Initial Vegetation Conditions in Study Sites of the ‘Forests Affected by Deer’ Project

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Summary

Project and Client

Landcare Research (Lincoln) was contracted by the Department of Conservation to contribute to the design of a study that would monitor and model the impacts of large-scale deer control on vegetation. Three of the four study sites selected are being subjected to experimental deer control until 2011 and here we describe the initial conditions for that long-term deer control experiment. The work was undertaken between October 2003 and June 2009.

Objectives

- Develop a strategy for monitoring the response of forest vegetation to deer control
- Divide four sites into comparable blocks and summarise vegetation in each block

Methods

- Investigating effects of deer control on forest maintenance requires a demographic approach, focusing on survival and growth of canopy tree seedlings. Determining effects on biodiversity focuses on the extent to which deer control shifts the proportion of highly palatable species, as well as the total biomass.
- Our approach was to obtain and appraise all relevant information for each candidate site based on its forest vegetation, geology, and physical environments. Then, if the candidate area was sufficiently homogeneous, we selected, on the basis of available information, two discrete geographic areas which could be used as paired treatment and non-treatment blocks within the area.

Results

- We chose two compositionally comparable blocks at each of the four candidate sites.
- Two sites are in the North Island: Waiotaka (Kaimanawa Ranges) and Waihaha Forest (West of Lake Taupo, central North Island).
- Two sites are in the South Island: Ruataniwha Conservation Area (Lake Ohau, Canterbury Ranges) and Anatoki (North West Nelson).
- The Pembroke Wilderness Area in Fiordland National Park (Southland Conservancy) was also considered as a potential site but was discarded because it was impossible to delineate blocks of adequate size which were similar environmentally – the area straddled a major geological boundary – and which had similar vegetation composition.

Key Findings

Vegetation composition was similar between the two blocks at the Waiotaka and Anatoki sites, but differed between blocks at the Ruataniwha and Waihaha sites. There are strong elevation gradients at all sites and elevation will be a key covariate in future plot analyses. Small differences in vegetation composition between blocks at the Ruataniwha site were attributable to sampling of subalpine and alpine vegetation in one block and not the other.

The Waihaha site has very little beech and is dominated by podocarps and various broadleaved trees. Vegetation composition between the two blocks was dissimilar in terms of some common canopy and understorey species and this will complicate interpretation of deer hunting treatments. Elevation, slope and landform accounted for some of the compositional

variation in this highly heterogeneous vegetation; composition is also likely to be determined by the legacies of volcanic activity over the last 2000 years and fire history over the last 800 years, and local influences of microclimate.

Seedlings of tree species from which to obtain demographic information were sampled at all sites, including canopy trees (beech species in three sites, kāmahi in three sites) and an understorey tree (putaputāwētā at Waihaha). Additional plots were required to obtain sufficient individuals at two sites (Waiotaka and Waihaha). In most cases, the height distributions of seedlings were similar (skewed to small individuals) and were not greatly different between blocks.

Understorey biomass, assessed by proxy methods, is likely to be greater in Waiotaka and Ruataniwha than in Waihaha and Anatoki. The proportion of the biomass in the understorey comprised of species that are preferred by deer was very low in three sites (<10% of measured points in the three beech-dominated sites: Waiotaka, Ruataniwha, and Anatoki) and was greater in the non-beech forests at Waihaha (14–18% of measured points).

Recommendations

- Establish the relationship between point height intercepts and measured cover and biomass, by species or by palatability class, at each site. Use accessible sites from which we can generalise to the entire catchment. These data will be publishable and of great use to future fieldworkers. They will also provide us with information on the variance in our biomass per subplot.
- Obtain data on soil nutrient concentrations and light environments at the subplot-level because these are very likely to determine seedling demography and understorey biomass and its composition.
- Combine the assessments of intra- and inter-site differences highlighted in this report alongside data on intra- and inter-site differences in deer (and other ungulate) densities to determine which sites should be prioritised for long-term inclusion in this project.

1. Introduction

Landcare Research (Lincoln) was contracted by the Department of Conservation to contribute to the design of a study that would monitor and model the impacts of large scale deer control on vegetation. In this report, we first describe how we developed a sampling framework to monitor the impact of deer control on vegetation; second, we summarise how comparable blocks of vegetation were selected at four sites and describe the vegetation conditions at each site. Three of these four sites are being subjected to experimental deer control until 2011 and the purpose of this report is to describe the initial conditions for that long-term deer control experiment. The work was undertaken between October 2003 and June 2009.

2. Background

The introduction of deer and other browsing herbivores to New Zealand in the 19th century ended a c. 300-year period, after the extinction of moa, in which there was no significant browsing of the understoreys of New Zealand forests (Bellingham & Lee 2006). Deer were liberated and spread throughout the three main islands of New Zealand, reaching most parts by 1985 and red deer (*Cervus elaphus scoticus*) were by far the most widespread of the nine wild deer species (Nugent & Fraser 2005). After liberation and on spreading to new areas of New Zealand, deer populations typically followed an irruptive pattern, i.e. with an increase to peak abundance, a crash to lower abundance, then an increase to a carrying capacity lower than peak abundance (Leopold 1943; Holloway 1950; Caughley 1970; Forsyth & Caley 2006). During the first stages of irruptions in New Zealand, deer have caused significant reductions of woody plant populations that are highly palatable to deer (e.g. Cockayne 1909; Mark & Baylis 1975; Wardle 1984). Most red deer populations in New Zealand are now at carrying capacity or below it because of sustained hunting pressure (Nugent & Fraser 2005).

There is considerable public debate about the ecological consequences of current deer populations for long-term maintenance of New Zealand’s forests and their biodiversity (Bain 2007 cf. New Zealand Deerstalkers’ Association 2007). Moreover, the alteration of plant communities caused during peak abundance of deer may not be reversible, even when deer are in low numbers. Reasons for this include diet-switching so that palatable plant species are highly browsed even at low deer densities, expansion of niches of non-palatable species to supplant reduced populations of plants, local extinction of seed sources, alterations of successional pathways, and shifts in ecosystem processes (Coomes et al. 2003). Even after nearly 30 years of maintaining deer at low numbers in forests of the Murchison Mountains in Fiordland National Park, there were only small and non-significant increases in the densities of seedlings and saplings of highly palatable tree and shrub species, suggesting that even low numbers of deer can influence forest dynamics and composition (Tanentzap et al. 2009). In contrast, Husheer & Robertson (2005) used faecal pellet indices and tagged canopy tree seedlings to demonstrate that intensive deer control in northern New Zealand successfully reduced deer abundance and resulted in significantly greater seedling growth rates by mountain beech (*Nothofagus solandri* var. *cliffortioides*).

This study is designed to evaluate whether deer control achieves goals of long-term maintenance of New Zealand's forests and their biodiversity at a range of sites across New Zealand, as well as other goals defined by learning groups convened for this adaptive management project (defined and described in Jacobson et al. 2009). This report describes the four areas selected for inclusion in this project: Waiotaka (Tongariro–Taupo Conservancy), Waihaha (Waikato Conservancy), Ruataniwha (Canterbury Conservancy), and Anatoki (Nelson–Marlborough Conservancy). These four areas were selected by the project leader (C. Veltman, Department of Conservation) to give geographic spread throughout New Zealand and because they satisfied the following criteria. First, candidate areas had to have indigenous forest cover. Second, the areas were required to have deer present and with other ungulates (e.g. chamois *Rupicapra rupicapra* and goats *Capra hircus*) rare or absent. Third, candidate areas were required to be sufficiently large that they could be subdivided into a treatment and non-treatment block (we use the word non-treatment in preference to the ambiguous term 'control'). Each block was required to be of a size typical of the Department of Conservation's operational scale of management used previously for the control of deer (i.e. c. 3500–5000 ha). Selection of areas was conducted in conjunction with Department of Conservation's Conservancy and Area Office staff, whose support of the project for its duration is important. The precise locations of each area largely reflect advice given at the conservancy level. This report describes the selection of treatment and non-treatment blocks within each of the four areas. It evaluates the similarity of forest vegetation, geology, and physical environments between blocks within each area. Candidate areas were evaluated in the following order: Waiotaka, Waihaha, Ruataniwha and Anatoki. The Pembroke Wilderness Area in Fiordland National Park (Southland Conservancy) was also considered as a potential site but was discarded because it was impossible to delineate blocks of adequate size which were similar environmentally – the area straddled a major geological boundary – and which had similar vegetation composition.

3. Objectives

- Develop a strategy for monitoring the response of forest vegetation to deer control
- Divide four sites into comparable blocks and summarise vegetation in each block

4. Developing a Monitoring Strategy

4.1 Strategy for monitoring forest vegetation response to deer control

Our approach to determining whether deer control results in changes to forest maintenance and biodiversity was twofold. Forest maintenance concerns the capacity of forest canopies to be maintained, i.e. for sufficient juvenile trees to grow to become potential canopy trees. Intense herbivory by deer can either prevent or retard growth of juveniles and enhance mortality. If intense herbivory is sustained, growth and survival of juveniles can be inadequate to offset mortality of adult trees (Duncan et al. 2006). Over time this results in non-replacement of canopies. Investigating effects of deer control on forest maintenance therefore requires a demographic approach, focusing on survival and growth of juveniles

(Allen et al. 2002). Determining responses to forest biodiversity requires an assessment of whether deer alter community composition, i.e. the species present and their abundance (biomass), especially plant species that are highly palatable to deer. Plant species that are consistently highly palatable to deer have been determined across a range of sites (Forsyth et al. 2002), and share some consistent foliar characteristics, especially low foliar fibre contents, low lignin concentration and high phosphorous concentrations (Forsyth et al. 2002, 2005). Determining effects on biodiversity focuses on the extent to which deer control shifts the proportion of highly palatable species, as well as the total biomass (Wardle et al. 2001). Our interpretation is based on general traits of species (such as foliar nutrients, investment in defence in leaves) to allow inter-site comparisons because some species are of local distributions and because there are links between the traits of species that are palatable to deer and long-term consequences for ecosystems and forest maintenance resulting from differences in litter quality and decomposition rates (Cornelissen et al. 1999; Wardle et al. 2002). Finally, a primary concern underpinning our choice of monitoring techniques was to maximise statistical power so as to detect vegetation responses to deer. The response by vegetation to deer control is likely to be slow in New Zealand's slow-growing evergreen forests, and is likely to vary spatially according to other factors limiting vegetation growth, such as light, fertility and competition from surrounding vegetation. Statistical concerns were presented to the learning groups and integrated, where possible, with the other wishes of the learning groups and with other constraints on the project (i.e. project duration).

4.2 Vegetation block selection and description

Our approach was to obtain and appraise all relevant information for each candidate site based on its forest vegetation, geology, and physical environments. Then, if the candidate area was sufficiently homogeneous, we selected, on the basis of available information, two discrete geographic areas, which could be used as paired treatment and non-treatment blocks within the area. Because this study employs a Before-After-Control-Impact (BACI) design, we were not seeking two statistically identical blocks for our treatment and non-treatment blocks; rather, our aim was to maximise overlap in geology and vegetation composition such that the two blocks contained approximately similar ecosystems that had similar capacities to respond to our deer control treatment. Vegetation information was based mostly on relevés (recce plots *sensu* Hurst & Allen 2007a) conducted in earlier surveys of the area, mostly since c. 1975. In some cases, data on forest structure, including seedlings and saplings as well as adult trees, were also available from existing permanent forest plots (Hurst & Allen 2007b). Vegetation data were derived from the National Vegetation Survey Databank (http://nvs.landcareresearch.co.nz/; Wiser et al. 2001). Geological information relied upon published maps.

4.3 Selecting vegetation attributes to measure

Longitudinal studies of deer invasion and exclosure studies widely report that deer (or ungulates more broadly) reduce the density of understorey vegetation in most indigenous forest types (e.g. Cockayne 1909; Mark & Baylis 1975; Allen et al. 1984; Smale et al. 1995; Wardle et al. 2001). Further, browsing of canopy tree seedlings within that understorey vegetation may limit recruitment of some tree species into the sapling and small-tree size classes. As these are the two most consistently reported effects of deer browse on forest vegetation, the learning groups elected to monitor the responses of understorey biomass and canopy-tree seedling growth and mortality to sustained deer control.

We advocated the use of permanent sampling plots for all vegetation measures as this greatly reduces the number of samples required to detect change over any given sampling interval. Much of the spatial variation in a BACI design can be reduced by using paired observations.

4.4 Sampling understorey biomass at a 3000-ha scale

We envisaged that the final analysis in this project would compare mean biomass in the treatment and non-treatment blocks at the beginning and end of the experiment to determine whether deer control had influenced understorey biomass, especially of palatable species. Variance around those means, variance around the change in biomass, and uncertainty surrounding the direction and size of change in each plot will reduce our ability to detect a deer control effect. In other words, understorey biomass could either increase or decrease or remain the same, and the size of that effect could vary greatly among plots. Ideally, we would have used existing data on these two forms of variance to conduct a power analysis, which would have indicated the number of permanent plots required to detect a specified difference between the treatment and non-treatment means. However, we did not have any a priori information on the variance of the change in biomass so we were not able to develop a power analysis for understorey biomass in permanent plots.

One approach available to us was to use an existing dataset on understorey biomass to calculate the probable limits of error (PLE) around mean biomass. The PLE is a simple statistic that expresses the 95% confidence interval (CI) around a mean as a percentage of that mean (Goulding & Lawrence 1992; Krebs 1999); the smaller the 95% CI, the lower the PLE, and the more confident we are about our mean. Ideally, one should aim for a PLE of 10% in ecological studies (Goulding & Lawrence 1992; Krebs 1999). The best source of information available for estimating the PLE of forest understorey biomass was a dataset on understorey biomass in temperate rainforest from Waitutu Forest in southern Fiordland (Table 1; Forsyth et al. 2005). We used this dataset to calculate the PLE and to estimate the number of samples we would need to generate a mean in the FAD project with a PLE of 10%. If we assume that forest understoreys in the FAD sites are at least as variable as those at Waitutu Forest then we estimated that we would need at least 314 plots in each treatment and non-treatment area per site. In forests where the understorey biomass is more variable among samples, many more samples would be required. Lastly, it is worth noting that Forsyth et al. (2005) sampled 102 taxa, many of which were represented in less than 5% of the plots, pointing to the fact that sampling needs to be extensive even to detect these species; reporting on changes in understorey biomass on a per species basis is unlikely to be feasible.

Although a PLE of 10% is a desirable benchmark to achieve, the actual PLE required depends on the size of the treatment effect one is expecting to detect (or willing to accept). If deer control has a 200% effect on understorey biomass then a larger PLE would be acceptable. If one is attempting to detect smaller differences (e.g. a 20% difference in mean biomass between non-treatment and treatment blocks) then a lower PLE will be essential. Finally, a posteriori power analysis will enable us to discuss whether non-significant results were a product of undersampling (a Type II error), or a true non-significant result.

Our initial intention was to avoid nested (hierarchical) data (i.e. subplots within plots) because of the analytical complications associated with such data. However, sampling 314 independent permanent plots at a 3000-ha scale was deemed unrealistic. We raised the possibility of subsampling the treatment and non-treatment blocks to select areas with homogeneous vegetation composition within which 314 plots could be contained, but this option was not selected because the learning groups wished to have coverage of the entire area. The option was available to attach the vegetation sampling to the faecal pellet sampling, which used 50 random points in the treatment and non-treatment blocks. To accommodate the difference in sampling effort between 50 points and 314 points, we subsampled each of our 50 plots using four subplots to try and increase information gained at each point. In so doing, we increased our sampling effort from 50 independent sampling plots to 200 nested sampling subplots.

Table 1 Summary of understorey biomass (0–2 m height) data from Waitutu Forest, southern Fiordland (Forsyth et al. 2005).

Measure	Value
No. plots	292
Size of each plot	1-m radius (3.14 m^2)
No. taxa sampled	102
No. people-days taken to sample plots	50
Mean biomass (g)	113.4
SD	103.4
SE	6.05
Coefficient of variation	0.91
95% CI	11.9
PLE	10.5 %
No. zero values	10
No. plots required to achieve a PLE of 10%	314
No. plots required to achieve a PLE of 5%	1114

Each plot was 10 × 10 m. Within that 100-m^2 plot the subcontractors laid out four 2 × 2 m subplots (Fig. 1). These subplots were slightly larger than the plots used by Forsyth et al. (2005; Table 1) based on the principle that larger plots homogenise spatial variation so our sampling should achieve at least the same PLE as Forsyth et al. (2005). Understorey biomass was measured in each subplot using the point height intercept (PHI) method (Scott 1965; Dickinson et al. 1992; Wiser & Rose 1997). This method uses a graded height pole (a point) with an imaginary cube of 5 × 5 × 5 cm around each 10-cm interval. Foliage present inside this imaginary cube was recorded by species for each 10-cm interval up to and including 30 cm (i.e. frequency of intercepts × species × height tier). We used 20 points (five points within each 2 × 2 m subplot; Fig. 1), and vegetation intercepts (instances where foliage was present within the imaginary cubed) were pooled per species across all five points in each subplot. Point height intercepts are a non-destructive proxy for biomass; our intention was to repeat this non-destructive measurement at the end of the experiment and then harvest the understorey biomass to determine the relationship between intercepts and actual biomass. Ideally, we would have conducted a pilot study to determine the number of points necessary in each subplot to adequately sample understorey vegetation to achieve a stable coefficient of variation around the mean (see Bråthen & Hagberg 2004), but time and resources were not available for such a study.

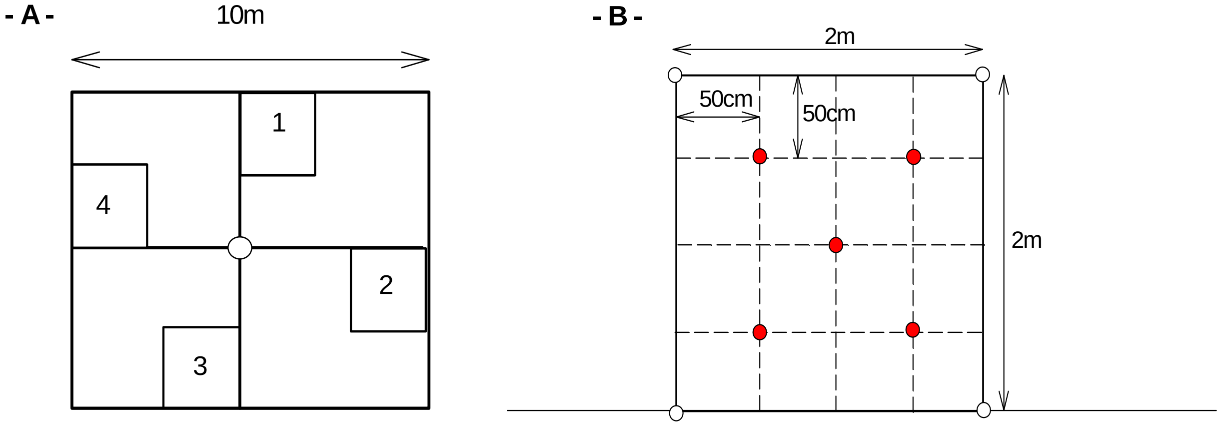

Fig. 1 (A) Layout of the 10 × 10 m plot around each sampling point containing four 2 × 2 m subplots (1–4). (B) Layout of five point-height-intercept points within each 2 × 2 m subplot.

4.5 Sampling canopy tree seedling growth and mortality at a 3000-ha scale

The candidate tree-seedling species was selected at each site by the learning groups (see descriptions of each site). Our concern was how to adequately sample tree seedlings to detect mortality over a 6-year period. We used the power analysis approach of Peltzer et al. (2005) to determine the number of permanently tagged seedlings we would require to estimate an annual mortality rate of 1.5% per year over 6 years of sampling; this rate of mortality is typical for New Zealand tree seedlings (Smale & Kimberley 1986; West 1995; Gillman & Ogden 2003; Bellingham & Richardson 2006; Kunstler et al. 2009). We estimated that a minimum of 44 seedlings would be required per species in the treatment and non-treatment blocks at each site. We elected to tag all seedlings of each target canopy tree species inside the four subplots at each plot (Fig. 1). A seedling was defined as being ≥ 15 cm in height and ≤ 2.5 cm in diameter at breast height (dbh). Epicormic seedlings (i.e. sprouts from adult individuals) were not tagged. For each seedling, the natural height and substrate (e.g. soil, fallen log, tree fern) were recorded.

4.6 Describing the forest composition inside each plot

We described forest community composition within each 10 × 10 m plot. Although we are not testing for an effect of deer control on forest community composition, we required this information to establish whether the treatment and non-treatment blocks at each site were compositionally comparable. Composition was measured using the relevé method of Hurst and Allen (2007a), which ascribes an ordinal cover score (1 = <1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = >76%) to all species in each of six fixed height tiers. In order to establish whether treatment and non-treatment blocks at each site were environmentally comparable we measured elevation, slope, aspect and angle to the horizon in eight compass directions (a landform index) at each plot to describe local environment. These data were collected at the start of the experiment and it is not our intention to measure them again at the end.

4.7 Data entry, correction and analysis

All data are stored as hard copies in the National Vegetation Survey (NVS) Databank at Lincoln, according to Department of Conservation Standard Operating Procedures (DOC 2007). All data were entered electronically either directly into NVS (the relevé descriptions) or into ancillary Access databases (point-height-intercept data and tagged seedlings), which are linked electronically to NVS.

Plot-level environmental data

Landform index was calculated by taking the mean of the eight angles to the horizon (after McNab 1993; see Richardson et al. 2008). Potential solar radiation was modelled as potential direct beam solar irradiance after Kaufmann & Weatherred (1982) using the *R* function *solrad* provided by R.P. Duncan (Lincoln University and Landcare Research, Lincoln). Missing values for slope and aspect took the mean for the site. Missing environmental data were either replaced with the mean for that site, excluded from analyses or, in the case of elevation which was missing on nearly half of the Recce descriptions (222 out of 481), modelled using LENZ surfaces. For the sake of consistency we used modelled elevations throughout. Data were summarised as arithmetic means per block and per site.

Plot-level vegetation composition

The relevé descriptions of vegetation contained a significant number of records where a plant had been identified only to genus. These genus-level records were divided into two types at each site. The first type was those records where the genus-level record was the only record from that genus. This type was retained in the data as it identifies a unique taxon and contains some information, albeit at a coarser taxonomic resolution than species-level data. The second type was those records where the genus-level record appeared alongside species-level records in the same genus. This type was deleted from the Recce data as we cannot be confident that records pertain to a unique taxon.

Recce data were checked for synonyms, invalid species codes (i.e. six-letter codes that could not be reconciled with an accepted vascular plant name), and unrealistic species records (i.e. recognised vascular plant species recorded substantially outside of their published range). Synonyms were corrected using Ngā Tipu Aotearoa – New Zealand Plantnames (http://nzflora.landcareresearch.co.nz/), invalid species codes were corrected where the intended species could be guessed and, where species codes were too obscure to be corrected, they were removed from the dataset. Missing cover values were ascribed a value of 1 (i.e. <1%).

We summarised vegetation composition within each block at each site using the relevé descriptions. We calculated a single importance value per species per plot by converting the ordinal cover scores to percentage cover midpoints, summing these across tiers, per species per plot, and then transforming them using the zero-adjusted log-transformation suggested by McCune et al. (2002, p. 69). The goal was to determine whether the measured composition was similar between the two blocks at each site, and to evaluate how dominant environment gradients (e.g. elevation) influenced vegetation composition. To achieve this we used non-metric multidimensional scaling (NMDS) ordination to organise the plots (samples) according to measured composition, and an associated procedure (*envfit*) to fit environmental variables (i.e. elevation, slope, landform index, potential solar radiation and block) to the

NMDS solution. This fit allows us to determine whether environment or block significantly influenced the dominant gradients of compositional variation. NMDS and *envfit* were both performed in *R* using the *vegan* library (Oksanen et al. 2008). We used function *metaMDS* with default settings to select the optimum number of axes in our NMDS. The interpretation of NMDS is the same as for other ordinations; the biplots can be used to visually examine how environmental variables influence the spread of plots along each axis. Finally, we calculated richness (of species and unique genus-level taxa) per block at each site to compare taxonomic overlap between blocks at each site.

Point-height-intercept data

Some of the understorey biomass data used obscure or invalid species names, or a species name was missing; these were grouped together without a taxonomic identity but retained in the data. No records were removed because we wished to minimise loss of information on biomass (i.e. we are more interested in the number of hits than the identity of the species). However, this is unsatisfactory as we have limited capacity to summarise understorey biomass according to palatability or growth form as we do not know the species encountered.

Intercepts were summed within each plot by taxa. Where possible, taxa were ascribed to one of three palatability classes: taxa preferred by deer, taxa not selected by deer, and taxa avoided by deer. Where possible we used the classification of Forsyth et al. (2002) based on ungulates. We supplemented that classification using published sources (Appendix 1). We reclassified species where information from literature sources conflicted substantially with the class chosen by Forsyth et al. (2002; see Appendix 2). We present the number of intercepts per block in each of these three palatability classes. Because the data contained a high proportion of zero values and the non-zero values followed a negative binomial distribution, we used zero-inflated negative binomial (ZINB) models to test for differences between FAD blocks in the mean number of intercepts per plot in each of the three palatability classes (preferred, not selected, and avoided). These models concurrently estimate the effect of FAD block on the occurrence of vegetation (i.e. a binomial probability for zero versus non-zero values) and on the abundance of vegetation where present (i.e. a negative binomial probability for the non-zero observations; Bolker 2009; Zuur et al. 2009).

Tagged seedling data

We present the number of seedlings per species, block and site; the distribution of seedlings by species across two broad substrates (the ground and all raised substrates); and the size-class distributions of each species at each site, by block. Contractors were requested to tag seedlings that were ≥ 15 cm in height with a diameter at breast height (dbh) of < 2.5 cm, but in practice, seedlings less than 15 cm in height were sometimes tagged and these seedlings have been retained in the dataset and included in our analyses.

All analyses were conducted in R v. 2.8.1 (R Development Core Team 2008).

5. Waiotaka, Kaimanawa Ranges, North Island

5.1 Selecting two compositionally comparable blocks at the Waiotaka site

The Waiotaka study area is in the north-west of the Kaimanawa Range and the geology of this area is uniform greywacke. Within the study area, two adjacent catchments, the Waiotaka and the Whitikau (a west-flowing river between the Waiotaka and Tongariro rivers), were chosen as blocks within which to conduct the investigation. Our goal was to establish whether a comparable block of indigenous forest could be found in each catchment. We used a map of forest classes and their attendant descriptions (Nicholls 1986) to inspect whether broad forest classes were similar between the Waiotaka and the Whitikau (Fig. 2). There was a clear altitudinal gradient from rimu (*Dacrydium cupressinum*) – mataī (*Prumnopitys taxifolia*) – hardwoods, through rimu–beeches (*Nothofagus* spp.), highland softwoods and hardwoods, to beeches at the highest elevations (Fig. 2). The Whitikau catchment had also an area of highland and steepland softwoods and hardwoods that was not present in the Waiotaka block. Further information on these altitudinal gradients (Elder 1962) provided reassurance that two approximately equal blocks of forest could be selected from these two catchments.

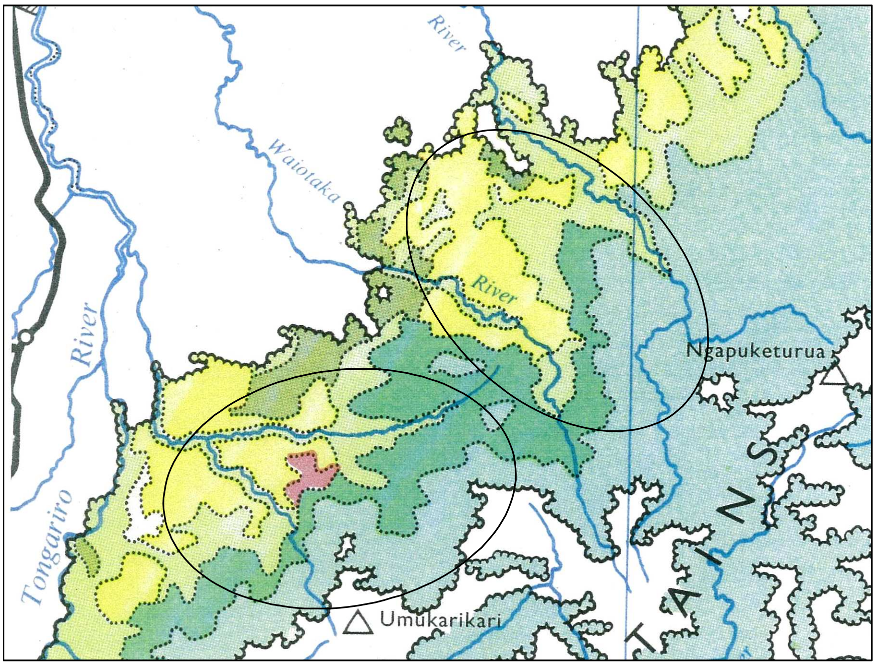

Fig. 2 Forest class map, Kaimanawa Ranges, showing the two general areas that were compared for the Waiotaka site. Forest classes approximately in sequence with increasing elevation: YELLOW = rimu–mataī–hardwoods; OLIVE GREEN = general hardwoods; PALE GREEN = rimu–beeches; DARK GREEN = highland softwoods–beeches; PINK = highland and steepland softwoods–hardwoods; GREY-GREEN = beeches.

Data were available from 40 historical relevé plots in the north-west of Kaimanawa Forest Park collected in 1980, which included parts of the Waiotaka and Whitikau catchments, and these were used to evaluate the comparability of the two proposed blocks. There was considerable floristic overlap in the composition of the two regions covered, based on the basal area of the trees (Appendix 2). Data from 40 permanent plots, measured in 1980, along five randomly located transects in the north-west of Kaimanawa Forest Park, were used to determine how comparable was forest structure. Although plots in the north, including the Waiotaka, had higher total tree basal area than plots in the south, including the Whitikau, the proportions of dominant trees, especially red beech (*Nothofagus fusca*) and kāmahi (*Weinmannia racemosa*), were similar between the two regions (Appendix 3).

Information from a remeasurement of 32 of those 40 permanent plots was also used to determine where seedlings of red beech, a target tree species for this study area, occurred and at what density. The data were collected in 2000 (described as part of a wider dataset in Husheer et al. 2003). The plots are either within or immediately adjacent to the two proposed catchments. Red beech seedlings ≤1.35 m tall were recorded in 24 subplots (0.75 m^2) within each 400-m^2 plot (total area sampled = 18 m^2, i.e. 4.5% of plot area). Red beech seedling densities were measured across all subplots for seedlings ≥0.15 m and ≤1.35 m tall, and presence only recorded for seedlings <0.15 m tall. Red beech dominates forest in the northern Kaimanawa Ranges and approximately follows the 600-m contour to 1100 m (Elder 1962). Therefore we segregated the existing plots into altitudinal bands and determined relative abundance and densities within them (Table 2). The results suggested that red beech seedlings were most likely to be encountered between 900 and 1099 m. Note, however, that even here seedling densities were not great (Table 2).

Table 2 Red beech (*Nothofagus fusca*) frequency of occurrence and seedling density in plots in three altitudinal bands in the northern Kaimanawa Ranges.

Elevation range (m)	No. plots	No. plots with seedlings	No. plots with saplings	No. plots with stems ≥ 2.5 cm dbh	Seedling density/ha (± 1SE)
700 – 899	8	2	1	1	79 ± 79
900–1099	15	4	6	10	593 ± 314
>1100	9	2	3	3	139 ± 90.9

5.2 FAD Waiotaka: environment

New plots were established during sampling of the Waiotaka study area in 2005. The goal was to sample 50 plots in each block, but additional sampling resulted in 75 plots in the Waiotaka block and 73 in the Whitikau block. The plot-level environments were similar between the two blocks (Table 3).

Table 3 Summary of mean environments and canopy height sampled by Recce plots. Data are presented as arithmetic means per site and for each of the two blocks at each site and the minimum and maximum elevations within each block are also presented.

SITE Block	No. plots	Elevation (m)	Slope (°)	Landform Index (°)	Potential solar radiation (% max)	Mean top height (m)
WAIOTAKA	148	940 (357–1389)	30	20	78	13.2
Waiotaka	75	936 (357–1353)	28	19	78	12.9
Whitikau	73	943 (580–1389)	33	21	77	13.7

5.3 FAD Waiotaka: vegetation composition

At the Waiotaka site, the two blocks shared 61% of their species (or, more strictly, their taxa; Table 4). Composition was strongly influenced by elevation and Landform Index, and there was no significant difference between the two blocks (Table 5; Fig. 3). However, there were a few notable compositional differences in canopy (12–20 m) species between the two blocks, with kāmahi (*Weinmannia racemosa*) more frequent in the Waiotaka than in the Whitikau (Table 6).

Table 4 Species richness (species or generic-level taxa) in the two blocks at the Waiotaka site.

Group	Taxa richness
Waiotaka site	198
Whitikau block	165
Waiotaka block	154
Shared	121 (61%)
Unique to Whitikau	44
Unique to Waiotaka	33

Table 5 Summary of environmental and FAD-block effects on vegetation composition at the Waiotaka site. r^2 is the squared correlation coefficient, a goodness-of-fit statistic.

Factor	r^2	Significance of influence on vegetation composition
FAD block	0.0085	0.2683
Altitude	0.7231	< 0.001
Slope	0.0272	0.12412
Landform Index	0.0555	0.01401
Potential solar radiation	0.0074	0.58058

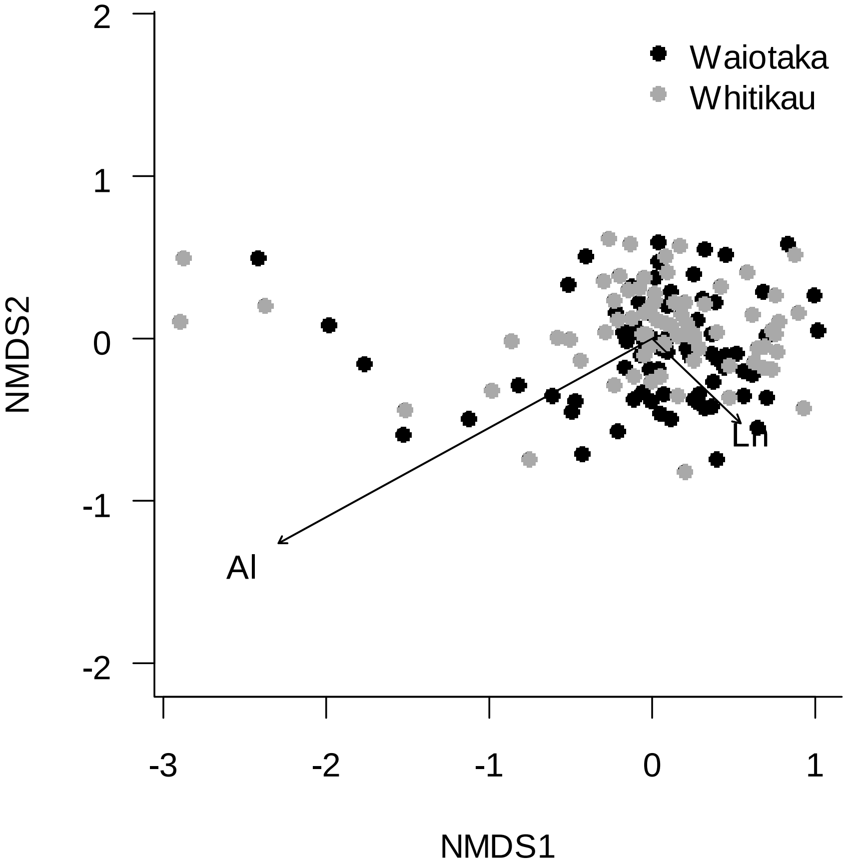

Fig. 3 NMDS ordination of vegetation cover data from two blocks at the Waiotaka site. Only two environmental factors were significant; Al (altitude) and Ln (landform Index) and there was no difference between the two FAD blocks (Waiotaka and Whitikau). Fitted lines (vectors) show the direction and strength of the relationship between an environmental factor and the sampled plots; in this instance, the strength of the relationship between compositional variation and altitude (Al) is much stronger than the relationship with Landform Index (Ln) and individual samples (plots) in the bottom left of the diagram are at higher altitudes than plots in the top right.

Table 6 Frequency of dominant species by Recce tier in each of two blocks at the Waiotaka site. A species was considered dominant if it was ever present in a plot with a cover score of 50% or more in any tier. Data are frequency (number of plots) per block with the frequency where dominant given in parentheses.

Tier	Species	Waiotaka *N = 75*	Whitikau *N = 73*
> 20 m	*Nothofagus fusca*	21 (6)	12 (5)
	Prumnopitys ferruginea	3 (1)	1 (0)
12–20 m	*Nothofagus fusca*	31 (13)	45 (14)
	Weinmannia racemosa	41 (9)	26 (4)
	Prumnopitys ferruginea	4 (1)	2 (0)
	Nothofagus solandri var. *cliffortioides*	4 (3)	1 (0)
	Nestegis cunninghamii	2 (1)	1 (0)
5–12 m	*Weinmannia racemosa*	54 (16)	49 (13)
	Nothofagus fusca	33 (7)	46 (22)
	Pseudowintera colorata	24 (2)	12 (1)
	Griselinia littoralis	13 (1)	18 (3)
	Cyathea smithii	6 (0)	6 (1)
	Nothofagus solandri var. *cliffortioides*	7 (4)	4 (1)
	Prumnopitys ferruginea	5 (0)	6 (1)
	Melicytus ramiflorus	2 (0)	8 (1)
	Nestegis cunninghamii	2 (1)	1 (0)
2–5 m	*Pseudowintera colorata*	64 (23)	57 (13)
	Weinmannia racemosa	52 (9)	49 (7)
	Carpodetus serratus	40 (1)	37 (1)
	Nothofagus fusca	33 (1)	42 (9)
	Podocarpus hallii	22 (1)	25 (0)
	Griselinia littoralis	17 (2)	24 (3)
	Coprosma tayloriae	16 (0)	14 (1)
	Neomyrtus pedunculata	21 (1)	2 (0)
	Cyathea smithii	8 (0)	13 (2)
	Nothofagus solandri var. *cliffortioides*	7 (2)	5 (3)
	Cyathea dealbata	5 (1)	6 (1)
	Melicytus ramiflorus	2 (0)	9 (1)
0.3–2 m	*Pseudowintera colorata*	70 (24)	68 (14)
	Blechnum discolor	40 (1)	64 (8)
	Weinmannia racemosa	53 (1)	51 (0)
	Microlaena avenacea	41 (0)	51 (2)
	Coprosma tayloriae	43 (3)	31 (3)
	Nothofagus fusca	34 (0)	38 (0)

	Griselinia littoralis	17 (0)	24 (1)
	Neomyrtus pedunculata	34 (3)	4 (0)
	Dicksonia lanata	7 (1)	12 (1)
	Phyllocladus alpinus	11 (1)	8 (0)
	Nothofagus solandri var. *cliffortioides*	7 (1)	5 (1)
	Podocarpus nivalis	3 (0)	3 (3)
	Olearia nummulariifolia	1 (0)	3 (2)
	Leptospermum scoparium	2 (1)	2 (0)
0–0.3 m	*Blechnum discolor*	43 (1)	65 (5)
	Histiopteris incisa	21 (1)	14 (0)
	Coprosma tayloriae	47 (0)	32 (1)
	Microlaena avenacea	44 (1)	56 (2)
	Pseudowintera colorata	69 (1)	68 (0)
	Blechnum novae-zealandiae	5 (0)	17 (1)
	Metrosideros diffusa	4 (0)	14 (1)
	Hymenophyllum multifidum	8 (0)	5 (1)
	Trichomanes reniforme	5 (1)	3 (0)
	Podocarpus nivalis	3 (0)	3 (3)
	Dracophyllum recurvum	1 (0)	3 (1)
	Celmisia spectabilis	1 (0)	3 (1)
	Olearia nummulariifolia	1 (0)	3 (2)

5.4 FAD Waiotaka: understorey biomass

The abundance of both ‘preferred’ and ‘not selected’ species was greater in the Whitikau block, relative to the Waiotaka block (Table 7).

Table 7 Understorey point height intercept (PHI) data for the Waiotaka site summarised by palatability class (Appendix 1). Data are presented as the total number of intercepts per block in each of four palatability classes and then as the mean number of intercepts per plot so as to standardise across blocks. Statistical differences in the number of intercepts per plot for each palatability class are indicated; means that share a letter within a row are not significantly different at $P \leq 0.05$.

Palatability class	Waiotaka	Whitikau
Total no. intercepts		
Preferred	60	132
Not selected	292	415
Avoided	1438	1275
Not classified	134	156
Total	1924	1978
No. intercepts per plot		
Preferred	0.8 a	1.8 b
Not selected	3.9 a	5.7 b
Avoided	19.2 a	17.5 a
Not classified	1.8	2.1
Total per plot	25.7	27.1

5.5 FAD Waiotaka: tagged canopy tree seedlings

The minimum sampling number of red beech and kāmahi seedlings was achieved in both blocks but required the establishment of additional plots (25 in the Waiotaka and 23 in the Whitikau). These additional plots were only established in the altitudinal strata where red beech seedlings are most abundant (900–1099 m; Table 8). In this stratum, the same sampling design was applied as described in section 4.4, i.e. along transects of randomised origins, with nested seedling subplots located along transects. In both blocks, this sampling design was applied until at least 80 seedlings of red beech and kāmahi were located and measured.

Red beech commonly regenerates on raised surfaces, especially on logs, and this is particularly prevalent when there are dense carpets of ferns in forests (June & Ogden 1975). Despite a higher frequency of ferns such as *Blechnum discolor* in ground tiers in the Whitikau block (Table 6), the percentage of red beech seedlings on raised surfaces was much lower in this block (13%) than in the Waiotaka block (48%; Table 8).

Table 8 Summary of the number of tagged seedlings of each species in each block and for the total Waiotaka site.

Species Substrate	Waiotaka *N* = 75 plots	Whitikau *N* = 73 plots	Total *N* = 148 plots
Nothofagus fusca	103	110	213
Ground	54	96	150
Raised	49	14	63
Weinmannia racemosa	121	83	204
Ground	80	52	132
Raised	41	31	72

Kāmahi also regenerates frequently on raised surfaces (Stewart & Veblen 1982; Lusk & Ogden 1992; Bellingham & Richardson 2006), but the percentages of kāmahi seedlings on raised surfaces were not greatly different between blocks (Waiotaka, 34%; Whitikau 37%; Table 8). Seedling size-class structures of kāmahi were very similar between the two blocks (Fig. 4) whereas red beech seedlings in the Waiotaka block had a greater frequency of smaller seedlings than in the Whitikau block (Fig. 4).

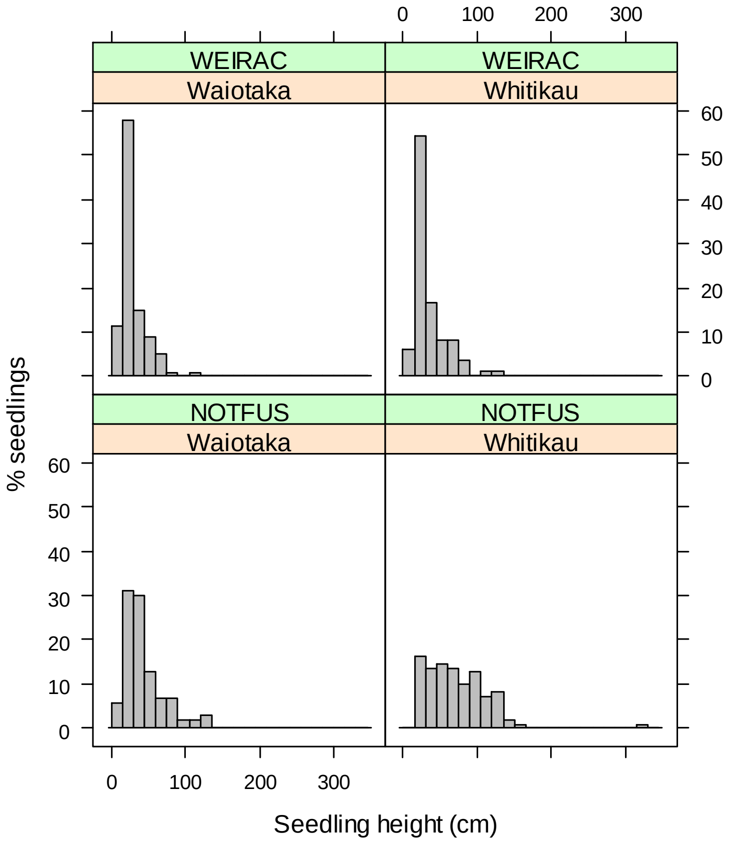

Fig. 4 Tagged seedling size class structures for the Waiotaka site; WEIRAC = kāmahi (*Weinmannia racemosa*), NOTFUS = red beech (*Nothofagus fusca*).

Seedling size structures of kāmahi from both blocks in the Waiotaka study area had a greater proportion of small-sized (<45 cm tall; Fig. 4) seedlings than in forests of similar canopy composition to the east (Husheer et al. 2003). Red beech seedlings in the Waiotaka study block were more similar in proportion of small-sized seedlings (<45 cm tall) to forests to the east than those in the Whitikau block (Husheer et al. 2003).

5.6 Waiotaka site summary

The two blocks (Waiotaka and Whitikau) are well matched in geology, physical environments, and forest composition, although kāmahi, a canopy species with seedlings that are preferred by deer, was more abundant in the Waiotaka block; canopy (>12 m) foliage of kāmahi was present in 55% of plots in the Waiotaka and only 36% of plots in the Whitikau block. The number of seedlings of kāmahi tagged was likewise greater in the Waiotaka block.

6. Waihaha Forest, West of Lake Taupo, Central North Island

6.1 Selecting two compositionally comparable blocks at the Waihaha site

The indigenous forests west of Lake Taupo are mostly those which have developed over the deep ignimbrite and pumice that resulted from the Taupo eruption. The axial Hauhungaroa Range to the west is greywacke, and ash from older eruptions is also evident. The present forests are compositionally complex reflecting heterogeneous volcanic disturbance, early Māori fires, and local microclimate such as frost hollows and elevation (Poole 1949; McKelvey 1963; Herbert 1978; Smale & Smale 2003). The Waihaha catchment contains the single largest area of dense podocarp forest in central North Island (Herbert 1978) with a particularly high component of mataī and rimu (McKelvey 1963). In terms of specific forest types, McKelvey (1963) mapped c. >70% of the Waihaha catchment as podocarp–kāmahi–scrub hardwood type (type M1; green symbols in Fig. 5) and dense mixed podocarp type (type L1; pink symbols in Fig. 5). The third most abundant forest type is rimu–tōtara–kāmahi–scrub type (type M7; blue symbols in Fig. 5), which occurs at higher elevations than either M1 or L1, towards the ridge crest of the Hauhungaroa Range (Fig. 5). Distribution of these forest types is directly associated with the depth of the Taupo pumice deposit and the proximity of the ignimbrite plateau to the surface (Nicholls 1986). The eastern margins of Waihaha Forest have abundant patches of fire-induced vegetation with kāmahi, rewarewa (*Knightia excelsa*), hīnau (*Elaeocarpus dentatus*), *Nestegis* spp. and shrubs. Druce (1952) described these post-fire successional communities and commented on the dominance of mānuka (*Leptospermum scoparium*), *Dracophyllum* spp. and bracken (*Pteridium esculentum*). Patches of successional vegetation occur within the Waihaha forest, also as a result of burning (Herbert 1978). In the Mangatu Stream there is a noteworthy area (‘less than a few hundred acres’) of silver beech (*Nothofagus menziesii*) forest (Poole 1949), which has developed where these is little or no pumice layer (McKelvey 1963). At high elevations, Hall’s tōtara (*Podocarpus hallii*) is dominant with scrub hardwoods (type G1 in Fig. 5).

Selecting two compositionally comparable blocks at the Waihaha site was likely to be difficult and to assist us with the process we requested that a subcontractor collect preliminary vegetation compositional data from two proposed blocks, on either side of the Waihaha River. We were particularly keen to identify regions with successional forest (blue symbols on Fig. 5) so that these could either be equally included in the two blocks, or excluded if they only occurred in one block. We advocated use of the relevé descriptions (Hurst & Allen 2007a) so as to be compatible with many other datasets in New Zealand. Unfortunately, data were collected only from the proposed northern block so differences between the two blocks could not be assessed before finalising our choice of blocks and implementing deer control. The two candidate blocks were on either side of the Waihaha River, with approximately equal areas of each forest type: Mangatu block to the north and Waihaha block to the south (Fig. 5).

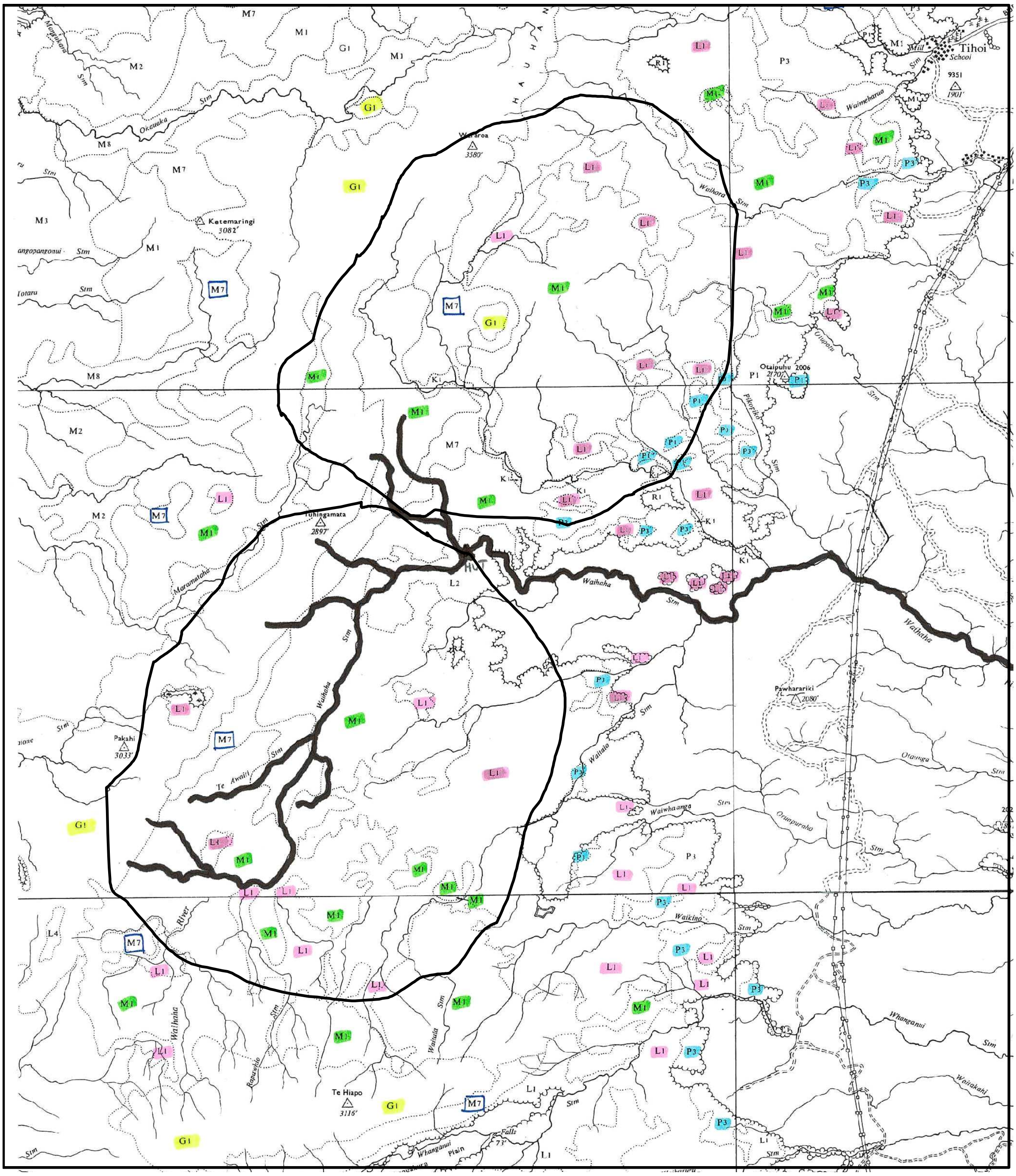

Fig. 5 Forest class map from Waihaha Forest. The black and white map was copied from McKelvey (1963) and the five major classes are denoted by colour (GREEN symbols = podocarp–kāmahi–scrub hardwood type; PINK symbols = mixed podocarp type; BLUE symbols = rimu–tōtara–kāmahi–scrub type (type L1; pink symbols to guide our selection of two blocks with approximately equal cover of each forest class. Part of the Waihaha River was marked with a thick line to emphasise the approximate boundary used for the northern, Mangatu block and southern, Waihaha block.

6.2 FAD Waihaha plots: environment

New plots were established in the Waihaha study area in 2006 with additional sampling in the same manner as for the Waiotaka site: 65 plots instead of 50 plots in the Mangatu block, and 67 plots instead of 50 plots in the Waihaha block. The Mangatu block samples a wider range of elevations but the plots in the two blocks are largely comparable (Table 9).

Table 9 Summary of mean environments and canopy height sampled by relevé plots. Data are presented as arithmetic means per site and for each of the two blocks at each site and the minimum and maximum elevations within each block are also presented.

SITE Block	No. plots	Elevation (m)	Slope (°)	Landform Index (°)	Potential solar radiation (% max)	Mean top height (m)
WAIHAHA	133	741 (513–970)	17	16	78	12.4
Mangatu	65	712 (513–970)	20	18	79	11.1
Waihaha	67	768 (635–920)	13	14	77	13.6

6.3 FAD Waihaha plots: vegetation composition

The two blocks shared more than two-thirds of their species (Table 10) although poor quality data (low resolution of species) may account for this apparent overlap. Our experience with contractors suggested appropriate quality control (e.g. audit) and assurance were necessary. There was a strong, significant difference in composition (cover by species) between the Mangatu and Waihaha blocks (Table 11; Fig. 6).

Table 10 Species richness in the two blocks at the Waihaha site. Taxa are not all species and unidentified generic records were deleted unless they were the only use in the dataset.

Group	Species richness
Waihaha site	161
Mangatu block	136
Waihaha block	135
Shared	110 (68%)
Unique to Mangatu	26
Unique to Waihaha	25

Table 11 Summary of environmental and FAD-block effects on vegetation composition at the Waihaha site. r^2 is the squared correlation coefficient, a goodness-of-fit statistic.

Factor	r^2	Significance of influence on vegetation composition
FAD block	0.1210	<0.001
Altitude	0.2389	<0.001
Slope	0.1970	<0.001
Landform Index	0.1002	0.002
Potential solar radiation	0.0058	0.707

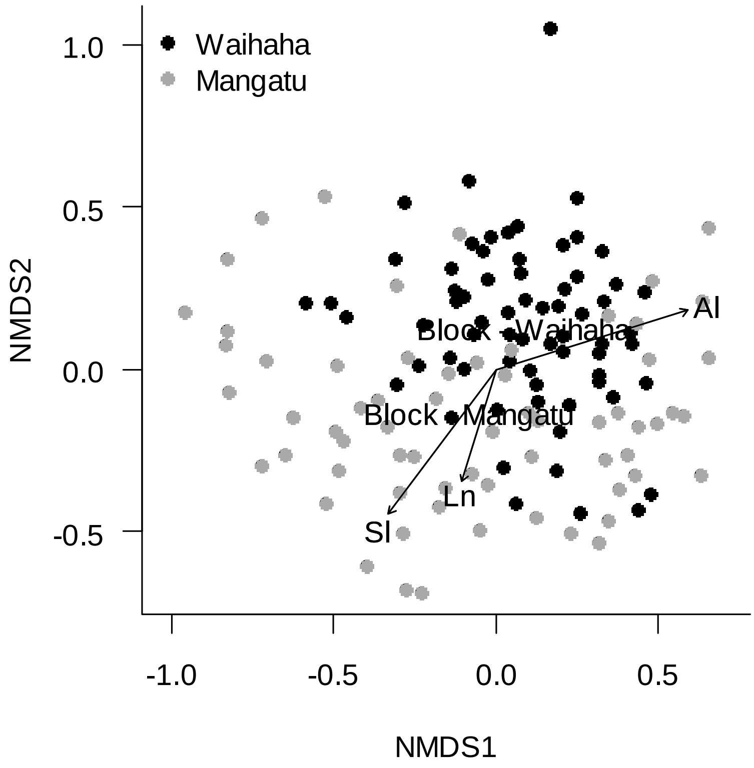

Fig. 6 NMDS ordination of vegetation cover data from the Waihaha site. There was a significant difference between the two blocks (illustrated by the position of centroids ('Block – Waihaha' and 'Block – Mangatu') for each block), and strong effects of altitude (Al), slope (Sl) and Landform Index (Ln) on vegetation composition (Table 11).

Tawa (*Beilschmiedia tawa*) and hīnau (*Elaeocarpus dentatus*) are moderately frequent in the Mangatu block but are scarcely present in the Waihaha block (Table 12). Descriptions of forest classes on the west of Lake Taupo by McKelvey (1963) separated forests with a significant component of tawa and hīnau (podocarp–tawa) as in the Mangatu block from those without tawa (podocarp–kāmahi–scrub hardwoods and dense mixed podocarps types) as in the Waihaha block. He interpreted these patterns along a gradient of successional development of forests according to soil development and depth of pumice resulting from the Taupo eruption of c. AD 232 (Sparks et al. 1995). Leathwick and Mitchell (1992) evaluated forest composition in the same forests and concluded that current mean annual temperature was also a likely determinant of the distribution of tawa, which had a higher probability of occurrence in warmer sites than some podocarps, in particular mataī, which had slightly higher frequency in the Waihaha block (Table 12).

Tānekaha (*Phyllocladus trichomanoides*) also is much more frequent in the Mangatu block than in the Waihaha block (Table 12). A possible reason for this could be that it is colonising sites that were previously burned; McKelvey (1963) stressed the role of past fires set by Māori as a determinant of current forest pattern in the area (see also Cameron 1955) and tānekaha is a common component of secondary successions after fire in northern New Zealand, where it is typically outcompeted by other conifers as succession proceeds (Ogden 1983; Burns & Smale 1990).

Table 12 Frequency of dominant species by tier in each of two blocks at the Waihaha site. A species was considered dominant if it was ever present in a plot with a cover score of 50% or more. Data are frequency (number of plots) per block with the frequency where dominant given in parentheses. †This record is likely to be incorrect as this species typically reaches a height of 13 m (McGlone et al. 2010).

Tier	Species	Mangatu *N = 65*	Waihaha *N = 67*
>20 m	*Dacrydium cupressinum*	13 (0)	8 (2)
	Prumnopitys taxifolia	6 (0)	9 (1)
	Podocarpus totara	2 (0)	4 (2)
	Prumnopitys ferruginea	0 (0)	5 (1)
	Elaeocarpus hookerianus †	0 (0)	1 (1)
12–20 m	*Quintinia serrata*	24 (3)	22 (7)
	Podocarpus hallii	12 (1)	19 (4)
	Dacrydium cupressinum	17 (3)	11 (1)
	Prumnopitys taxifolia	7 (1)	16 (5)
	Weinmannia racemosa	9 (0)	12 (1)
	Elaeocarpus dentatus	16 (3)	4 (0)
	Prumnopitys ferruginea	2 (0)	16 (3)
	Beilschmiedia tawa	14 (1)	1 (0)
	Podocarpus totara	3 (3)	8 (3)
	Elaeocarpus hookerianus	4 (0)	5 (1)
	Phyllocladus trichomanoides	7 (1)	1 (0)
	Griselinia littoralis	3 (2)	5 (0)
	Nestegis cunninghamii	3 (0)	3 (1)
	Nestegis lanceolata	3 (1)	3 (0)
5–12 m	*Weinmannia racemosa*	35 (1)	39 (4)
	Quintinia serrata	36 (9)	36 (15)
	Carpodetus serratus	21 (0)	35 (2)
	Podocarpus hallii	25 (3)	30 (0)
	Pseudowintera colorata	23 (4)	26 (2)
	Myrsine salicina	10 (0)	32 (4)
	Griselinia littoralis	12 (2)	23 (2)
	Dacrydium cupressinum	19 (1)	16 (0)
	Pseudopanax crassifolius	16 (0)	13 (1)
	Dicksonia squarrosa	25 (1)	3 (0)
	Elaeocarpus dentatus	23 (4)	5 (0)
	Prumnopitys ferruginea	8 (0)	20 (1)
	Elaeocarpus hookerianus	9 (0)	15 (2)
	Cyathea smithii	14 (2)	10 (1)

	Beilschmiedia tawa	18 (7)	2 (0)
	Prumnopitys taxifolia	6 (0)	14 (1)
	Podocarpus totara	6 (1)	11 (0)
	Melicytus ramiflorus	15 (1)	0 (0)
	Nestegis cunninghamii	8 (1)	7 (0)
	Nestegis lanceolata	7 (1)	6 (0)
	Phyllocladus trichomanoides	9 (1)	2 (0)
	Fuchsia excorticata	9 (1)	0 (0)
	Phyllocladus alpinus	3 (0)	5 (1)
	Phyllocladus toatoa	5 (1)	3 (0)
	Dicksonia fibrosa	6 (1)	0 (0)
2–5 m	*Beilschmiedia tawa*	19 (1)	2 (0)
	Cyathea smithii	31 (0)	23 (1)
	Dicksonia fibrosa	10 (1)	4 (0)
	Dicksonia squarrosa	29 (4)	15 (0)
	Griselinia littoralis	12 (0)	25 (1)
	Melicytus ramiflorus	18 (1)	1 (0)
	Myrsine salicina	10 (0)	35 (1)
	Neomyrtus pedunculata	23 (0)	45 (1)
	Phyllocladus alpinus	3 (1)	5 (1)
	Pseudowintera colorata	43 (4)	56 (14)
	Quintinia serrata	39 (0)	39 (1)
	Weinmannia racemosa	39 (1)	41 (2)
0.3–2 m	*Blechnum discolor*	31 (3)	16 (0)
	Leptospermum scoparium	0 (0)	1 (1)
	Metrosideros diffusa	16 (1)	1 (0)
	Neomyrtus pedunculata	31 (0)	55 (1)
	Phyllocladus alpinus	3 (0)	7 (1)
	Pseudowintera colorata	60 (2)	66 (13)
	Quintinia serrata	42 (0)	41 (1)
0–0.3 m	*Blechnum discolor*	32 (1)	16 (0)
	Blechnum fluviatile	40 (0)	44 (2)
	Trichomanes reniforme	16 (2)	9 (1)

In contrast to tawa and tānekaha, which are more frequent in the Mangatu block, miro (*Prumnopitys ferruginea*) and toro (*Myrsine salicina*) are more frequent in the Waihaha block (Table 12), but we do not know of likely reasons for this. The ground cover fern *Blechnum discolor* is twice as frequent in the Mangatu block as in the Waihaha block.

In summary, complex compositional variation between the two blocks at Waihaha reflects both the mosaic of historical disturbance, and current environments such as soil fertility. If differences in vegetation composition influence understorey light environments, then the capacity of each block to respond to deer control may not be equal; light is a critical resource limiting understorey dynamics. To account for this in our final analysis, we intend to measure canopy openness (light) on each subplot when the plots are revisited at the end of the experiment. In order to keep the approach equal at all four sites, we will complete these measurements at all sites.

6.4 FAD Waihaha plots: understorey biomass

The number of intercepts in the browse tier (a proxy for biomass) and the relative proportions of ‘preferred’, ‘not-selected’, and ‘avoided’ species within the intercepts were similar between the two blocks, although there were slightly more intercepts of ‘not selected’ species in the Waihaha block, relative to the Mangatu block (Table 13).

Table 13 Understorey point height intercept (PHI) data summarised by palatability class (Appendix 1). Data are presented as the total number of intercepts per block in each of four palatability classes and then as the number of intercepts per plot, so as to standardise across blocks. Statistical differences in the number of intercepts per plot for each palatability class are indicated; means that share a letter within a row are not significantly different at $P \leq 0.05$.

Palatability class	Mangatu	Waihaha
Total no. intercepts		
Preferred	179	160
Not selected	226	320
Avoided	550	617
Not classified	55	53
Total	1010	1150
No. intercepts per plot		
Preferred	2.8 a	2.4 a
Not selected	3.5 a	4.8 b
Avoided	8.5 a	9.2 a
Not classified	0.8	0.8
Total per plot	15.5	17.2

6.5 FAD Waihaha plots: tagged canopy tree seedlings

To obtain the minimum number of kāmahi and putaputawētā (*Carpodetus serratus*) seedlings required the establishment of additional plots in both blocks (i.e. 65 rather than 50 plots in the Mangatu, and 67 rather than 50 plots in the Waihaha). This was achieved by laying out new transects of maximum length 300 m from randomised origins, along which 2 × 2 m plots were established (see section 4.4) and seedlings of kāmahi and putaputawētā were tagged and measured within them; this process continued until the required number was reached.

The percentage of kāmahi seedlings on raised surfaces was much lower in the Mangatu block (28%) than in the Waihaha block (38%, Table 14). Because putaputawētā has very small seeds (0.4–0.6 mg; Wardle 1991; Burrows 1996), although not as small as kāmahi (0.1 mg; Wardle 1991), it is unsurprising that it too is well represented as seedlings on raised surfaces. Like kāmahi, the percentage of putaputawētā seedlings on raised surfaces was much lower in the Mangatu block (21%) than in the Waihaha block (34%, Table 14). Seedling size-class structures of kāmahi and putaputawētā were very similar between the two blocks (Fig. 7).

Table 14 Summary of the number of tagged seedlings of each species in each block and for the total Waihaha site.

Species Substrate	Mangatu *N* = 65 plots	Waihaha *N* = 67 plots	Total *N* = 132 plots
Carpodetus serratus	156	162	318
Ground	124	107	231
Raised	32	55	87
Weinmannia racemosa	214	156	370
Ground	155	97	252
Raised	59	59	118

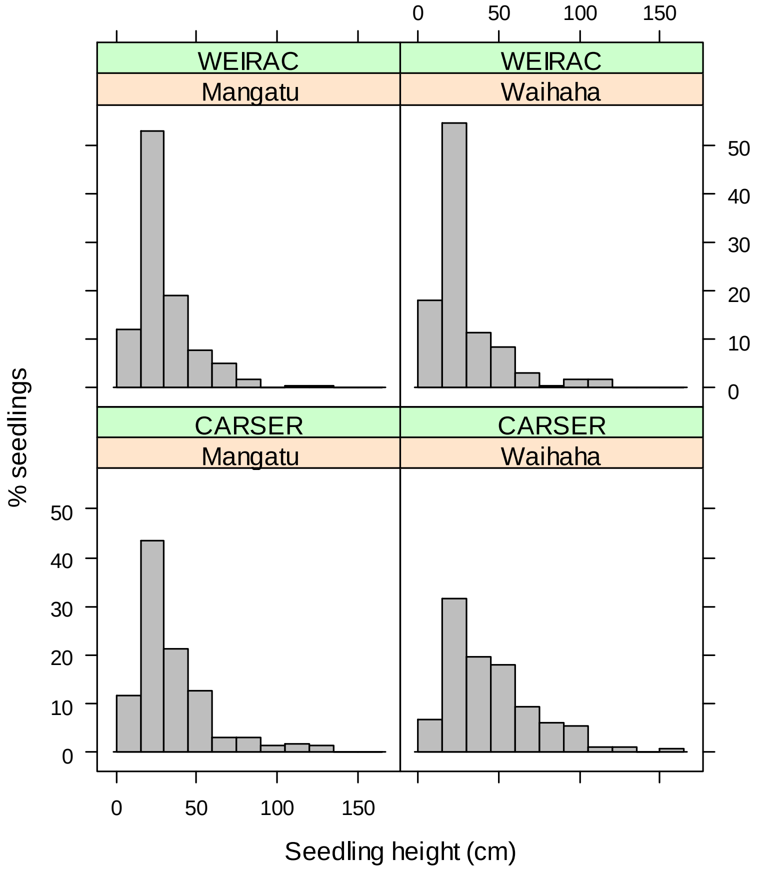

Fig. 7 Tagged seedling size class structures for the Waihaha site; WEIRAC = kāmahi (*Weinmannia racemosa*), CARSER = putaputawētā (*Carpodetus serratus*).

6.6 Waihaha site summary

The two blocks (Waihaha and Mangatu) are well matched in geology. Their physical environments are quite similar although the Waihaha block is of slightly higher elevation and has more dissected terrain. There are some differences in forest composition, which could reflect differences between the two blocks in terms of long-term successional patterns resulting from the Taupo eruption, mean annual temperature, and fire history or interactions between all three of these factors. Understorey biomass and representation of palatable biomass was quite similar between the two blocks.

7. Ruataniwha Conservation Area, Lake Ohau, Canterbury Ranges, South Island

7.1 Selecting two compositionally comparable blocks at the Ruataniwha site

The Hopkins and Huxley catchments in the Ruataniwha Conservation Park, Lake Ohau, are close to the Main Divide of the Southern Alps and are uplifted, metamorphosed sedimentary rocks (semi-schist). Forests in this region are compositionally simple being an admixture of silver beech (*Nothofagus menziesii*) and mountain beech (*N. solandri* var. *cliffortioides*; Wardle & Guest 1977). The presence and abundance of subordinate species in the forest understorey reflect elevation; species typical of open valley floor communities (e.g. pastoral species) are found in low-elevation forests, while high-elevation forests progressively include species from open subalpine and alpine communities. A substantial rainfall gradient (2900–4250 mm; see Table 27 in Discussion for an explanation of how these data were derived) occurs across the two catchments with greater rainfall at high elevation and close to the Main Divide. The dominant beech species close to the divide is silver beech, shifting to mountain beech away from the divide, partially reflecting rainfall gradients (Wardle & Guest 1977). The forests of the Huxley and Hopkins catchments were mapped as being largely similar according to Wardle and Guest (1977) so we were confident that any compositional gradients in that region were shared between the two catchments.

To evaluate compositional similarity between the Hopkins and Huxley catchments, we re-examined the permanent forest plot data used by Wardle and Guest (1977; Ahuriri Survey 1973/4 archived in the NVS Databank). These data indicated that composition was indeed similar between the two catchments with approximately equal basal area and density of dominant species (Appendix 4). This was the basis for the delineation of two equal-sized blocks of forest within the two catchments, avoiding the wetter headwaters of the Hopkins catchment to minimise differences in rainfall between the two blocks.

7.2 FAD Ruataniwha plots: environment

Plot-level environments in new plots established within the two blocks in 2007 were similar between the two blocks although mean canopy top height was much higher in the Hopkins block (18.7 m) than in the Huxley block (13.4 m; Table 15); this may have arisen because some plots in the Huxley block sampled short-statured subalpine forest and alpine heath vegetation.

Table 15 Summary of mean environments and canopy height sampled by Recce plots. Data are presented as arithmetic means per site and for each of the two blocks at each site and the minimum and maximum elevations within each block are also presented.

SITE Block	No. plots	Elevation (m)	Slope (°)	Landform Index (°)	Potential solar radiation (% max)	Mean top height (m)
RUATANIWHA	101	940 (663–1175)	26	20	70	16.0
Hopkins	50	939 (758–1159)	25	20	70	18.7
Huxley	51	941 (663–1175)	27	20	70	13.4

7.3 FAD Ruataniwha plots: vegetation composition

Dominant subalpine species such as *Phyllocladus alpinus*, *Podocarpus nivalis* and *Coprosma pseudocuneata* were all more frequent in the Huxley block, relative to the Hopkins block (Table 16). The Huxley block had more species than the Hopkins block and less than half the species were shared between the two blocks (Table 17). Greater species richness in the Huxley block reflected a few plots that sampled subalpine forest and alpine heath vegetation. Greater sampling of high-elevation communities in the Huxley block relative to the Hopkins resulted in a strong significant difference in composition between the Huxley and Hopkins blocks (Table 18, Fig. 8).

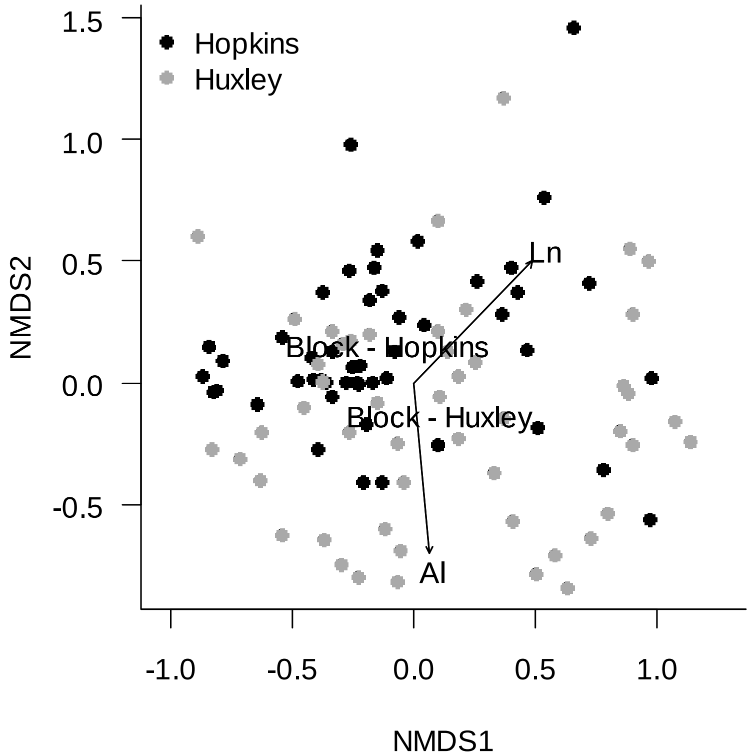

Fig. 8 NMDS ordination of vegetation cover data from the Ruataniwha site. There was a significant difference between the two blocks (illustrated by the position of centroids (‘Block – Hopkins’ and ‘Block – Huxley’) for each block), and strong effects of altitude (Al) and Landform Index (Ln) on vegetation composition.

Table 16 Frequency of dominant species by tier in each of two blocks at the Ruataniwha site. A species was considered dominant if it was ever present in a plot with a cover score of 50% or more. Data are frequency (number of plots) per block with the frequency where dominant given in parentheses.

Tier	Species	Hopkins *N* = 50	Huxley *N* = 51
>20 m	*Nothofagus solandri* var. *cliffortioides*	6 (1)	0 (0)
12–20 m	*Nothofagus solandri* var. *cliffortioides*	38 (25)	19 (14)
	Nothofagus menziesii	25 (9)	16 (10)
5–12 m	*Nothofagus solandri* var. *cliffortioides*	44 (7)	32 (18)
	Nothofagus menziesii	37 (8)	34 (11)
2–5 m	*Nothofagus solandri* var. *cliffortioides*	45 (0)	36 (6)
	Nothofagus menziesii	40 (1)	36 (2)
0.3–2 m	*Nothofagus solandri* var. *cliffortioides*	47 (10)	37 (6)
	Nothofagus menziesii	41 (0)	39 (2)
	Coprosma pseudocuneata	12 (0)	31 (3)
	Podocarpus nivalis	9 (2)	22 (8)
	Polystichum vestitum	14 (5)	14 (2)
	Phyllocladus alpinus	6 (0)	22 (1)
	Cortaderia fulvida	1 (0)	1 (1)
0–0.3 m	*Nothofagus solandri* var. *cliffortioides*	48 (11)	39 (11)
	Nothofagus menziesii	44 (0)	40 (1)
	Coprosma pseudocuneata	14 (0)	33 (2)
	Polystichum vestitum	22 (5)	24 (2)
	Hymenophyllum multifidum	17 (3)	21 (4)
	Blechnum penna-marina	18 (0)	18 (2)
	Coprosma depressa	18 (5)	18 (2)
	Podocarpus nivalis	8 (4)	28 (11)
	Hymenophyllum revolutum	11 (6)	11 (2)
	Rytidospermum gracile	2 (0)	3 (1)
	Cortaderia fulvida	1 (0)	1 (1)
	Hymenophyllum sanguinolentum	2 (1)	0 (0)
	Pratia angulata	1 (1)	2 (1)

Table 17 Species richness in the two blocks at the Ruataniwha site. Taxa are not all species and unidentified generic records were deleted unless they were the only use in the dataset.

Group	Species richness
Ruataniwha site	134
Hopkins block	89
Huxley block	99
Shared	54 (40%)
Unique to Hopkins	35
Unique to Huxley	45

Table 18 Summary of environmental and FAD block effects on vegetation composition at the Ruataniwha site. r^2 is the squared correlation coefficient, a goodness of fit statistic.

Factor	r^2	Significance of influence on vegetation composition
FAD block	0.0733	0.0020
Altitude	0.1520	<0.001
Slope	0.0066	0.7297
Landform index	0.1950	<0.001
Potential solar radiation	0.0313	0.2162

7.4 FAD Ruataniwha plots: understorey biomass

In contrast to the Waiotaka and Waihaha study areas, the understorey biomass (intercepts as a proxy) was greater in one block (Hopkins) than the other, and the relative proportion of ‘avoided’ species in that block (at a plot level, Table 19, and overall, i.e. 66.9% of all intercepts) was greater than in the Huxley block (52.9% of all intercepts). The proportionately greater biomass of ‘avoided’ species could be a result of past herbivory, resulting in greater inertia in response to deer control, i.e. established unpalatable species may outcompete newly established palatable species (Coomes et al. 2003).

Table 19 Understorey point height intercept (PHI) data summarised by palatability class (Appendix 1). Data are presented as the total number of intercepts per block in each of four palatability classes and then as the number of intercepts per plot so as to standardise across blocks. Statistical differences in the number of intercepts per plot for each palatability class are indicated; means that share a letter within a row are not significantly different at $P \leq 0.05$.

Palatability class	Hopkins	Huxley
Total no. intercepts		
Preferred	115	46
Not selected	131	337
Avoided	828	541
Not classified	164	99
Total	1238	1023

Table 19 continued

Palatability class	Hopkins	Huxley
No. intercepts per plot		
Preferred	2.3 a	0.9 b
Not selected	2.6 a	6.6 a
Avoided	16.6 a	10.6 b
Not classified	3.3	1.9
Total per plot	24.8	20.1

7.5 FAD Ruataniwha plots: tagged seedlings

The designated number of mountain beech seedlings was readily achieved within the plots established in both blocks (Table 20).

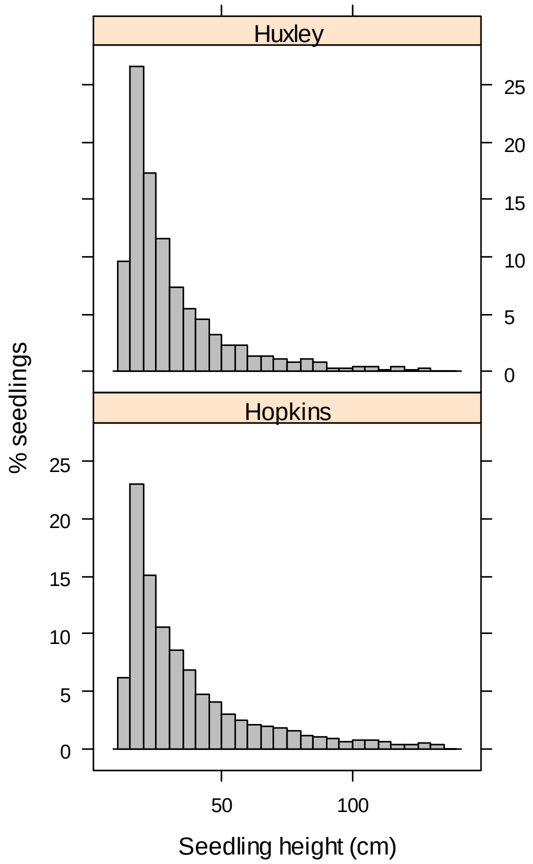

Fig. 9 Seedling height class structure of mountain beech (*Nothofagus solandri* var. *cliffortioides*) in two blocks at the Ruataniwha site. Each bar represents a 5-cm height class bin. Median seedling height was 28 cm in the Hopkins block and 24 cm in the Huxley block. These height-class structures are not representative below 50 cm because the contractors raised the minimum sampling height from 15 cm to 50 cm during the fieldwork.

Although more seedlings were in plots in the Hopkins block (Table 14), the total number in both blocks were high and we are confident that, as a result, demographic data (survival and growth) will be statistically sound in both blocks. The demographic data on mountain beech in the two blocks will be readily comparable with equivalent data on mountain beech in the Kaweka Range in the North Island, which is subject locally to intense browsing by sika deer (*Cervus nippon*; Husheer et al. 2006). Population size structures in both blocks in Ruataniwha are similar (Fig. 9). Mountain beech is much less dependent on raised surfaces for its regeneration than red beech (as in Waiotaka, Table 8), with a low percentage of seedlings on raised surfaces overall (2.8%); the percentage was higher in the Huxley block (3.5%) than in the Hopkins block (2.3%; Table 20).

Table 20 Summary of the number of tagged seedlings in each block and for the total Ruataniwha site.

Species Substrate	Hopkins *N* = 50	Huxley *N* = 51	Total *N* = 101
Nothofagus solandri var. *cliffortioides*	5371	3163	8534
Ground	5247	3052	8299
Raised	124	111	235

7.6 Ruataniwha site summary

The two blocks (Huxley and Hopkins) are well matched in geology and physical environments. The Huxley block sampled more subalpine vegetation than the Hopkins block, possibly because of past avalanche disturbance or more disrupted treelines. As a result it had higher species richness because there were more alpine plants in the plots. Tree canopy compositions were similar between the two blocks.

8. Anatoki, North West Nelson, South Island

8.1 Selecting two compositionally comparable blocks at the Anatoki site

The Anatoki River drains east out of the Kahurangi National Park into Golden Bay. Selection of two comparable blocks centred on the Anatoki River catchment was a challenge because this area contains some of the oldest and most diverse bedrocks in New Zealand, along with forests and alpine vegetation containing many endemic plant taxa (Williams 1993). To address these issues, we used a combination of fine-scale geological maps and plot-level-measured vegetation composition data to identify two comparable blocks of forest that could be used as a potential study site for the project. The option to stratify by bedrock type was not available to us because of the constraint of applying the same sampling design to all of the four sites.

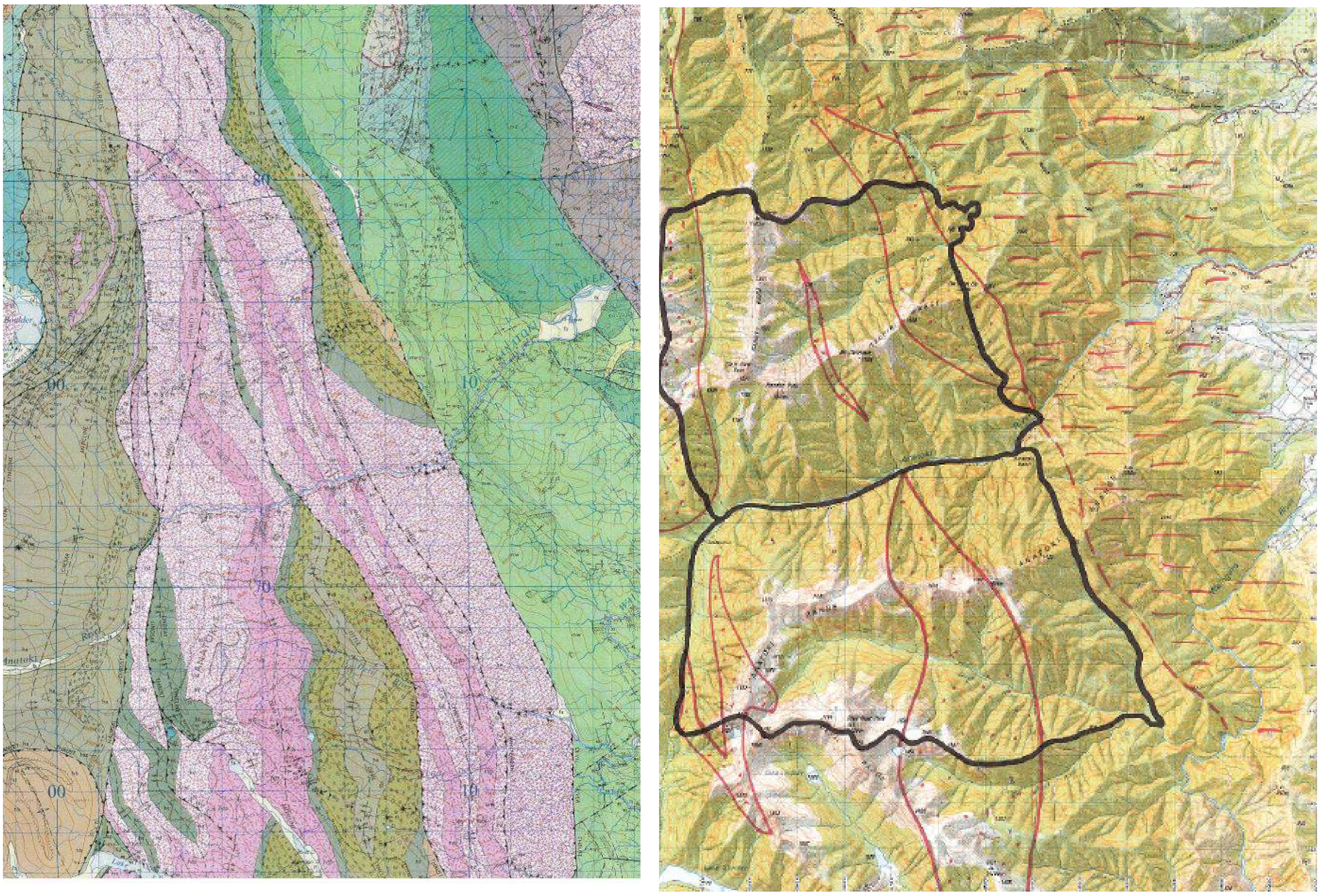

Fig. 10 LEFT: Geological map of the Takaka region (Grindley 1971) showing diverse bands of bedrocks. RIGHT: Topographic map of the same area with two suggested blocks (in black) selected by equalising the areas of bedrock (sketched on in red) in each block. The Anatoki River forms the boundary between the two blocks.

The Anatoki area contains bands of early Palaeozoic rocks in two terranes (Müncker & Cooper 1999; Fig. 10) and bands of deformation along the Anatoki Fault (Jongens 2006). The only possible configuration that could delimit two blocks of comparable geology was to delimit one to the north and one to the south, with the same large differences in rock type occurring within each block.

We then used existing vegetation data (relevé data) to determine whether composition was approximately similar between the two blocks. These data are unpublished (C. Newell and R. Allen, Landcare Research; Department of Conservation, Nelson) and are archived in the NVS Databank. We used these data to examine whether there was compositional overlap and whether elevation was a principal environmental gradient in each block. Composition overlapped well (Appendix 5) and was strongly related to elevation in both areas examined (Appendix 6). We were strongly encouraged by these outcomes and proceeded with our two adjacent blocks separated by the Anatoki River: the Devil block to the north and the Haupiri block to the south (Fig. 10).

8.2 FAD Anatoki plots: environment

New plots were established in 2007 in both blocks. The Devil block samples a broader elevation band and, given the importance of elevation for composition, we anticipated that this would affect compositional overlap (Table 21). The Devil sites received more potential solar radiation than the Haupiri sites. Potential solar radiation is probably only important in gaps but is likely to influence composition.

Table 21 Summary of mean environments and canopy height sampled by relevé plots at the Anatoki site. Data are presented as arithmetic means and the minimum and maximum elevations within each block are also presented.

SITE Block	No. plots	Elevation (m)	Slope (°)	Landform Index (°)	Potential solar radiation (% max)	Mean top height (m)
ANATOKI	100	924 (338–1488)	32	23	76	12.7
Devil	50	932 (338–1488)	33	22	83	12.6
Haupiri	50	917 (356–1393)	31	24	70	12.9

8.3 FAD Anatoki plots: vegetation composition

The Devil block had more species than the Haupiri block and only 53% of the species were shared between the two blocks (Table 22). Many of the unique species in the Devil block were in species-rich alpine genera such as *Hebe*, *Celmisia* and *Olearia* that were sampled in a few high-elevation plots that were not matched in the Haupiri block. There was no significant difference in composition between the two blocks (Table 23, Fig. 11).

In addition to differences related to sampling alpine vegetation, there were some differences in the frequency of dominant forest species (Table 24).

Table 22 Richness in the two blocks at the Anatoki site. Taxa are not all species and unidentified generic records were deleted unless they were the only use in the dataset.

Group	Species richness
Anatoki site	183
Devil block	156
Haupiri block	124
Shared	97 (53%)
Unique to Devil	59
Unique to Haupiri	27

Table 23 Summary of environmental and FAD block effects on vegetation composition summarised by NMDS at the Anatoki site. r^2 is the squared correlation coefficient, a goodness of fit statistic.

Factor	r^2	Significance of influence on vegetation composition
FAD block	0.0027	0.7618
Altitude	0.8495	<0.001
Slope	0.1416	<0.001
Landform Index	0.0642	0.0470
Potential solar radiation	0.0204	0.3824

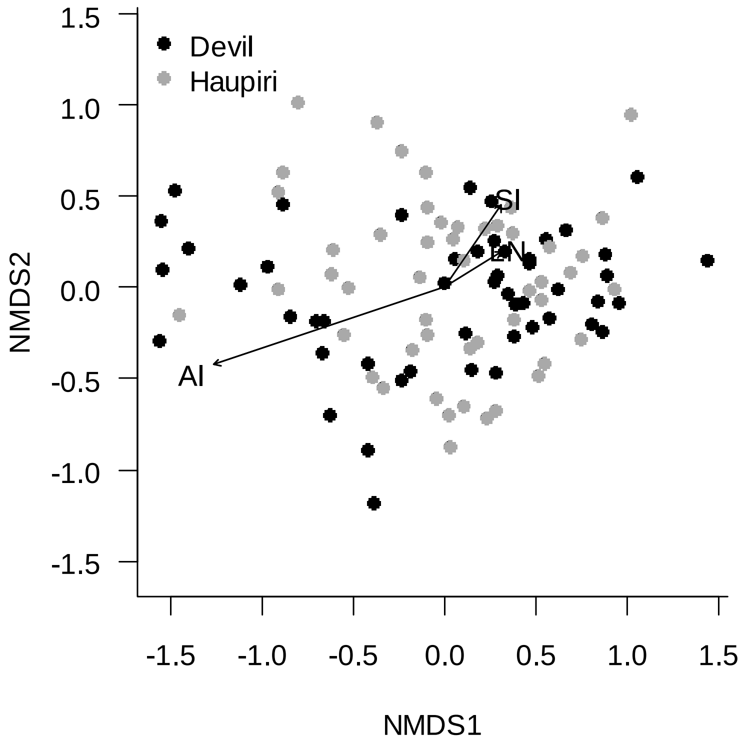

Fig. 11 NMDS ordination of vegetation cover data from the Anatoki site. There were significant effects of altitude (Al), slope (Sl) and Landform Index (Ln) on vegetation composition, but no effect of FAD block.

Table 24 Frequency of dominant species by tier in each of two blocks at the Anatoki site. A species was considered dominant if it was ever present in a plot with a cover score of 50% or more. Data are frequency (number of plots) per block with the frequency where dominant given in parentheses. *N* = 50 plots per block.

Tier	Species	Devil	Haupiri
>20 m	*Nothofagus fusca*	3 (0)	3 (1)
	Nothofagus menziesii	1 (0)	2 (2)
12–20 m	*Nothofagus menziesii*	29 (2)	28 (6)
	Nothofagus fusca	25 (6)	23 (8)
	Weinmannia racemosa	12 (0)	11 (3)
5–12 m	*Nothofagus menziesii*	35 (4)	31 (4)
	Weinmannia racemosa	27 (7)	26 (5)
	Nothofagus fusca	26 (3)	24 (4)
	Quintinia serrata	25 (2)	22 (4)
	Nothofagus solandri var. *cliffortioides*	14 (2)	13 (1)
	Griselinia littoralis	4 (0)	8 (1)
	Hedycarya arborea	2 (0)	1 (1)
2–5 m	*Nothofagus menziesii*	36 (2)	35 (0)
	Weinmannia racemosa	27 (1)	29 (0)
	Quintinia serrata	28 (0)	23 (1)
	Nothofagus solandri var. *cliffortioides*	15 (2)	13 (0)
	Archeria traversii	6 (0)	11 (2)
	Dracophyllum longifolium	2 (0)	4 (1)
	Cyathea smithii	3 (0)	2 (1)
0.2–2 m	*Coprosma foetidissima*	25 (1)	37 (0)
	Quintinia serrata	29 (1)	24 (0)
	Blechnum discolor	20 (3)	13 (1)
	Nothofagus solandri var. *cliffortioides*	15 (1)	14 (0)
	Pseudowintera colorata	12 (0)	16 (3)
	Archeria traversii	9 (0)	18 (2)
	Uncinia uncinata	2 (0)	14 (5)
	Dracophyllum longifolium	6 (0)	5 (1)
	Cyathea smithii	4 (0)	3 (1)
	Leptospermum scoparium	0 (0)	2 (1)
0–0.3 m	*Blechnum discolor*	21 (1)	15 (0)
	Uncinia uncinata	7 (0)	23 (6)
	Myrsine salicina	5 (0)	6 (1)
	Dracophyllum longifolium	5 (0)	5 (1)
	Metrosideros fulgens	5 (2)	1 (1)

The forest sedge *Uncinia uncinata* and the shrub *Archeria traversii* were both more frequent in the Haupiri block than in the Devil block (Table 24). Further, *Uncinia uncinata* was frequently dominant at a plot-level in the Haupiri block. This species is found in high-light environments where moisture is not limiting, perhaps suggesting that the Haupiri block had more clearings or gaps. *Archeria traversii* is associated with extremely poor soils, higher elevations and often a high proportion of cloudy days, again suggesting that these environments were sampled more frequently in the Haupiri block (Table 24).

8.4 FAD Anatoki plots: understorey biomass

Point height intercept data were summarised by adding the intercepts within each block by palatability class (see Appendix 1). As in Ruataniwha and in contrast to the Waiotaka and Waihaha study areas, the understorey biomass (intercepts as a proxy) was greater in one block (Haupiri) than the other, and the relative proportion of 'avoided' species in that block (at a plot level, Table 25, and overall, i.e. 65.1% of all intercepts) was greater than in the Haupiri block (50.1% of all intercepts). As in Ruataniwha, greater understorey biomass in one block than the other could reflect different levels of past disturbance to canopies, and the higher proportion of 'avoided' biomass in the Haupiri block could be a confounding influence on potential recruitment of 'preferred' species after controlling ungulates.

Table 25 Understorey point height intercept (PHI) data summarised by palatability class (see Appendix 3). Data are presented as the total number of intercepts per block in each of four palatability classes and then as the number of intercepts per plot so as to standardise across blocks. Statistical differences in the number of intercepts per plot for each palatability class are indicated; means that share a letter within a row are not significantly different at $P \leq 0.05$.

Palatability class	Devil	Haupiri
Total no. intercepts		
Preferred	54	53
Not selected	190	186
Avoided	309	529
Not classified	59	45
Total	612	813
No. intercepts per plot		
Preferred	1.1 a	1.1 a
Not selected	3.8 a	3.7 a
Avoided	6.2 a	10.6 b
Not classified	1.2	0.9
Total per plot	12.2	16.3

8.5 FAD Anatoki plots: tagged canopy tree seedlings

The minimum number of seedlings (44) was achieved for silver beech (*Nothofagus menziesii*) in both blocks but was not achieved for red beech (*N. fusca*) or kāmahi (*Weinmannia racemosa*) in the Devil block (Table 26). Seedling size class structures were approximately similar for all three species (Fig. 12). Median seedling heights were: 30 cm in the Haupiri block and 32 cm in the Devil block for kāmahi; 34 cm in the Haupiri block and 30 cm in the Devil block for red beech; and 24 cm in the Haupiri block and 28 cm in the Devil block for silver beech.

The percentage of seedlings of red beech, silver beech, and kāmahi on raised surfaces in the Devil block were very low (7%, 5%, and 3% respectively), and less than in the Haupiri block (11%, 18%, and 32% respectively, Table 26). A greater proportion of seedlings on raised surfaces in the Haupiri block again could be a result of greater past disturbances of canopies, resulting in more fallen logs as sites for seedlings to colonise (cf. section 8.4). The very low percentage of red beech and kāmahi seedlings on raised surfaces in the Devil block also contrast with both blocks in the Waiotaka study area (section 5.5).

Table 26 Summary of the number of tagged seedlings of each species in each block and for the total Anatoki site.

Species Substrate	Devil *N* = 50	Haupiri *N* = 50	Total *N* = 100
Nothofagus fusca	28	89	117
Ground	26	79	105
Raised	2	10	12
Nothofagus menziesii	75	112	187
Ground	71	92	163
Raised	4	20	24
Weinmannia racemosa	40	69	109
Ground	39	47	86
Raised	1	22	23

8.6 Anatoki site summary

The diverse geologies within both blocks are as evenly matched as possible. Existing plot data and newly established plots as part of this project suggest that the areas have comparable vegetation, with small differences that arise from uneven sampling of alpine vegetation. Elevation is a strong gradient underpinning compositional variation. The Haupiri block has a denser understorey with more unpalatable cover than the Devil block.

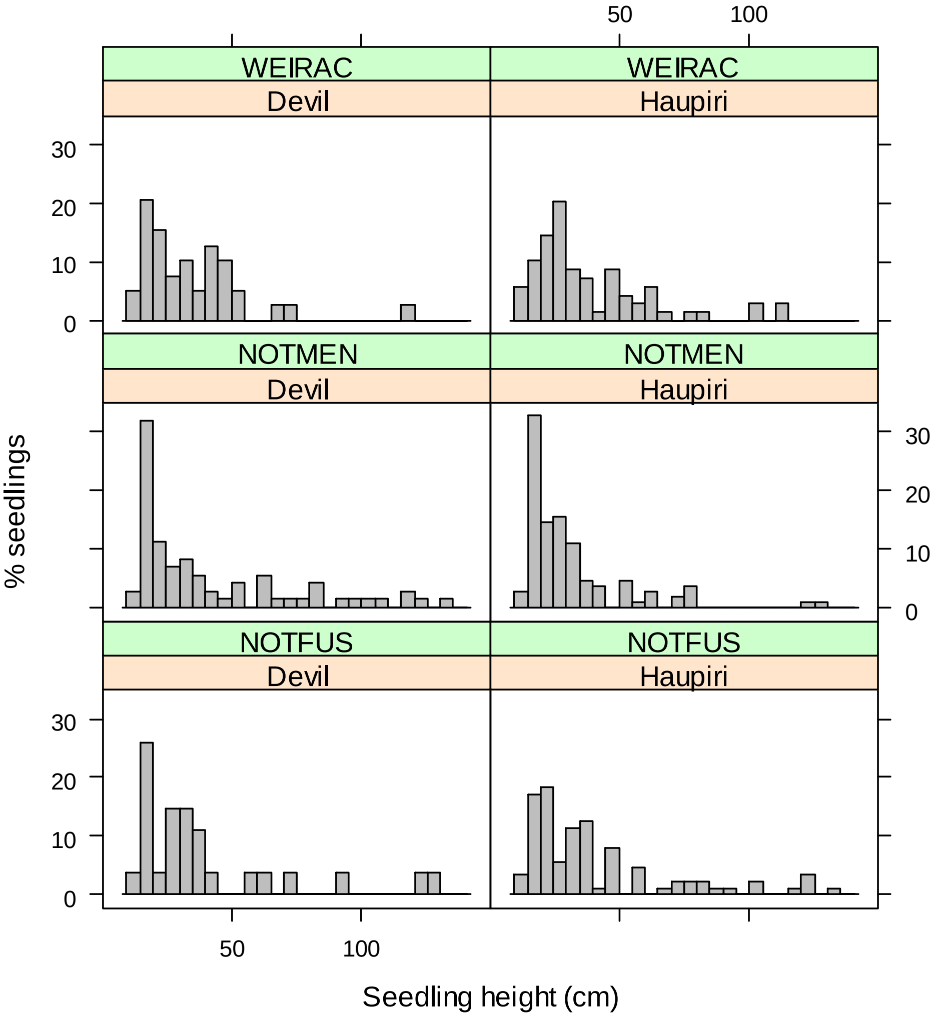

Fig. 12 Seedling height class structure of three species in two blocks at the Anatoki site. Each bar represents a 15-cm height class bin. WEIRAC = kāmahi (*Weinmannia racemosa*), NOTMEN = silver beech (*Nothofagus menziesii*), NOTFUS = red beech (*N. fusca*).

9. Discussion

9.1 General discussion of approach taken to develop the study and the four sites we chose

We adopted a consistent approach of delineating comparable sized blocks within candidate study areas. The first criterion was to have comparable geologies within both blocks. If this criterion could be met then we evaluated as much existing forest compositional data as existed to determine if the blocks were comparable. Further criteria (e.g. whether deer were present in sufficient numbers, whether sustained possum control was being implemented, whether ungulates other than deer were present) were applied in the selection of study sites but not in the component of the project that we report here. When one proposed study area (Pembroke Wilderness Area) could not be subdivided into areas of comparable geology and forest composition, it was rejected as a potential site in which to work (Appendix 7).

Four candidate sites could be delineated into two blocks of a size suitable for operational scales of management on the basis of comparable geology, physiography, and vegetation composition (Table 27), and for three of these, treatment and non-treatment blocks were assigned after selection by a coin toss. Geologies of all four sites differ from one another: Waiotaka and Ruataniwha are most similar to one another geologically but the other two sites (Anatoki and Waihaha) are very dissimilar to all other sites.

Table 27 Summary of the four FAD sites. For each block we indicate whether it was ascribed the experimental non-treatment (NT) or the experimental treatment (T). Bedrock, rainfall and mean annual temperature (MAT) were estimated for each georeferenced FAD plot using thin-plate splines fitted to data from nearby meteorological stations (Leathwick 2001; Leathwick et al. 2003).

Site	Blocks	Bedrock	Rainfall (mm)	MAT (ºC)
Waiotaka	Whitikau (NT) Waiotaka (T)	Greywacke	2241	8.5
Waihaha	Mangatu (NT) Waihaha (T)	Lavas, ignimbrite, hard volcanic rocks, ancient ash and greywacke (to the west)	1618	9.8
Ruataniwha	Huxley (NT) Hopkins (T)	Semi-schist	3523	7.5
Anatoki	Haupiri * Devil *	Highly diverse ancient volcanics with minor intrusives (Fig. 10)	3071	7.9

* Experimental treatments were not allocated to the Anatoki blocks

9.2 Composition

Forest composition is dominated by beech (*Nothofagus* spp.) in Waiotaka, Ruataniwha, and Anatoki, whereas beech is nearly absent from Waihaha, which is instead dominated by a diverse mixture of angiosperm and conifer species. Elevation is a strong determinant of compositional variation at all sites. In Waihaha, legacies of past disturbance (volcanism and fire) and microclimate are also likely determinants of current vegetation composition. The proportion of trees in Waihaha comprised of species that are preferred in deer diets (Forsyth et al. 2002) is greater than in the other sites but all sites contain understorey species that are preferred in deer diets.

9.3 Point height intercept data

Methods for quantifying the vertical distribution of biomass have been used in vegetation studies in New Zealand (Scott 1965; Park 1972) and elsewhere (McArthur & Horn 1969; Wardle & Zackrisson 2005). The strength of relationships between the proxy measurements of biomass, using intercepts, and actual biomass is unknown and will be determined after harvests at the end of the project. Nonetheless, there were differences in proxy measurements of biomass (intercepts) between the study sites.

It seems likely that understorey biomass, assessed by intercepts, is lower in the Waihaha and Anatoki sites (the average intercepts per plot across the four blocks in these sites range from 12 to 17) than in the Waiotaka and Ruataniwha sites (range 20–27 intercepts per plot). Furthermore the proportion of understorey biomass of species preferred by deer in the beech-dominated sites (Waiotaka, Ruataniwha, and Anatoki) is lower (3–9% of intercepts per plot were on preferred species across the six blocks in these sites) than in Waihaha, a non-beech site (14% of intercepts per plot, Waihaha block; 18%, Mangatu block). A low proportion of preferred species in three sites could be a legacy of previous deer herbivory, which could have altered the competitive balance to favour less preferred species currently (Coomes et al. 2003). It could also be a result of lower resource levels (soil nutrients, light) on average in the beech-dominated sites because many species which are preferred in deer diets grow in resource-rich situations, i.e. with high levels of soil nitrogen and phosphorus or light (Bellingham & Lee 2006). Quantifying resource levels, including soil nutrient concentrations and light environments, would aid interpretation of changes in understorey biomass during this study.

At the end of the experiment, the effect of deer control on understorey biomass will be measured as the difference between treatment and non-treatment blocks in intercept frequency in each of the three palatability classes. Intercept frequency will be converted to biomass by harvesting each subplot, weighing the material, and using regression analysis to convert intercept frequencies to biomass. As with seedling demography, environmental variation among plots will be accommodated in the analyses using the plot-level measurements of elevation and landform described here, and subplot-level measurements of canopy openness, which will be completed at the end of the experiment.

9.4 Seedling populations

Seedling size structures of beeches from the three sites where they are dominant canopy trees show distributions skewed towards small seedlings, which typically self-thin during onward growth, especially after canopy disturbance (Wardle 1984; Coomes & Allen 2007). The height distribution of red beech seedlings in Waiotaka and Anatoki are quite similar to those reported from the Tararua Range (June & Ogden 1975) and mountain beech seedlings ≥50 cm (where data are representative) in Ruataniwha have a similar height distribution to those in the Kaweka Range (Duncan et al. 2006).

Kāmahi was widespread across the study sites, occurring in all but Ruataniwha, and in most sites seedling height distributions were skewed towards smaller seedlings. There is little published information on seedling height distributions of kāmahi (but see Husheer et al. 2003; Section 5.5 this report). Seedlings of kāmahi are not strongly responsive to increased light in old-growth forests (Bellingham & Richardson 2006; Coomes et al. 2009) although this species features prominently in secondary successions (Wardle 1966), after wind disturbance (Stewart 1986), after earthquakes (Wells et al. 2001) and after fire (Payton et al. 1984; Wilmshurst et al. 1999). It is unknown whether seedlings of kāmahi self-thin during onward growth. Putaputawētā seedlings were only sampled in the Waihaha study site, where their height distribution was similar to that of kāmahi. We know of no published accounts of the seedling sizes of putaputawētā with which to compare those from Waihaha.

Across sites, red beech and kāmahi had a high percentage of seedlings on raised surfaces, and this was also the case for putaputawētā at Waihaha. In five blocks in three sites, more than 30% of kāmahi seedlings occurred on raised surfaces, with the exception of the Devil block at Anatoki where only 3% occurred on raised surfaces. The percentage of kāmahi seedlings on raised surfaces in the other five blocks (32–38%) was low compared with that in montane rainforests in central Westland (42–80%; Stewart & Veblen 1982) and in lowland forests of Bench Island (41–50%; Veblen & Stewart 1980), but greater than that in lowland forests of eastern Stewart Island (12–28%; Veblen & Stewart 1980). The percentage of red beech seedlings on raised surfaces was quite similar at the two blocks in Anatoki (7%, Devil block; 11% Haupiri block) and similar to that at the Whitikau block (12%) in Waiotaka, but at the Waiotaka block the percentage on raised surfaces (42%) was much greater, although not as great as that from a 3-year-old cohort of red beech seedlings on raised surfaces (c. 80%) in the Tararua Range (June & Ogden 1975). Remeasurements of tagged seedlings of these species across the treatment and non-treatment blocks could reveal whether the benefits of reduced competition from other plants on the ground offset slightly greater mortality rates on raised surfaces (Bellingham & Richardson 2006) and the interaction of these with herbivory.

At the end of the experiment, the effect of deer control on seedling demography will be measured as the difference between the change in the treatment block and the change in the non-treatment block, in both tagged seedling growth and mortality rates. Environmental variation among seedlings will be accommodated in the analyses using the plot-level measurements of elevation and landform described here, and subplot-level measurements of canopy openness, which will be completed at the end of the experiment.

10. Key Findings and Recommendations

10.1 Key findings

Vegetation composition was similar between the two blocks at the Waiotaka and Anatoki sites, but differed between blocks at the Ruataniwha and Waihaha sites. There are strong elevation gradients at all sites and elevation will be a key covariate in future plot analyses. Small differences in vegetation composition between blocks at the Ruataniwha site were attributable to sampling of subalpine and alpine vegetation in one block and not the other.

The Waihaha site has very little beech and is dominated by podocarps and various broadleaved trees. Vegetation composition between the two blocks was dissimilar in terms of some common canopy and understorey species and this will complicate interpretation of deer hunting treatments. Elevation, slope and landform accounted for some of the compositional variation in this highly heterogeneous vegetation; composition is also likely to be determined by the legacies of volcanic activity over the last 2000 years and fire history over the last 800 years, and local influences of microclimate.

Seedlings of tree species from which to obtain demographic information were sampled at all sites, including canopy trees (beech species in three sites, kāmahi in three sites) and an understorey tree (putaputawētā at Waihaha). Additional plots were required to obtain sufficient individuals at two sites (Waiotaka and Waihaha). In most cases, the height distributions of seedlings were similar (skewed to small individuals) and were not greatly different between blocks.

Understorey biomass, assessed by proxy methods, is likely to be greater in Waiotaka and Ruataniwha than in Waihaha and Anatoki. The proportion of the biomass in the understorey comprised of species that are preferred by deer was very low in three sites (<10% of measured points in the three beech-dominated sites: Waiotaka, Ruataniwha, and Anatoki) and was greater in the non-beech forests at Waihaha (14–18% of measured points).

10.2 Recommendations

- Establish the relationship between point height intercepts and measured cover and biomass, by species or by palatability class, at each site. Use accessible sites from which we can generalise to the entire catchment. These data will be publishable and of great use to future fieldworkers. They will also provide us with information on the variance in our biomass per subplot.
- Obtain data on soil nutrient concentrations and light environments at the subplot-level because these are very likely to determine seedling demography and understorey biomass and its composition.
- Combine the assessments of intra- and inter-site differences highlighted in this report alongside data on intra- and inter-site differences in deer (and other ungulate) densities to determine which sites should be prioritised for long-term inclusion in this project.

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12. References

Allen RB, Payton IJ, Knowlton JE 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.

Allen RB, Stewart G, Rogers G 2002. Maintenance of key tree species. Science for Conservation 190. Wellington, Department of Conservation. 60 p.

Bain H 2007. Wild deer – like possums on stilts. Forest and Bird 325: 23–25.

Bellingham PJ, Lee WJ 2006. Distinguishing natural processes from impacts of invasive mammalian herbivores. In: Allen RB, Lee WG eds Biological invasions in New Zealand. Berlin, Springer. Pp. 321–336.

Bellingham PJ, Richardson SJ 2006. Tree seedling growth and survival over 6 years across different microsites in a temperate rain forest. Canadian Journal of Forest Research 36: 910–918.

Bolker BM 2009. Ecological models and data in R. New Jersey, Princeton University Press.

Bråthen KA, Hagberg O 2004. More efficient estimation of plant biomass. Journal of Vegetation Science 15: 653–660.

Burns BR, Smale MC 1990. Changes in structure and composition over fifteen years in a secondary kauri (*Agathis australis*) – tanekaha (*Phyllocladus trichomanoides)* forest stand, Coromandel Peninsula, New Zealand. New Zealand Journal of Botany 28: 141–158.

Burrows CJ 1996. Germination behaviour of seeds of seven New Zealand woody plant species. New Zealand Journal of Botany 34: 355–367.

Cameron RJ 1955. Mosaic and cyclic regeneration in North Island podocarp forests. New Zealand Journal of Forestry 7: 55–64.

Caughley G 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology 51: 53–72.

Clarkson BR 1984. Vegetation of three mountain mires, west Taupo, New Zealand. New Zealand Journal of Botany 22: 361–375.

Cockayne L 1909. Report on a botanical survey of Stewart Island. Government Printer, Wellington.

Coomes DA, Allen RB 2007. Mortality and tree-size distributions in natural mixed-age forests. Journal of Ecology 95: 27–40.

Coomes DA, Allen RB, Forsyth DM, Lee WG 2003. Factors preventing the recovery of New Zealand forests following control of invasive deer. Conservation Biology 17: 450–

459.

Coomes DA, Kunstler G, Canham CD, Wright E 2009. A greater range of shade-tolerance niches in nutrient-rich forests: and explanation for positive richness–productivity relationships? Journal of Ecology 97: 705–717.

Cornelissen JHC, Pérez-Harguindeguy N, Díaz S, Grime JP, Marzano B, Cabido M, Vendramini F, Cerabolini B 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. New Phytologist 143: 191–200.

Cuddihy MJ 1978. Forests and the influence of deer in the catchments of the Kaipo and John O'Groats / M.J. Cuddihy Southland Conservancy, New Zealand Forest Service.

Cunningham A 1979. A century of change in the forests of the Ruahine Range, North Island, New Zealand: 1870-1970. New Zealand Journal of Ecology 2: 11–21.

Department of Conservation 2007. National Vegetation Survey (NVS) Databank data entry, archiving and retrieval SOP (DOCDM-39000).

Dickinson KJM, Mark AF, Lee WG 1992. Long-term monitoring of non-forest communities for biological conservation. New Zealand Journal of Botany 30: 163–179.

Druce AP 1952. The vegetation of Western Taupo. New Zealand Science Review 10: 89–91.

Duncan R, Ruscoe W, Richardson S, Allen R 2006. Consequences of deer control for Kaweka mountain beech forest dynamics. Landcare Research Contract Report LC0607/021 for the Department of Conservation.

Elder NL 1962. Vegetation of the Kaimanawa Ranges. Transactions of the Royal Society of New Zealand Botany 2: 1–37.

Forsyth DM, Caley P 2006. Testing the irruptive paradigm of large-herbivore dynamics. Ecology 87: 297–303.

Forsyth DM, Coomes DA, Nugent G, Hall GMJ 2002. Diet and diet preferences of introduced ungulates (order: Artiodactyla) in New Zealand. New Zealand Journal of Zoology 29: 323–343.

Forsyth DM, Richardson SJ, Menchenton K 2005. Foliar fibre predicts diet selection by invasive red deer *Cervus elaphus scoticus* in a temperate New Zealand forest. Functional Ecology 19: 495–504.

Gillman LN, Ogden J 2003. Seedling mortality and damage due to non-trophic animal interactions in a northern New Zealand forest. Austral Ecology 28: 48–52.

Goulding CJ, Lawrence ME 1992. Inventory Practice for Managed Forest. Ministry of Forestry, FRI Bulletin. No 171.

Grindley GW 1971. Takaka. Geological Map of New Zealand S8. New Zealand Geological Survey.

Herbert J 1978. Forest pattern and regeneration ecology of the Rangitoto-Hauhungaroa forests. Indigenous Silviculture Report 19. Rotorua, New Zealand Forest Service, Forest Research Institute. 26 p.

Holloway JT 1950. Deer and the forests of western Southland. New Zealand Journal of Forestry 6: 123–137.

Hurst JM, Allen RB 2007a. The Recce method for describing New Zealand vegetation – field methods. Lincoln, Landcare Research.

Hurst JM, Allen RB 2007b. A permanent plot method for monitoring indigenous forests – field methods. Lincoln, Landcare Research.

Husheer SW, Coomes DA, Robertson AW 2003. Long-term influences of introduced deer on the composition and structure of New Zealand *Nothofagus* forests. Forest Ecology and Management 181: 99–117.

Husheer SW, Robertson AW 2005. High-intensity deer culling increases growth of mountain beech seedlins in New Zealand. Wildlife Research 32: 273–280.

Husheer SW, Allen RB, Robertson AW 2006. Suppression of regeneration in New Zealand mountain beech forests is dependent on species of introduced deer. Biological Invasions 8: 823–834.

Jacobson C, Allen W, Veltman C, Ramsey D, Forsyth DM, Nicol S, Allen R, Todd C, Barker R 2009. Collaborative learning as part of adaptive management of forests affected by deer. In: Allan C, Stanley GH eds Adaptive environmental management: a practitioner's guide. Dordrecht, Springer. Pp. 275–294.

James IL, Wallis FP 1969. A comparative study of the effects of introduced mammals on *Nothofagus* forest at Lake Waikareiti. Proceedings of the New Zealand Ecological Society 16:1–6.

Jongens R 2006. Structure of the Buller and Takaka Terrane rocks adjacent to the Anatoki Fault, northwest Nelson, New Zealand. New Zealand Journal of Geology and Geophysics 49: 443–461.

June SR, Ogden J 1975. 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.

Kaufmann MR, Weatherred JD 1982. Determination of potential direct beam solar irradiance. Rocky Mountain Forest and Range Experiment Station, Series Research paper RM 242. Fort Collins, Colorado, USA, Forest Service, U.S. Dept. of Agriculture. 23 p.

Krebs CJ 1999. Ecological Methodology, 2nd ed. Addison-Wesley Educational Publishers, Inc.

Kunstler G, Coomes DA, Canham CD 2009. Size-dependence of growth and mortality influence the shade tolerance of trees in a lowland temperate rain forest. Journal of Ecology 97: 685–695.

Leathwick JR 2001. New Zealand's potential forest pattern as predicted from current species-environment relationships. New Zealand Journal of Botany 39: 447−464.

Leathwick JR, Mitchell ND 1992. Forest pattern, climate and vulcanism in central North island, New Zealand. Journal of Vegetation Science 3: 603–616.

Leathwick JR, Morgan F, Wilson G, Rutledge D, McLeod M, Johnston K 2003. Land environments of New Zealand: technical guide. Manaaki Whenua Press, New Zealand.

Leopold A 1943. Deer irruptions. Wisconsin Conservation Bulletin 8: 3–11.

Lusk C, Ogden J 1992. Age structure and dynamics of a podocarp–broadleaf forest in Tongariro National Park, New Zealand. Journal of Ecology 80: 379–393.

Mark AF, Baylis GTS 1975. Impact of deer on Secretary Island, Fiordland, New Zealand. Proceedings of the New Zealand Ecological Society 22: 19–24.

McArthur RH, Horn HS 1969. Foliage profile by vertical measurements. Ecology 50: 802–804.

McCune B, Grace JB, Urban DL 2002. Analysis of ecological communities. Oregon, USA, MjM Software Design.

McGlone MS, Richardson SJ, Jordan GJ 2010. Trees in New Zealand: heights, species richness and range size. New Zealand Journal of Ecology 33: 137–151.

McKelvey P 1963. The synecology of the West Taupo indigenous forests. Bulletin of the New Zealand Forest Service 14.

McNab WH 1993. A topographic index to quantify the effect of mesoscale landform on site productivity. Canadian Journal of Forest Research 23: 1100–l 107.

Münker C, Cooper RA 1999. The Cambrian arc complex of the Takaka Terrane, New Zealand: an integrated stratigraphical, paleontological and geochemical approach. New Zealand Journal of Geology and Geophysics 42: 415–445.

New Zealand Deerstalkers' Association 2007. Preservationists scaremongering over big game management. http://www.deerstalkers.org.nz/Site/Press_Releases/Press_Releases.aspx

Nicholls J 1986. A descriptive overview of the central North Island volcanic upland. In: Veale BJ, Innes JG eds Ecological research in the central NI Volcanic Plateau region. Proceedings of a NZ Forest Science FRI workshop, Pureora. Pp. 2–17.

Nugent G, Fraser W 2005. Red deer. In: King CM ed. The handbook of New Zealand mammals. South Melbourne, Oxford University Press. Pp. 401–420.

Ogden J 1983. Community matrix model predictions of future forest composition at Russell State Forest. New Zealand Journal of Ecology 6: 71–77.

Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson GL, Solymos P, Stevens MHH, Wagner H 2008. Vegan: Community ecology package. R package version 1.16-5. http://vegan.r-forge.r-project.org/

Park GN 1972. Point height intercept analysis: a refinement of point analysis for structural quantification of low arboreal vegetation. New Zealand Journal of Botany 11: 103–114.

Payton IJ, Allen RB, Knowlton JE 1984. A post-fire succession in the northern Urewera forests North Island, New Zealand. New Zealand Journal of Botany 22: 207–222.

Peltzer DA, Allen RB, Rogers GM 2005. Dieback and recruitment of the forest dominants *Nothofagus fusca* and *Libocedrus bidwillii*, central North Island, New Zealand. Science for Conservation 255. Wellington, Department of Conservation.

Poole AL 1949. A pocket of silver beech – West Taupo. New Zealand Journal of Forestry 6:144–145.

R Development Core Team 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Richardson SJ, Allen RB, Doherty JE 2008. Shifts in leaf N:P ratio during resorption reflect soil P in temperate rainforest. Functional Ecology 22: 738–745.

Rogers GM, Leathwick JR 1997. Factors predisposing forests to canopy collapse in the southern Ruahine Range, New Zealand. Biological Conservation 80: 325–338.

Rose AB, Platt KH 1987. Recovery of northern Fiordland alpine grasslands after reduction in the deer population. New Zealand Journal of Ecology 10: 23–33.

Scott D 1965. A height frequency method for sampling tussock and shrub vegetation. New Zealand Journal of Botany 3: 253–260.

Smale MC, Kimberley MO 1986. Growth of naturally regenerated *Beilschmiedia tawa* and podocarps in unlogged and selectively logged forest, Pureora (New Zealand). New Zealand Journal of Forestry Science 16: 131–141.

Smale MC, Smale PN 2003. Dynamics of upland conifer/broadleaved forest at Waihaha, central North Island, New Zealand. Journal of the Royal Society of New Zealand 33: 509–528.

Smale MC, Hall GMJ, Gardner RO 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.

Sparks RJ, Melhuish WH, McKee JWA, Ogden J, Palmer JG, Molloy BPJ 1995. C-14 calibration in the southern hemisphere and the date of the last Taupo eruption: evidence from tree-ring sequences. Radiocarbon 37: 155–163.

Stewart GH 1986. Forest dynamics and disturbance in a beech/hardwood forest, Fiordland, New Zealand. Vegetatio 68: 115–126.

Stewart GH, Veblen TT 1982. Regeneration patterns in southern rata (*Metrosideros umbellata*) – kamahi (*Weinmannia racemosa*) forest in central Westland, New Zealand. New Zealand Journal of Botany 20: 55–72.

Stewart GH, Wardle JA, Burrows LE 1987. Forest understorey changes after reduction in deer numbers, northern Fiordland, New Zealand. New Zealand Journal of Ecology 10: 35–42.

Tanentzap AJ, Burrows LE, Lee WG, Nugent G, Maxwell JM, Coomes DA 2009. Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. Journal of Applied Ecology 46: 1064–1072.

Veblen TT, Stewart GH 1980. Comparison of forest structure and regeneration on Bench and Stewart Islands, New Zealand. New Zealand Journal of Ecology 3: 50–68.

Wardle J, Guest R 1977. Forests of the Waitaki and Lake Hawea catchment. New Zealand Journal of Forestry Science 7:44–67.

Wardle DA, Zackrisson O 2005. Effects of species and functional group loss on island ecosystem properties. Nature 435: 806–810.

Wardle DA, Barker GM, Yeates GW, Bonner KI, Ghani A 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecological Monographs 71: 587–614.

Wardle DA, Bonner KI, Barker GM 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. Functional Ecology 16: 585–595.

Wardle J, Hayward J 1970. The forests and scrublands of the Taramakau and the effects of browsing by deer and chamois. Proceedings of the New Zealand Ecological Society 17: 80–91.

Wardle J 1967. Vegetation of the Aorangi Range, Southern Wairarapa. New Zealand Journal of Botany 5: 22–48.

Wardle J 1971. The forests and shrublands of the Seaward Kaikoura Range. New Zealand Journal of Botany 9: 269–292.

Wardle J 1974. Influence of introduced mammals on the forest and scrublands of the Grey River headwaters. New Zealand Journal of Forestry Science 4: 459–186

Wardle JA 1984. The New Zealand beeches. Christchurch, New Zealand Forest Service.

Wardle J, Hayward J, Herbert J 1973. Influence of ungulates in the forests and scrublands of South Westland. New Zealand Journal of Forestry Science 3: 3–36.

Wardle P 1966. Biological flora of New Zealand. 1. *Weinmannia racemosa* Linn. f. (Cunoniaceae). Kamahi. New Zealand Journal of Botany 4: 114–131.

Wardle P 1991. Vegetation of New Zealand. Cambridge University Press.

Wells A, Duncan RP, Stewart GH 2001. Forest dynamics in Westland, New Zealand: the importance of large, infrequent earthquake-induced disturbance. Journal of Ecology 89: 1006–1018.

West CJ 1995. Sustainability of *Beilschmiedia tawa*-dominated forest in New Zealand: population predictions based on transition matrix model analysis. Australian Journal of Botany 43: 51–71.

Williams PA 1993. The sub-alpine and alpine vegetation on the central sedimentary belt of Paleozoic rocks in north-west Nelson, New Zealand. New Zealand Journal of Botany 31: 65–90.

Wilmshurst JM, Eden DN, Froggatt PC 1999. Late Holocene forest disturbance in Gisborne, New Zealand: a comparison of terrestrial and marine pollen records. New Zealand Journal of Botany 37: 523–540.

Wiser SK, Rose AB 1997. Two permanent plot methods for monitoring changes in grasslands: A field manual. Manaaki Whenua Press, Lincoln, New Zealand.

Wiser SK, Bellingham PJ, Burrows LE 2001. Managing biodiversity information: development of New Zealand’s National Vegetation Survey databank. New Zealand Journal of Ecology 25 (2): 1–17.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM 2009. Mixed effects models and extensions in ecology with R. New York, Springer.

Appendix 1 Classification of plant taxa into ordinal palatability categories

Classification of species (or taxa) into ordinal palatability categories. Total number of intercepts that were not classified (Class = ‘NC’) is 765 out of a total of 9748 (8%). Congenerics ONLY used if all species are in the same category (e.g. all species of *Dracophyllum* are always avoided; the same cannot be said of *Olearia*). *Polystichum vestitum* and *Asplenium bulbiferum* were classified as ‘Preferred’ after Mark & Baylis (1975), Wardle (1971), Wardle (1974), and Wardle & Hayward (1970), rather than ‘Not selected’ (after Forsyth et al. 2002).

Species (or taxa)	Class	Source(s)	No. intercepts in FAD dataset
Polystichum vestitum	P	Not selected Forsyth et al. (2002); Preferred Mark & Baylis (1975)	285
Griselinia littoralis	P	Forsyth et al. (2002)	151
Weinmannia racemosa	P	Forsyth et al. (2002)	131
Pseudopanax crassifolius	P	Forsyth et al. (2002)	68
Coprosma tenuifolia	P	Forsyth et al. (2002)	48
Pseudopanax colensoi	P	Forsyth et al. (2002)	22
Asplenium bulbiferum	P	Not selected Forsyth et al. (2002); Preferred Mark & Baylis (1975)	17
Aristotelia serrata	P	Forsyth et al. (2002)	11
Asplenium flaccidum	P	Forsyth et al. (2002)	10
Ripogonum scandens	P	Forsyth et al. (2002)	9
Melicytus ramiflorus	P	Forsyth et al. (2002)	8
Coprosma grandifolia	P	Forsyth et al. (2002)	7
Coprosma lucida	P	Forsyth et al. (2002)	6
Myrsine australis	P	Forsyth et al. (2002)	5
Schefflera digitata	P	Forsyth et al. (2002)	5
Anisotome haastii	P	Rose & Platt (1987)	3
Geniostoma ligustrifolium	P	Forsyth et al. (2002)	2
Raukaua edgerleyi	P	Forsyth et al. (2002)	2
Pseudopanax arboreus	P	Forsyth et al. (2002)	1
Hoheria lyallii	P	Hoheria glabrata is preferred (Stewart et al. 1987)	1
Chionochloa pallens	P	Preferred (Rose & Platt 1987); Avoided (Wardle 1974, but probably ranked too low – Wardle 1991)	1
Podocarpus nivalis	NS	Wardle (1974); Wardle (1991)	455
Blechnum fluviatile	NS	Forsyth et al. (2002)	368
Metrosideros diffusa	NS	Forsyth et al. (2002)	230

Blechnum procerum	NS	Forsyth et al. (2002)	142
Leptopteris superba	NS	Avoided Forsyth et al. (2002); Not selected Wardle (1974)	116
Coprosma foetidissima	NS	Forsyth et al. (2002)	105
Blechnum penna-marina	NS	Forsyth et al. (2002)	97
Coprosma pseudocuneata	NS	Not selected (Stewart et al. 1987); Avoided (Wardle 1974; Wardle & Hayward 1970)	96
Raukaua anomalus	NS	Stewart et al. (1987)	39
Rubus cissoides	NS	Forsyth et al. (2002)	33
Dicksonia squarrosa	NS	Forsyth et al. (2002)	30
Myrsine salicina	NS	Forsyth et al. (2002)	29
Carpodetus serratus	NS	Forsyth et al. (2002)	28
Elaeocarpus hookerianus	NS	Forsyth et al. (2002)	25
Chionochloa species	NS	Not selected (Wardle 1991; rather generic hint that they are often eaten)	22
Pseudopanax linearis	NS	Wardle (1974); Stewart et al. (1987)	21
Coprosma rhamnoides	NS	Forsyth et al. (2002)	19
Muehlenbeckia australis	NS	Forsyth et al. (2002)	18
Cyathea colensoi	NS	Wardle (1974)	17
Coprosma colensoi	NS	Wardle (1974); Stewart et al. (1987)	16
Hebe stricta	NS	Forsyth et al. (2002)	13
Raukaua simplex	NS	Forsyth et al. (2002)	13
Astelia fragrans	NS	Wardle (1984) lists *Astelia* spp. as currently eaten	12
Chionochloa rigida	NS	Not selected (Wardle 1991; rather generic suggestion that they are often eaten)	11
Coprosma propinqua	NS	Forsyth et al. (2002)	7
Metrosideros umbellata	NS	Forsyth et al. (2002)	6
Astelia nervosa	NS	Not selected (Wardle 1971, 1974); Preferred (James & Wallis 1969)	6
Coprosma ciliata	NS	Preferred (Wardle & Hayward 1970); Not selected (Wardle 1974; Stewart et al. 1987)	5
Hebe odora	NS	Stewart et al. (1987)	5
Nothofagus truncata	NS	Wardle (1974)	4
Astelia trinervia	NS	Wardle (1984) lists *Astelia* spp. as currently eaten	4
Clematis paniculata	NS	Forsyth et al. (2002)	3
Hedycarya arborea	NS	Forsyth et al. (2002)	3
Pennantia corymbosa	NS	Forsyth et al. (2002)	3
Astelia solandri	NS	Wardle (1984) lists *Astelia* spp.	3

		as currently eaten	
Tmesipteris spp.	NS	Forsyth et al. (2002)	2
Coprosma cheesemanii	NS	Rose & Platt (1987)	2
Asplenium polyodon	NS	Forsyth et al. (2002)	1
Rubus spp.	NS	Forsyth et al. (2002)	1
Tmesipteris elongata	NS	Forsyth et al. (2002)	1
Nothofagus solandri	NS	Forsyth et al. (2005)	1
Aristotelia fruticosa	NS	Stewart et al. (1987)	1
Olearia lacunosa	NS	Wardle (1974)	1
Elaeocarpus dentatus	NS	Forsyth et al. (2002)	
Nothofagus solandri var. *cliffortioides*	AV	Forsyth et al. (2002)	840
Microlaena avenacea	AV	Wardle (1991, p. 202)	603
Blechnum discolor	AV	Forsyth et al. (2002)	557
Pseudowintera colorata	AV	Forsyth et al. (2002)	520
Uncinia uncinata	AV	'the large-leaved spp. of *Uncinia*' (Wardle 1967)	509
Leptopteris hymenophylloides	AV	Forsyth et al. (2002)	308
Hymenophyllum revolutum	AV	Forsyth et al. (2002)	202
Hymenophyllum multifidum	AV	Forsyth et al. (2002)	194
Neomyrtus pedunculata	AV	Forsyth et al. (2002)	192
Uncinia filiformis	AV	'the large-leaved spp. of *Uncinia*' (Wardle 1967)	157
Hymenophyllum spp.	AV	Forsyth et al. (2002)	152
Coprosma tayloriae	AV	Husheer et al. (2006)	151
Trichomanes reniforme	AV	Forsyth et al. (2002)	138
Nothofagus menziesii	AV	Forsyth et al. (2002)	132
Uncinia spp.	AV	'the large-leaved spp. of *Uncinia*' (Wardle 1967)	109
Hymenophyllum demissum	AV	Forsyth et al. (2002)	81
Dracophyllum recurvum	AV	Stewart et al. (1987) for congenerics	65
Phyllocladus alpinus	AV	Wardle & Hayward (1970); Wardle et al. (1973); Stewart et al. (1987)	62
Dicksonia lanata	AV	Cunningham (1979); James & Wallis (1969); Wardle (1991)	61
Nothofagus fusca	AV	Forsyth et al. (2002)	52
Uncinia rupestris	AV	'the large-leaved spp. of *Uncinia*' (Wardle 1967)	51
Podocarpus hallii	AV	Forsyth et al. (2002)	49
Cyathea smithii	AV	Forsyth et al. (2002)	45
Nestegis cunninghamii	AV	Forsyth et al. (2002)	39
Blechnum chambersii	AV	Forsyth et al. (2002)	38

Grammitis billardierei	AV	Forsyth et al. (2002)	35
Histiopteris incisa	AV	Forsyth et al. (2002)	34
Gaultheria antipoda	AV	Forsyth et al. (2002)	33
Prumnopitys ferruginea	AV	Forsyth et al. (2002)	31
Cortaderia fulvida	AV	*C. toetoe* is according to Rogers & Leathwick (1997).	28
Blechnum colensoi	AV	Forsyth et al. (2002)	27
Lepidothamnus laxifolius	AV	Forsyth et al. (2002)	26
Lepidothamnus laxifolius	AV	*Lepidothamnus intermedius* is avoided (Stewart et al. 1987)	26
Hymenophyllum sanguinolentum	AV	Forsyth et al. (2002)	23
Nestegis lanceolata	AV	Forsyth et al. (2002)	23
Dacrydium cupressinum	AV	Forsyth et al. (2002)	21
Gahnia procera	AV	Wardle (1974)	21
Hymenophyllum dilatatum	AV	Forsyth et al. (2002)	20
Hypolepis distans	AV	Forsyth et al. (2002)	20
Archeria traversii	AV	Wardle & Hayward (1970); Stewart et al. (1987)	20
Dracophyllum traversii	AV	Wardle & Hayward (1970)	18
Phormium cookianum	AV	Wardle (1974)	16
Dracophyllum longifolium	AV	Forsyth et al. (2002)	15
Hypolepis millefolium	AV	Forsyth et al. (2002)	15
Pentachondra pumila	AV	Epacrids are avoided (Wardle 1991)	13
Celmisia spectabilis	AV	Wardle (1971)	13
Nertera dichondrifolia	AV	Wardle (1991, p. 202)	13
Phyllocladus trichomanoides	AV	Forsyth et al. (2002)	11
Prumnopitys taxifolia	AV	Forsyth et al. (2002)	11
Gaultheria depressa	AV	*Gaultheria antipoda* and *G. ruprestris* are avoided (Stewart et al. 1987)	11
Dracophyllum menziesii	AV	Stewart et al. (1987)	11
Cyathodes juniperina	AV	Forsyth et al. (2002)	10
Androstoma empetrifolia	AV	Epacrids are avoided (Wardle 1991)	8
Grammitis spp.	AV	Forsyth et al. (2002)	8
Parsonsia spp.	AV	Forsyth et al. (2002)	6
Cortaderia toetoe	AV	Rogers & Leathwick (1997)	6
Podocarpus totara	AV	Wardle (1971)	6
Lagenifera strangulata	AV	Wardle (1991, p. 202)	6
Rytidosperma gracile	AV	Wardle (1991, p. 202)	6
Cyathea dealbata	AV	Forsyth et al. (2002)	5
Leptospermum scoparium	AV	Forsyth et al. (2002)	5

Gahnia spp.	AV	*G. procera* is avoided (Wardle 1974)	5
Dracophyllum spp.	AV	Congenerics are avoided and Epacrids are avoided (Wardle 1991)	4
Beilschmiedia tawa	AV	Forsyth et al. (2002)	3
Hymenophyllum rufescens	AV	Forsyth et al. (2002)	3
Hymenophyllum villosum	AV	Forsyth et al. (2002)	3
Olearia colensoi	AV	Wardle (1974); Stewart et al. (1987)	3
Nertera depressa	AV	Wardle (1991, p. 202)	3
Uncinia banksii	AV	'the large-leaved spp. of *Uncinia*' (Wardle 1967)	2
Uncinia nervosa	AV	'the large-leaved spp. of *Uncinia*' (Wardle 1967)	2
Asplenium hookerianum	AV	Forsyth et al. (2002)	2
Hymenophyllum bivalve	AV	Forsyth et al. (2002)	2
Hymenophyllum flabellatum	AV	Forsyth et al. (2002)	2
Hymenophyllum scabrum	AV	Forsyth et al. (2002)	2
Nothofagus solandri var. *cliffortioides* × *fusca*	AV	Forsyth et al. (2002) lists the two parent species as avoided	2
Gaultheria species	AV	*Gaultheria antipoda* and *G. ruprestris* are avoided (Stewart et al. 1987)	2
Dracophyllum uniflorum	AV	Wardle (1971, 1974)	2
Rytidosperma spp.	AV	Wardle (1991, p. 202)	2
Phyllocladus toatoa	AV	'most podocarps' Wardle (1991); James & Wallis (1969)	1
Hymenophyllum lyallii	AV	Forsyth et al. (2002)	1
Hymenophyllum rarum	AV	Forsyth et al. (2002)	1
Leptopteris spp.	AV	Forsyth et al. (2002)	1
Melicope simplex	AV	Forsyth et al. (2002)	1
Pteridium esculentum	AV	Forsyth et al. (2002)	1
Rhabdothamnus solandri	AV	Forsyth et al. (2002)	1
Gaultheria crassa	AV	*Gaultheria antipoda* and *G. ruprestris* are avoided (Stewart et al. 1987)	1
Halocarpus bidwillii	AV	*Halocarpus biforme* is Avoided (Wardle & Hayward 1970; Stewart et al. 1987)	1
Ozothamnus leptophyllus	AV	Wardle (1971)	1
Coprosma depressa	NC		132
Blechnum novae-zealandiae	NC		59
Unknown species	NC		42
Coprosma microcarpa	NC		35
Sticherus cunninghamii	NC		31
Olearia nummulariifolia	NC		30

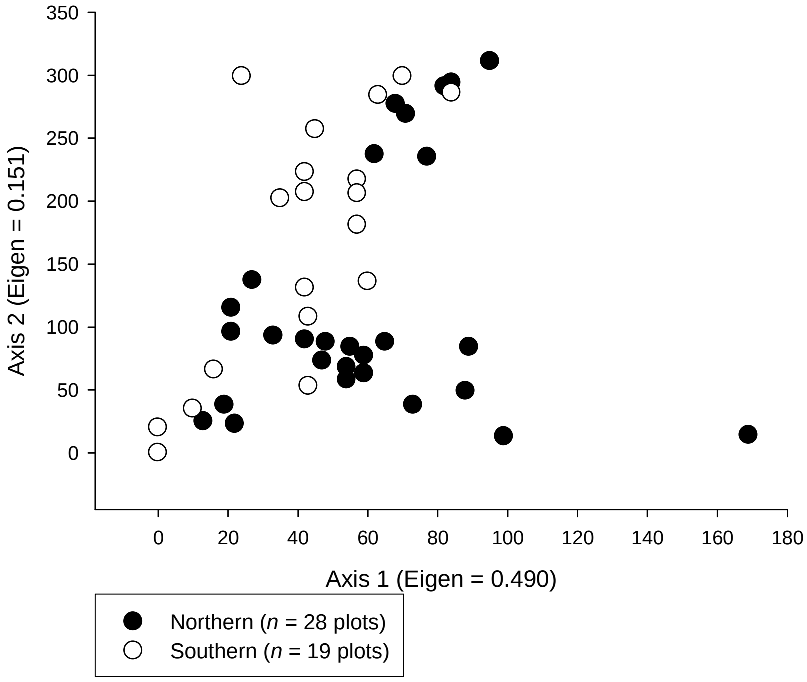
Polystichum silvaticum	NC	25
Poa cita	NC	22
Holcus lanatus	NC	18
Brachyglottis bidwillii	NC	17
Coprosma species ‘p’ *dumosa*	NC	17
Nertera villosa	NC	17
Coprosma pseudociliata	NC	16
Cardamine spp.	NC	14
Blechnum vulcanicum	NC	13
Agrostis capillaris	NC	11
Anthoxanthum odoratum	NC	10
Libertia micrantha	NC	10
Anisotome aromatica	NC	9
Coprosma spp.	NC	9
Crepis capillaris	NC	9
Viola filicaulis	NC	9
Pratia angulata	NC	8
Trifolium repens	NC	8
Luzuriaga parviflora	NC	7
Polygonum salicifolium	NC	7
Blechnum spp.	NC	6
Hebe gracillima	NC	6
Corybas species	NC	5
Hebe tetragona	NC	5
Knightia excelsa	NC	5
Muehlenbeckia species	NC	5
Nertera ciliata	NC	5
Parahebe lyallii	NC	5
Acaena anserinifolia	NC	4
Asplenium spp.	NC	4
Coriaria angustissima	NC	4
Lycopodium spp.	NC	4
Nertera spp.	NC	4
Oxalis lactea	NC	4
Poa breviglumis	NC	4
Pseudowintera axillaris	NC	4
Urtica incisa	NC	4
Carmichaelia spp.	NC	3
Cerastium fontanum	NC	3

Coprosma spathulata	NC	3
Hieracium praealtum	NC	3
Hydrocotyle spp.	NC	3
Lastreopsis glabella	NC	3
Lindsaea trichomanoides	NC	3
Luzula picta	NC	3
Ranunculus reflexus	NC	3
Trichomanes venosum	NC	3
Blechnum filiforme	NC	2
Brachyglottis repanda	NC	2
Cardamine debilis	NC	2
Cyathea spp.	NC	2
Dichelachne crinita	NC	2
Hebe canterburiensis	NC	2
Helichrysum bellidioides	NC	2
Hydrocotyle pterocarpa	NC	2
Lycopodium scariosum	NC	2
Myrsine nummularia	NC	2
Nestegis spp.	NC	2
Oxalis spp.	NC	2
Pyrrosia eleagnifolia	NC	2
Schizeilema haastii	NC	2
Taraxacum officinale	NC	2
Brachyglottis elaeagnifolia	NC	1
Brachyglottis laxifolia	NC	1
Centella uniflora	NC	1
Collospermum hastatum	NC	1
Coprosma perpusilla	NC	1
Cordyline banksii	NC	1
Dicksonia fibrosa	NC	1
Earina autumnalis	NC	1
Forstera sedifolia	NC	1
Forstera tenella	NC	1
Hebe topiaria	NC	1
Hypochoeris radicata	NC	1
Luzula spp.	NC	1
Lycopodium australianum	NC	1
Lycopodium fastigiatum	NC	1
Microseris scapigera	NC	1

Mycelis muralis	NC	1
Ourisia sessilifolia	NC	1
Parahebe spp.	NC	1
Rumex acetosella	NC	1
Stellaria parviflora	NC	1

Appendix 2 Detrended correspondence analysis of tree basal area

Detrended correspondence analysis of the basal area of tree species ≥ 2.5 cm in diameter at 1.35 m height in 40 permanent plots in the north-west Kaimanawa Forest Park surveyed in 1980: northern plots include some plots from the Waiotaka block, and southern plots include some plots from the Whitikau block.



Appendix 3 Summary of Kaimanawa forest plot measurements

Summary of tree basal area, tree, sapling and seedling densities and local environment in north-west Kaimanawa Forest Park based on 40 permanent forest plots measured in 1980: northern plots include some plots from the Waiotaka block, and southern plots include some plots from the Whitikau block.

	Northern Area (*n* = 26)		Southern Area (*n* = 14)	
Basal area (m^2/ha ± SD)				
Nothofagus solandri	4	± 11	5	± 9
Nothofagus fusca	23	± 40	14	± 23
Nothofagus menziesii	2	± 7	8	± 14
Griselinia littoralis	3	± 5	3	± 4
Weinmannia racemosa	26	± 26	11	± 15
Pseudowintera colorata	5	± 5	1	± 1
All species	68	± 42	50	± 18
Tree stems/ha ± SD				
Nothofagus solandri	465	± 4305	185	± 280
Nothofagus fusca	161	± 250	148	± 375
Nothofagus menziesii	24	± 68	267	± 422
Griselinia littoralis	39	± 51	62	± 71
Weinmannia racemosa	410	± 348	269	± 376
Pseudowintera colorata	2566	± 2657	496	± 572
All species	4568	± 2761	2366	± 711
Small seedling (< 15 cm) freq occur (%)				
Griselinia littoralis	66		65	
Neomyrtus pedunculata	8		10	
Uncinia spp.	40		42	
Coprosma ‘tayloriae’	31		46	
Microlaena avenacea	17		7	
Raukaua simplex	21		27	
Myrsine divaricata	26		39	
Nothofagus solandri	13		23	
Nothofagus menziesii	0		31	
Nothofagus fusca	11		17	
Weinmannia racemosa	9		9	
Pseudowintera colorata	46		42	

Seedling density ± SD (15–135 cm tall stems/ ha)				
Griselinia littoralis	70	± 950	80	± 1020
Neomyrtus pedunculata	1810	± 10310	4810	± 20033
Coprosma ‘tayloriae’	2500	± 10530	4540	± 11210
Raukaua simplex	880	± 5010	240	± 2030
Myrsine divaricata	1740	± 6380	1620	± 4910
Nothofagus solandri	1260	± 7260	670	± 3840
Nothofagus menziesii	170	± 2020	1260	± 4750
Nothofagus fusca	790	± 5610	630	± 4050
Weinmannia racemosa	70	± 1510	240	± 2500
Pseudowintera colorata	5830	± 10380	3270	± 9570
Sapling density ± SD (>135 cm tall, <2.5 cm dbh)				
Pseudowintera colorata	1950	± 2520	530	± 860
Site variables				
Altitude	1006	± 151	1046	± 167
Aspect	318	± 97	170	± 111
Slope	25	± 9	25	± 10

Appendix 4 Summary of Hopkins–Huxley forest plot measurements

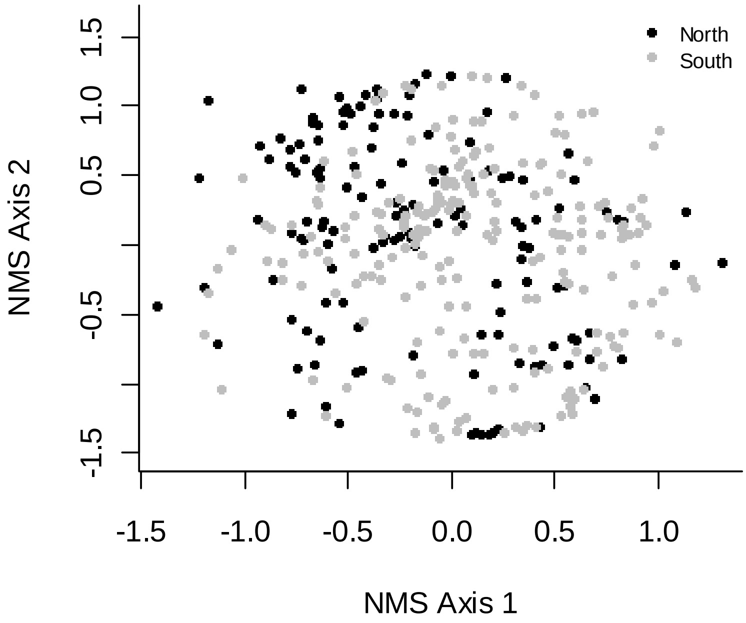
Summary of tree basal area, tree, sapling and seedling densities and local environment in the Hopkins and Huxley river catchments based on 35 permanent forest plots.

	Hopkins (n = 21)		Huxley (n = 14)	
Basal area (m^2/ha ± SD)				
Nothofagus solandri	48	± 26	37	± 28
Nothofagus menziesii	14	± 19	20	± 24
Phyllocladus alpinus			0.4	± 0.9
Podocarpus hallii	0.1	± 0.5	0.4	± 1.2
Dracophyllum longifolium			0.1	± 0.3
Griselinia littoralis			0.1	± 0.4
Hoheria glabrata	0.1	± 0.5		
All species	62	± 20	58	± 17
Tree stems/ha ± SD				
Nothofagus solandri	909	± 687	612	± 577
Nothofagus menziesii	272	± 425	394	± 443
Phyllocladus alpinus			110	± 307
Podocarpus hallii	10	± 39	51	± 102
Dracophyllum longifolium			44	± 104
Griselinia littoralis			10	± 40
Hoheria glabrata	41	± 190		
All species	1244	± 676	1246	± 543
Small seedling (< 15 cm) freq occur (%)				
Nothofagus solandri	77		66	
Nothofagus menziesii	14		22	
Podocarpus nivalis			13	
Hoheria glabrata	3		1	
Griselinia littoralis	1		7	
Phyllocladus alpinus	0.4		5	
Coprosma tayloriae			2	
Podocarpus hallii			1	
Raukaua simplex	0.4			
Seedling density ± SD (15–135 cm tall stems/ha)				
Nothofagus solandri	18680	± 45060	29160	± 68970
Nothofagus menziesii	2100	± 13730	1100	± 5100
Podocarpus nivalis			4500	± 24640

Phyllocladus alpinus	210	± 2760	510	± 4250
Hoheria glabrata	390	± 3570		
Dracophyllum longifolium			280	± 3750
Raukaua simplex	240	± 3490		
Griselinia littoralis	110	± 1180		
Podocarpus hallii	50	± 1180	240	± 3690
Coprosma tayloriae			80	± 1450
Aristotelia fruticosa			40	± 720
Sapling density ± SD (>135 cm tall <2.5 cm dbh)				
Nothofagus solandri	1000	± 3390	1170	± 68970
Nothofagus menziesii	40	± 190	20	± 110
Hoheria glabrata	120	± 780		
Raukaua simplex	10	± 90		
Site variables				
Altitude	1005	± 148	911	± 150
Slope	25	± 13	28	± 12

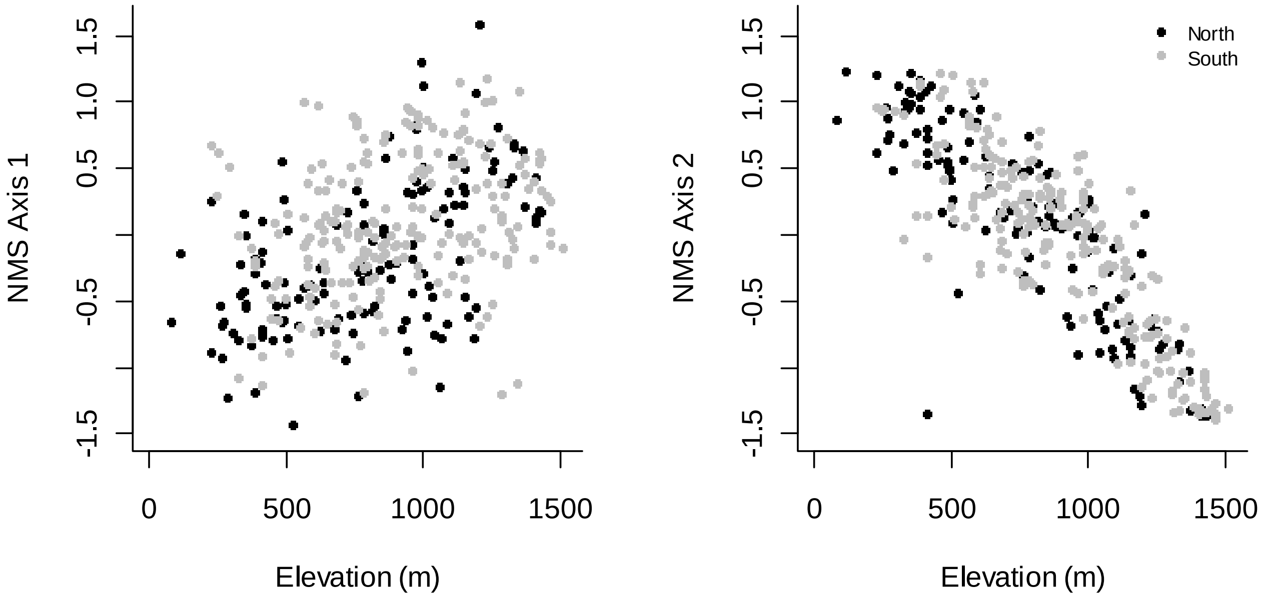
Appendix 5 NMDS ordination of vegetation composition data, Kahurangi National Park

NMDS ordination of vegetation composition data (collected using Recce relevé plots) from two areas either side of the Anatoki River, Kahurangi National Park. NMDS performed in PC-Ord. Final stress = 22.8 for two-dimensional solution; final instability = 0.03035 after 200 iterations



Appendix 6 Elevation vs NMDS axes 1 and 2 for Kahurangi National Park

Relationships between elevation and the NMDS axes 1 and 2 scores for each vegetation plot. Data are presented for two areas either side of the Anatoki River, Kahurangi National Park.



Appendix 7 Pembroke Wilderness Area site that was considered but not selected

We were asked to assess whether two comparable blocks of forest could be selected from the Pembroke Wilderness Area in northern Fiordland. The area is confined by the Tasman coast to the west, the Tutuko massif to the east, Milford Sound to the south, and the Hollyford River to the north. The terrain is extremely steep through much of the area but a strong appeal of the area is that it is purported to have high deer densities because difficult access limits hunting pressure (D.M. Forsyth, pers. comm.).

We summarised Recce relevé data collected by Cuddihy (1978) from the study region (Table S1; Fig. S1). We divided the area thus: North block is tentatively from Sydney Beach to Mount Sutherland north to the May Hills and includes the Kaipo River west of the Alpine Fault. South block is tentatively from south of the ridge from Sydney Beach to Mount Sutherland to south of the John O'Groats River including land west of the Alpine Fault. These data revealed that forests in the north were dominated by silver beech while those in the south were more diverse and variously dominated by kāmahi, southern rātā (*Metrosideros umbellata*), silver beech and mountain beech. An NMDS ordination was used to organise the plots according to composition (Fig. S1) and this clearly revealed that there was limited overlap in composition between the two blocks. Forest types were never mapped in this area of New Zealand. Geology was similar in the north and the south (greywacke with alluvial deposits along river courses). We concluded that compositional differences between the two blocks were too great to justify establishment of two comparable blocks.

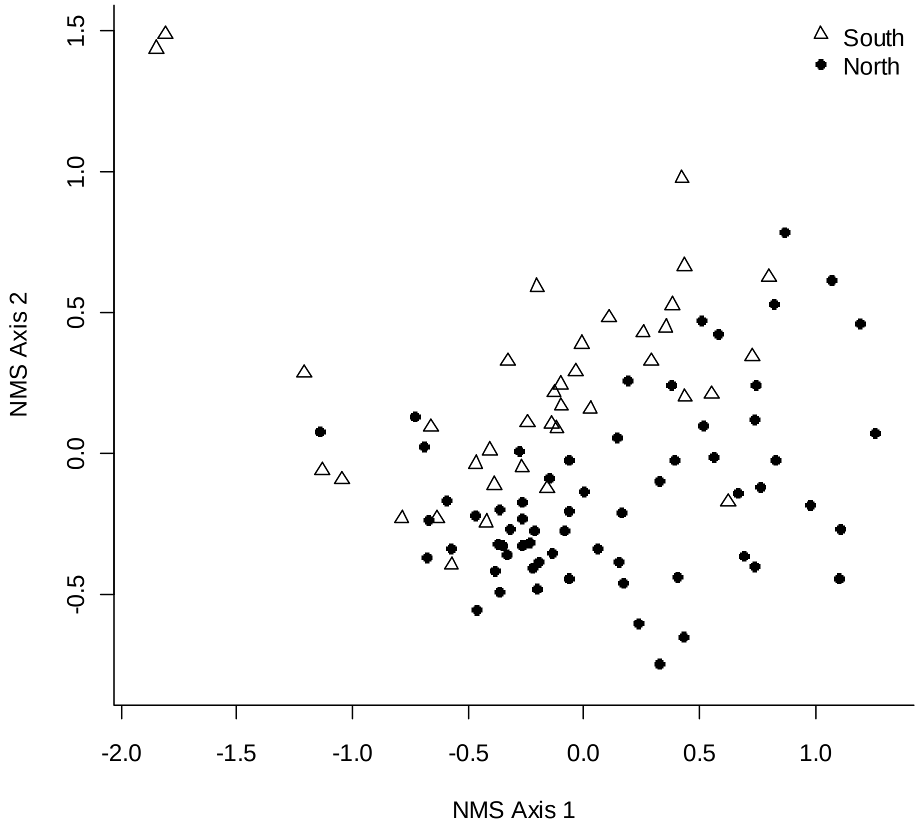


Fig. S1 NMDS ordination of vegetation composition data from the Pembroke Wilderness Area divided into two tentative blocks that had been suggested as two blocks for use in FAD.

Table S1 Frequency of species recorded as dominant cover in fixed tier heights in two blocks within the Pembroke Wilderness Area. Data from plots on randomly located lines throughout the area in 1977. Data in table are frequency of plots in which species were recorded as dominant (and present). Dominance was scored directly in the field and was not ascribed from cover class scores.

		North Block	South Block
		n = 64 plots	n = 38 plots
Tier	Species	% of plots	% of plots
>20 m	*Dacrydium cupressinum*	22 (23)	11 (11)
12–20 m	*Nothofagus menziesii*	52 (59)	16 (32)
	Weinmannia racemosa	9 (14)	26 (45)
	Metrosideros umbellata	9 (36)	16 (68)
	Dacrydium cupressinum	6 (25)	11 (32)
	Nothofagus solandri var. *cliffortioides*	3 (6)	13 (16)
5–12 m	*Weinmannia racemosa*	63 (80)	61 (89)
	Fuchsia excorticata	19 (34)	3 (16)
	Nothofagus menziesii	13 (52)	5 (26)
	Melicytus ramiflorus	6 (20)	11 (32)
	Hedycarya arborea	3 (16)	11 (29)
2–5 m	*Weinmannia racemosa*	34 (75)	16 (79)
	Cyathea smithii	27 (83)	13 (53)
	Pseudowintera colorata	17 (41)	0 (5)
	Coprosma foetidissima	11 (48)	18 (53)
	Dicksonia squarrosa	9 (56)	29 (61)
	Freycinetia baueriana subsp. banksii	2 (9)	13 (45)
0.3–2 m	*Blechnum discolor*	47 (72)	29 (68)
	Cyathea smithii	28 (77)	24 (58)
	Pseudowintera colorata	17 (53)	0 (13)
	Dicksonia squarrosa	3 (47)	11 (63)
0–0.3 m	*Metrosideros diffusa*	22 (61)	16 (61)
	Blechnum novae-zelandiae	16 (53)	29 (68)
	Metrosideros perforata	14 (23)	0 (5)
	Nertera depressa	2 (13)	11 (37)
	Metrosideros fulgens	0 (11)	11 (61)