest over a period of twenty years (1951-1971). *New Zealand Journal of Forestry* 19: 102-113.
- June, S.R.; Ogden, J. 1978. Studies on the vegetation of Mount Colenso, New Zealand. 3. The population dynamics of red beech seedlings. *Proceedings of the New Zealand Ecological Society* 22: 61-66.
- King, C.M. 2005 (Editor). *The handbook of New Zealand mammals*, Second edition. Oxford University Press, Melbourne, Australia.
- Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs* 36: 239-273.
- Krebs, C.J. 1989. *Ecological methodology*. HarperCollins, New York, NY, U.S.A.
- Lawton, J.H. 1994. What do species do in ecosystems? *Oikos* 71: 367-374.
- Mark, A.F.; Grealish, G.; Ward, C.M.; Wilson, J.B. 1988. Ecological studies of a marine terrace sequence in the Waitutu Ecological District of southern New Zealand. Part 1: The vegetation and soil patterns. *Journal of the Royal Society of New Zealand* 18: 29-58.
- Mattson, W.J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11: 119-161.
- May, R.M. 1973. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, NJ, U.S.A.
- McIlroy, J.C. 2001. Advances in New Zealand mammalogy 1990-2000: Feral pig. *Journal of the Royal Society of New Zealand* 31: 225-231.
- McKelvey, P.J. 1973. *The pattern of the Urewera forests*. Technical Paper no. 59. New Zealand Forest Service, Wellington, N.Z.
- McNaughton, S.J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs* 53: 291-320.
- Miller, A.P.; Webb, P.I. 2001. Diet of house mice (*Mus musculus* L.) on coastal sand dunes, Otago, New Zealand. *New Zealand Journal of Zoology* 28: 49-55.
- Mills, J.N. 1986. Herbivores and early postfire succession in Southern California chaparral. *Ecology* 67: 1637-1649.
- Mooney, H.A. 1986. Photosynthesis. In: Crawley, M.J. (Editor), *Plant ecology*, pp. 345-373. Blackwell, Oxford, U.K.
- NPCA 2004. Possum population monitoring: using the trap-catch method: protocol. National Possum Control Agencies, N.Z. 30 p.
- Nugent, G.; Fraser, K.W.; Sweetapple, P.J. 1997. *Comparison of red deer and possum diets and impacts on Podocarp-hardwood forest, Waihaha catchment, Pureora Conservation Park*. Science for conservation 50. Department of Conservation, Wellington, N.Z.
- Ogden, J. 1985. An introduction to plant demography with special reference to New Zealand trees. *New Zealand Journal of Botany* 23: 751-772.
- Payton, I.J.; Allen, R.B.; Knowlton, J.E. 1984. A post-fire succession in the northern Urewera forests, North Island, New Zealand. *New Zealand Journal of Botany* 22: 207-222.
- Pimm, S.L. 1982. *Food webs*. Chapman and Hall, London, U.K.
- Quinn, R.D. 1986. Mammalian herbivory and resilience in Mediterranean-climate ecosystems. In: Dell, B.; Hopkins A.J.M.; Lamont B.B. (Editors), *Resilience in Mediterranean-type ecosystems*, pp. 113-128. Dr W. Junk Publishers, Dordrecht, Netherlands.
- Ruscoe, W.A. 2004. A new location record for kiore (*Rattus exulans*) on New Zealand's South Island. *New Zealand Journal of Zoology* 31: 1-5.
- Ruscoe, W.A. and Murphy, E.C. 2005. House mouse. In: King, C.M. (Editor), *The Handbook of New Zealand Mammals*, Second edition, pp. 204-221. Oxford University Press, Melbourne, Australia.
- Ruscoe, W.A.; Wilson, D.; McElrea, L.; McElrea, G.; Richardson, S.J. 2004. A house mouse (*Mus musculus*) population eruption in response to heavy rimu (*Dacrydium cupressinum*) seedfall in southern New Zealand. *New Zealand Journal of Ecology* 28: 259-265.
- Schauber, E.M.; Kelly, D.; Turchin, P.; Simon, C.; Lee, W.G.; Allen, R.B.; Payton, I.J.; Wilson, P.R.; Cowan, P.E.; Brockie, R.E. 2002. Masting by eighteen New Zealand plant species: The role of temperature as a synchronizing cue. *Ecology* 83: 1214-1225.
- Smale, M.C.; Hall, G.M.J.; Gardiner, R.O. 1995. Dynamics of kanuka (*Kunzea ericoides*) forest on south Kaipara Spit, New Zealand, and the impact of fallow deer (*Dama dama*). *New Zealand Journal of Ecology* 19: 131-141.
- Stewart, G.H. 1986. Forest dynamics and disturbance in a beech/hardwood forest, Fiordland, New Zealand. *Vegetatio* 68: 115-126.
- Stewart, G.H.; Burrows, L.E. 1989. The impact of white-tailed deer *Odocoileus virginianus* on regeneration in the coastal forests of Stewart Island, New Zealand. *Biological Conservation* 49: 275-293.

- Suominen, O.; Danell, K.; Bergstrom, R. 1999. Moose, trees, and ground-living invertebrates: indirect interactions in Swedish pine forests. *Oikos* 84: 215-226.
- Sweetapple, P.J.; Nugent, G. 2004. Seedling ratios: a simple method for assessing ungulate impacts on forest understories. *Wildlife Society Bulletin* 32: 137-147.
- Tilman, D. 1983. Plant succession and gopher disturbance along an experimental gradient. *Oecologia* 60: 285-292.
- Tyler, C.M. 1996. Relative importance of factors contributing to postfire seedling establishment in maritime chaparral. *Ecology* 77: 2182-2195.
- Veblen, T.T.; Stewart, G.H. 1980. Comparison of forest structure and regeneration on Bench and Stewart Islands. *New Zealand Journal of Ecology* 3: 50-68.
- Vesey-Fitzgerald, D.F. 1960. Grazing succession among East African mammals. *Journal of Mammalogy* 41: 161-172.
- Wallis, F.P.; James, I.L. 1972. Introduced animal effects and erosion phenomena in the northern Urewera forests. *New Zealand Journal of Forestry* 17: 21-36.
- Ward, C.M. 1988. Marine terraces of the Waitutu district and their relation to the late Cenozoic tectonics of the southern Fiordland region, New Zealand. *Journal of the Royal Society of New Zealand* 18: 1-28.
- Wardle, D.A.; Bardgett, R.D.; Klironomos, J.N.; Setälä, H.; van der Putten, W.H.; Wall, D.H. 2004. Ecological linkages between aboveground and belowground biota. *Science* 304: 1629-1633.
- Wardle, D.A.; Barker, G.M.; Yeates, G.W.; Bonner, K.I.; Ghani, A. 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecological Monographs* 71: 587-614.
- Wardle, D.A.; Bonner, K.I.; Barker, G.M. 2000. Stability of ecosystem properties in response to above-ground functional group richness and composition. *Oikos* 89: 11-23.
- Wardle, J.A. 1984. *The New Zealand beeches: ecology, utilisation and management*. New Zealand Forest Service, Christchurch, N.Z.
- Wardle, P. 1980. Ecology and distribution of silver beech (*Nothofagus menziesii*) in the Paringa district, South Westland, New Zealand. *New Zealand Journal of Ecology* 3: 23-36.
- Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge, U.K.
- White, G.C.; Burnham, K.P. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 Supplement: 120-138.
- Williamson, W.M.; Wardle, D.A.; Yeates, G.W. 2005. Changes in soil microbial and nematode communities during ecosystem decline across a long-term chronosequence. *Soil Biology and Biochemistry* 37: 1289-1301.
- Wilson, D.J.; Lee, W.G.; Webster, R.A.; Allen, R.B. 2003. Effects of possums and rats on seedling establishment at two forest sites in New Zealand. *New Zealand Journal of Ecology* 27: 147-155.

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