Ungulate effects on tawa *(Beilschmiedia tawa)* forest in Urewera National Park

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Published by
Department of Conservation
Head Office, PO Box 10-420
Wellington, New Zealand

This report was commissioned by East Coast Conservancy

ISSN 1171-9834

Reference to material in this report should be cited thus:

Bockett, F.K. 1998.
Ungulate effects on tawa *(Beilschmiedia tawa)* forest in Urewera National Park. *Conservation Advisory Science Notes No. 196.* Department of Conservation, Wellington.

Keywords: *Beilschmiedia tawa,* taws forest, deer browsing, `mainland island', Urewera National Park

Abstract

In early - mid 1997 five exclosures located in or adjoining the northern part of Te Urewera National Park were remeasured in order to assess changes in species composition and structure due to the influence of feral pigs and deer. These plots were last assessed in 1980/81, and it was hoped that any difference in vegetation outside would give an indication of change in browsing pressure since this time.

The main aim of the study, however, was to obtain data to compare with a mainland island area located in the northern reaches of the park.

Results were obtained only from exclosures sited within tawa *(Beilschmiedia tawa)* forest in order to be comparable with the `mainland island' area in which this was the dominant canopy species.

The main results for exclosure/adjacent control comparisons were similar to those obtained in 1980/81. In summary, density and diversity of sapling and tree (2-10 cm dbh) species was found to be significantly greater within exclosures compared with unprotected areas. Plots located within the mainland island area were not significantly different from browsed control areas at exclosure locations. This indicates that browsing ungulates are exerting similar pressure on forest dynamics of this area.

At most control and mainland island sites very few species were found in the sapling and small tree tiers whereas within exclosures subcanopy species such as kanono *(Coprosma grandifolia)*, hangehange *(Geniostoma ruprestre* var. *ligustrifolium)*, mahoe *(Melicytus ramiflorus)* and pate *(Schefflera digitata)* formed a dense understorey.

These results would suggest that ungulates are still influencing the structure and composition of taws forest within Urewera National Park. This continued removal of palatable subcanopy and sapling tiers by ungulates (in particular deer) has important implications for the ecological restoration of the 'mainland island' area.

1. Introduction

In studies concerning herbivore effects on vegetation, an important objective is the assessment of long term changes in forest structure, composition and regeneration potential. However, because of the immediate need to provide management decisions, predictions of future conditions of the forest must sometimes be made on the basis of existing patterns (Veblen & Stewart 1982).

One way of directly assessing the influence of browsing animals on plant communities over time is by the use of exclosure studies.

These allow a direct comparison between browsed and unbrowsed areas and therefore indicate the species assemblages which may develop in the absence of browsing pressure.

During the period 1961-1968 the New Zealand Forest Service erected several exclosure plots in order to determine the influence of ungulate browsing on the forests of the Urewera ranges (Knowlton et al. 1982).

Red deer *(Cervus elaphus)* and pigs *(Sus scrofa)* were well established throughout the area, along with sambar *(C. unicolor)* and rusa *(C. timorensis)* in less widespread distributions (Knowlton 1981), and browsing was implicated in observed depletion of plant cover and accelerated erosion.

It was not until some years later (1980/81) that these exclosure plots were first quantitatively assessed, and it was found that, despite recent reductions in ungulate number throughout the area, density and diversity of small diameter trees were still being affected (Knowlton et al. 1982).

In early 1997 it was decided to obtain remeasurements of exclosure plots located in the northern reaches of Urewera National Park.

This was in order to re-assess the condition of browsed control plots and investigate understorey composition within exclosures after approximately thirty years' protection from ungulate browsing. Data obtained were also to be compared with various plots located within a mainland island at Otamatuna to assess impacts of ungulate browsing on the vegetation of this area.

The `mainland island' area is a tract of forest in the northern Urewera which has undergone extensive introduced pest control since it was first identified as an important kokako habitat in 1991. Possum control began in 1993 and present possum numbers are very low within the area. Mustelid control was initiated more recently in 1996/97.

This study was initiated to complement the existing ecological restoration programmes already in place at Otamatuna, by assessing the impact of deer on the vegetation.

The predominant canopy species of the mainland island area is tawa *(Beilschmiedia tawa)*, and in order to make a valid comparison, exclosure plots also had to be located in forest of this type, *Beilschmiedia tawa* dominant broadleaf canopy with scattered emergent podocarps.

Only one exclosure in the northern Urewera, however, was sited in the forest type required for study, so additional plots in taws were located further south and used for remeasurement.

A full description of exclosure locations, topography, soils and climate is given in Allen et al. (1984). The plots used for remeasurement varied in size from 7.5x7.5 m to 9x9 m and ranged in altitude from 260 m to 530 m, covering an array of different aspects (Appendix 8.1). Plates 1 and 2 (Appendix 8.6) show exclosures at Horomanga and Central Waikare sites.

Exclosures were concentrated on river flats or terraces and therefore were not representative of the Urewera area as a whole, the Urewera ranges being described as steep sloped (30° to 50°) mountain ranges (Wallis & James 1972, Allen et al. 1984), which cover an altitudinal range from 80 m to 1392 m above sea level.

2. Methods

2.1 FIELD MEASUREMENTS

Exclosures and adjacent controls

Vegetation

The field methodology for measurement of exclosure and adjacent control plots follows that used by Allen et al. (1982).

In summary, at each exclosure location two similarly sized control plots were located systematically at a distance of 5 m from the exclosure fence according to similarity of canopy cover and topographic features. Within the exclosures, plot size was determined by the maximum number of 1.5 m^2 subplots that could be fitted in a square or rectangular grid-like fashion. Within each plot - trees > 2 cm dbh (diameter) were recorded by species and dbh and saplings >1.4 m in height, <2 cm dbh were recorded by species. Seedlings were recorded by species for different height classes within 1 m^2 circular seedling plots which were located at the intersections of the 1.5 x 1.5 m grid system.

Non-woody species were also surveyed by recording percentage occurrence within the 1 m^2 seedling plots.

Animal density

At each exclosure location an assessment of browsing animal density was achieved by an adaptation of the faecal presence/absence technique (Baddeley 1985, Beadel 1988).

This technique was designed to cover an area of 1 km^2 using four 500 m transect lines run out along opposing compass bearings off exclosure boundaries.

Every 20 m along each line a circular plot of 1.14 m radius was located within which presence/absence of deer and possum pellets was recorded and pig sign measured by presence of faeces or evidence of rooting behaviour.

This method was recommended by Graham Nugent (pers. comm. 1997), the area covered being an estimate of the home range of a deer.

Mainland island plots

To enable a direct comparison between exclosure plots and the mainland island area, five 9x9 m plots were located along river flats or terraces using a stratified random sampling technique. With this method, suitable areas (i.e. river flats/terraces) were subjectively chosen and plots located using random number tables along 100 m lines.

Another series of five 9x9 m plots were established in the core of the study area along bait station lines which occurred at 485 m and 560 m. In this case, however, random numbers were used for every 100 m along 1000 m lines in order to correspond to an existing bait station.

Plots within this area typically occurred on steep slopes and were more representative of the area as a whole.

Methodology used for measurement was the same as that used for the exclosure and adjacent control plots.

Animal densities for this area were not recorded, but have recently been surveyed by Dave Wilson (1997) for another study.

2.2 STATISTICAL ANALYSIS

To correct for variations in exclosure and control plot sizes, data from sapling and tree (2-10 cm dbh) tiers were converted to densities/100 m^2 and data from 1 m^2 seedling subplots were converted to densities/ m^2.

Because plot size tended to be less than the minimum area of the vegetation for large trees (minimum area - the smallest area on which the species composition of a plant community is adequately represented), trees greater than 10 cm in diameter were not included in the analysis. This was also to give a snapshot of fairly recent browsing influence on the various areas.

Statistical analyses for comparisons between exclosure and adjacent control plots on parameters such as average density or diversity were carried out using Wilcoxin Signed Rank test. This is the non-parametric equivalent of a two-sample paired data t-test. For comparisons involving unpaired data (exclosure/mainland island terrace plots, etc.) a Mann-Whitney U-Test was used.

These non-parametric tests were used because they do not require an assumption of the normal distribution or the equality of variances.

In addition to this, a multivariate analysis of variance (MANOVA) was carried out on sapling and tree data. This test gives the combined response of every variable (species) to a treatment (browsing/non browsing) and therefore does not require that species data for density be pooled across all sites.

MANOVA programmes produce four test statistics; Pillai's trace was used for greatest robustness and power.

Because of the limited number of plots that were measured, univariate comparisons of individual species were not possible.

3. Results

3.1 TREES (2-10 CM DBH) AND SAPLINGS

Figures 1-5 show densities of tree and sapling species across the five exclosure and adjacent control sites surveyed. Species abbreviations are given in full in Appendix 8.2.

The general trend within exclosures shows kanono *(Coprosma grandifolia)* forming the dominant subcanopy tree in the 2-10 cm diameter range. Other species such as hangehange *(Geniostoma rupestre* var *ligustrifolium),* pate *(Schefflera digitata)* and putaputaweta *(Carpodetus serratus)* are also commonly present.

Within control plots for the first four sites (Figs 1-4) the only species to occur in the tree classes are pigeonwood *(Hedycarya arborea)* and tawa *(Beilschmiedia tawa).* At the fifth site (Waihua) large numbers of small-leaved tree and shrub species occur outside the exclosures (putaputaweta, *Pseudopanax anomalus, Coprosma rotundifolia* and *Pennantia corymbosa).*

At this site, however, larger-leaved palatable trees, such as mahoe *(Melicytus ramiflortis),* five finger *(Pseudopanax arboreus),* tarata *(Pittosporum eugenioides),* kanono, karamu *(Coprosma robusta)* and *Coprosma lucida,* occur only within the exclosure.

Sapling results show similar trends. Within exclosures a large variety of palatable species are present. Outside in adjacent browsed controls, only tawa, pigeonwood and rewarewa are present in the first four plots. At the last site (Waihua) more species are present in the sapling tier compared with other sites. These are predominantly small-leaved species similar to those in the tree tier and unpalatable species such as *Pseudowintera* sp.

For sapling and tree tiers, between-site variation occurs in both the species present and density at which they occur, but in general, exclosures show large and consistent differences in diversity and density when compared with their respective controls.

Animal densities as assessed by pellet frequencies are shown in conjunction with graphs for each exclosure site. Waihua and Horomanga sites have the highest results for deer, at 18% and 19% respectively, with other sites ranging from 3% to 8%. Pig density ranges between 1% and 6% and possum density between 5% and 24%.

Figures 6 and 7 give species density in tree and sapling tiers averaged across all sites for exclosure and control plots.

Kanono dominates the results for both the sapling and tree tiers within the exclosures while control plots are influenced largely by the high abundances of small-leaved species encountered at Waihua. The main canopy species (tawa) does not appear to be regenerating within the exclosures to any great extent and is more prevalent in the control plots in both the tree and sapling tiers.

Figure 8 gives density of tree and sapling species for plots located within the mainland island area. Both density and diversity of woody species at these sites are less than those seen within the exclosure plots. For plots located on river terraces, saplings of mahoe, tawa, pigeonwood and *Coprosma rotundifolia* occur in low densities. Tree species at these sites consist of taws, kahikatea *(Dacrycarpus dacrydioides),* rewarewa *(Knightia excelsa)* and pukatea *(Laurelia novo-zelandiae).* Within ridge face plots located on steeper slopes, a greater diversity of species in the tree tier occur. These include some palatable species such as hangehange, mahoe, kamahi *(Weinmannia racemosa)* and mapou *(Myrsine australis).* Fewer species of saplings than trees were found in these higher plots.

The main species in both the sapling and tree tiers within all mainland island plots is the canopy species, tawa.

Tables 1-4 present the results of statistical analyses on both density and diversity measurements across all the different plot types.

Significant differences were found between exclosure and adjacent control plots, and exclosures and mainland island terrace plots in the sapling and tree tier for both density and diversity.

Differences between exclosure and control plots in the sapling tier were less obvious than other differences ($P<0.1$) due to the influence of the Waihua site, where large numbers of small-leaved saplings occurred.

Mainland island terrace plots were not significantly different from the control areas adjacent to exclosures in either sapling or tree tiers. Likewise, plots located on ridge faces at higher altitudes (steep plots) within the mainland island area were not significantly different from lower plots (terrace plots) for density in the sapling and tree tiers.

There was, however, a statistical difference detected in the diversity of tree 2-10 cm species between ridge face and river plots within the mainland island area.

Multivariate analysis (MANOVA) results for sapling and tree density are presented in Tables 5 and 6. These results support the findings of the univariate density tests. Exclosures are once again significantly different from associated controls and from mainland island terrace plots in both tree (2-10 cm) and sapling densities. Control plots are not significantly different from mainland island terrace plots and these in turn are not significantly different from steep face plots.

3.2 SEEDLINGS 0-15 CM AND 15-140 CM

Figures 9 and 10 show average seedling density in two size classes (0-15 and 15-140 cm) for both exclosure and control plots. Differences between exclosure and control plots are less obvious than in sapling or tree tiers. Tawa is the most abundant species in both seedling tiers within the exclosure plots, followed by kahikatea, pigeonwood, *Alseuosmia macrophylla* and kanono. Tawa and kahikatea are also predominant in the control plots, with a variety of other species occurring at lower densities.

Tawa, pigeonwood, *Alseuosmia macrophylla* and kanono appear to occur at greater densities in both size classes within the exclosures compared with controls.

Tables 7 and 8 give results from statistical analyses of density in seedling tiers. Exclosures and adjacent controls are not significantly different for density in 0-15 cm and 16-140 cm seedling tiers.

Statistical comparisons involving these sites show significant differences between exclosures and mainland island terrace plots and adjacent controls and mainland island terrace plots for density of seedlings in the 15-140 cm tier.

Figures 11 and 12 give seedling density for mainland island river terrace and steep slope plots.

In river terrace plots, tawa, rewarewa and pigeonwood are the most common species. Very few species occur in the higher seedling tiers. In the steeper slope plots at higher altitudes a greater diversity of species occur in both size tiers, with hangehange dominating in the 0-15 cm tier and *Olearia rant* in the 16-140 cm tier.

Diversity was not analysed for seedling tiers.

Many palatable understorey species (e.g. *Coprosma* species, hangehange, mahoe, mapou and pate) absent in the sapling and small tree tiers in browsed plots are present in these plots in smaller seedling tiers.

3.3 NON-WOODY SPECIES

Figures 13, 14 and 15 show proportions of non-woody species found within exclosure, control and mainland island seedling subplots. No species appears to occur more predominantly inside exclosures compared with outside, but in browsed control plots some ferns, the dicot herb *Hydrocotyle elongata,* the sedge *Uncinia uncinata,* and the grass *Microlaena avenacea,* appear to be more abundant. Mainland island steep plots appear to be more diverse than river terrace plots in terms of non-woody vegetation species. No statistical analyses were carried out on non-woody vegetation classes.

Figure 16 shows density of tree ferns (above 1.4 m in height) by species for exclosure, control and mainland island plots. Differences in species distribution between the different plots does not appear to be due to browsing. Species composition is fairly similar between sites and no species appears significantly more abundant within exclosures compared with browsed plots. High densities of *Dicksonia squarrosa* occur within mainland island terrace plots.

4. Discussion

Decimation of the forest understorey by introduced animals has been a prevailing theme of ecological writing in New Zealand (Veblen & Stewart 1982), the depletive effects of deer colonisation having been described in a number of papers (e.g. Allen et al. 1984). Even at reduced densities, deer and other animals affect a wide range of palatable species, so their long-term effect on biodiversity is severe (Veblen & Stewart 1982). This has particularly been found to apply to numerous subcanopy hardwood tree species, which in many cases are so highly preferred that nearly total ungulate removal is required before any widespread recovery can occur (Nugent & Fraser 1993).

Results from this study tend to conform to trends described for other exclusion studies and in general do not appear significantly different from those found by Knowlton et al in their 1982 study. This would indicate that recent browsing pressure is similar to that around or before 1982 at the sites surveyed.

Results for exclosures, controls and mainland island plots are discussed in more detail in following sections.

4.1. EXCLOSURES/CONTROLS

Vegetation

After approximately thirty years exclusion of browsing animals within exclosures, a fully developed subcanopy of palatable species including shrubs and subcanopy trees of *Coprosma* sp., *Pseudopanax* sp., tarata, mahoe, mapou and pate has developed.

Outside of exclosures, however, subcanopy species are considerably less frequent, a significant difference in both density and diversity for woody saplings and small trees being found.

Species which occur in the sapling and small tree tier outside of exclosures consist of moderate or least preferred woody plant species according to preference groupings of woody plant species for deer (see Appendix 8.4). The only exception being pigeonwood and putaputaweta, both classed as highly preferred food species for deer, which occur in lower densities outside the exclosures compared with inside.

A list of pig preferred plant species is also given in Appendix 8.5.

A study by Thompson and Challies (1988) on pig diet in the Urewera ranges has shown that fruit and carrion are the most important food for pigs, with browsing and grazing providing a relatively small component of the diet.

This would indicate that pigs are not contributing greatly to the understorey decimation seen at these exclosure locations compared with the effect of deer, although rooting and browsing may have some influence on seedling survival.

Cyathea spp. formed the only major component of leaf material taken by pigs in Thompson and Challies (1988) paper and there was no apparent difference between exclosures and controls in numbers of this species. In fact, tree ferns were the most predominant species found outside exclosures above the height of the seedling tiers.

The canopy species tawa, classed by many authors as a broad-leaved species of low palatability to deer (Knowles & Beveridge 1982, Allen et al. 1984), occurs as both a sapling and small tree outside exclosures.

This would tend to indicate that browsing at the sites surveyed is not impeding the regeneration of the canopy species to the same extent as in other larger-leaved palatable subcanopy species.

Tawa is described as a `K' selected shade-tolerant type species which during the juvenile phase is capable of rapid response to changes in light conditions (West 1986).

Absence of tawa within the exclosures in the sapling tier and low numbers (cf. control) in the tree tiers may be due to competition from more rapidly growing `R' type species which have flourished in the absence of browsing.

In the seedling tiers no notable differences were detected between exclosure and control plots for overall density of seedlings in both 0-15 and 16-140 cm classes.

Small differences between species such as tawa, pigeonwood, *Alseuosmia macrophylla* and kanono, which occur at greater densities in both size classes within the exclosures compared with controls, could be a result of browsing, although other palatable species such as mahoe and hangehange occur at similar densities inside and out of exclosures.

Seedling results indicate that potential for regeneration of the subcanopy is viable in adjacent control plots given that browsing pressure was removed, the suite of subcanopy species present in higher sapling and tree tiers within exclosures also occurring outside, though only in lower seedling tiers.

Outside exclosures it does not appear that species composition is changing in any way towards favouring unpalatable species except for possibly the Waihua site, where the unpalatable shrub *Pseudowintera axillaris* was found in low numbers outside the exclosure along with various small-leaved tree species. Small leaves may possibly confer some resistance to browse because of the greater effort required per unit intake of nutrients.

These findings are similar to those described by Allen et al. (1984).

Non-woody vegetation results are also similar to those described in Allen et al. The turf-forming species *Uncinia uncinata* and *Microlaena avenacea* are still more frequent outside exclosures compared with inside. Grazing can stimulate species such as grasses to grow vigorously (Crawley 1986) and perhaps explains why the two species of grass are more successful within external controls.

Animal densities

Figures for animal density could not be correlated with vegetation results found at each site. The method used, however, only gave an instantaneous measure for animal density at the time of measurement and therefore could not be directly related to differences between exclosure and control plots, these having taken many years to establish. Also, measurements were carried out over a three-month period from March to June 1997, whereas ideally they should have been taken over a much shorter period earlier in the year to combat the influence of increased litter fall and seasonal deer movements on the results. Logistical factors prevented this from being possible.

Despite this, results show that pigs, possums and deer were present around the sites surveyed at the time of measurement.

4.2 MAINLAND ISLAND PLOTS

Results for mainland island plots were essentially similar to those found at controls adjacent to exclosure locations. Species composition differed slightly and cumulative results for diversity appeared much less than cumulative exclosure and control diversity results, probably because plots were located within a smaller area.

Statistical analysis involving a direct comparison between exclosures/controls and mainland island plots could only be carried out on the plots located at lower altitudes on flatter terrain, but these could then be compared to plots located at higher altitudes on steeper slopes and a secondary relationship back to exclosures inferred.

A significant difference in both density and diversity of woody saplings and small trees between exclosures and river terrace plots and no significant difference between controls and river terrace plots indicates that browsing animals are exerting similar pressure on forest of mainland island flat terrace/bench areas to that of other areas surveyed.

Differences between terrace plots and steeper ridge face plots were essentially non-significant, a true difference only being found in the diversity of trees (2-10 cm), which is greater in the steeper plots.

In a Fiordland survey on deer browsing it was found that terraces and toe slopes were most utilised by deer, followed by ridges/spurs/side slopes and finally blockfields and moraines (Nugent et al. 1987, Stewart et al. 1987). Differential choice of location by browsers may have influenced the difference in the results found.

Within the mainland island, palatable species such as mahoe, hangehange and mapou were still being found in tree and sapling tiers (although in very low densities) compared with a complete absence of these species at the controls outside of exclosure locations. Large-leaved *Coprosma* species, as in control plots, were notably absent.

The situation with the canopy species tawa, however, was similar to that seen at control plots. The presence of tawa as the predominant sapling and small tree in both types of mainland island plots implies that regeneration is less affected by browsing animals than with larger-leaved subcanopy species.

Seedling densities for mainland island plots show that the palatable subcanopy-forming species absent from sapling and small tree tiers are present as small seedlings (although in low numbers) within both types of plot.

It could be envisaged that removal of browsing pressure would lead to a situation similar to that seen within the exclosures, with a dense understorey of species such as kanono, mahoe, mapou, pate, hangehange and pigeonwood developing.

This has important implications for the kokako population which resides within the Otamatuna mainland island area in that many of these species have been identified as important kokako foods. Leathwick et al. (1983) conclude from a Pureora survey that "red deer have a considerable dietary overlap with kokako" particularly in species such as lancewood *(Pseudopanax crassifolium),* five finger *(P. arboreum),* raukawa *(P. edgerleyi),* mahoe, pigeonwood, kanono and putaputaweta.

5. Conclusion and recommendations

The main findings of this study show that browsing animals, particularly deer, are still strongly influencing the structure and composition of taws forest by inhibiting the development of subcanopy trees and shrubs.

The mainland island area at Otamatuna is no exception, and deer control within this area would complement the already existing programmes on single species conservation. The release of species important in kokako diet is an example of one benefit to be gained.

Exclosures within the mainland island area would allow the effect of browsing ungulates on regeneration to be investigated more directly and could provide a method of monitoring the effectiveness of any animal control programme in conjunction with pellet analyses.

It is recommended that any subsequent exclosures or permanent plots placed within the Urewera for long-term monitoring of forest dynamics be of the 20 m x 20 m variety. This size more adequately samples tall forest type vegetation and reduces the influence of edge effects. Also this type of plot has been used in other parts of the Urewera since the early 1980s, e.g. Waikare permanent plots/exclostires and exclosures at Te Pua.

It is also recommended that new plots be established at sites which are representative of the area as a whole, if this is logistically possible. This would allow greater generalisation of results.

Plots in this study were concentrated on flat benches and were generally adjacent to a river or stream. This limits the ability to generalise because it was not the typical topography encountered in Urewera National Park. New plots if possible should cover a range of slopes and not be concentrated on the flat, which has been identified as a favoured topography for deer browse.

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7. Figures and tables

TABLE 1: Average density ± standard error in tree (2-10cm) tier for all plots including statistical comparisons.

Plot	Average density (stems/100m2)	Statistical comparison	P <
Exclosures (Ex)	34.7 ± 6.6	Ex/Co	0.05
Controls	10.0 ± 7.9	Ex vs T	0.01
Mainland island terrace plots (T)	11.9 ± 4.5	Co vs T	N.S
Mainland island steep plots (S)	3.21 ± 2.1	T vs S	N.S

TABLE 2 :Average diversity ± standard error in tree (2-10cm) tier for all plots including statistical comparisons.

Plot	Av. diversity (#sp/100m2)	Statistical comparison	P <
Exclosures (Ex)	9.16 ± 2.1	Ex/Co	0.01
Controls	2.91 ± 1.6	Ex vs T	0.01
Mainland island terrace plots (T)	3.95 ± 1.06	Co vs T	N.S
Mainland island steep plots (S)	1.23 ± 0.55	T vs S	0.05

TABLE 3: Average density ± standard error in sapling tier for all plots including statistical comparisons.

Plot	Av. density (Stems/100m2)	Statistical comparison	P <
Exclosures (Ex)	56.0 ± 18.1	Ex/Co	0.1
Controls	21.4 ± 18.7	Ex vs T	0.01
Mainland island terrace plots (T)	3.76 ± 1.3	Co vs T	N.S
Mainland island steep plots (S)	2.22 ± 1.1	T vs S	N.S

TABLE 4: Average diversity ± standard error in sapling tier for all plots including statistical comparisons.

Plot	Av. diversity (#sp/100m2)	Statistical comparison	P <
Exclosures (Ex)	11.8 ± 2.7	Ex/Co	0.01
Controls	2.8 ± 1.7	Ex vs T	0.01
Mainland island terrace plots (T)	1.2 ± 0.40	Co vs T	N.S
Mainland island steep plots (S)	2.0 ± 0.63	T vs S	N.S

TABLE 5: Multivariate Analysis of Variance results for sapling density. Variable = species, test statistic = Pillai's trace.

Site comparison	P <
Exclosure/Control	0.0001
Exclosure/ Mainland island terrace plots	0.0001
Control/ Mainland island terrace plots	N.S
Mainland island terrace plots/ steep plots	N.S

TABLE 6: Multivariate Analysis of Variance results for tree (2-10cm) density. Variable = species, test statistic = Pillai's trace.

Site comparison	P <
Exclosure/Control	0.0001
Exclosure/ Mainland island terrace plots	0.0001
Control/ Mainland island terrace plots	N.S
Mainland island terrace plots/ steep plots	N.S

TABLE 7: Average density ± standard error in (0-15cm) seedling tier for all plots including statistical comparisons.

Plot	Av. density (Seedlings/m2)	Statistical comparison	P <
Exclosures (Ex)	8.45 ± 5.65	Ex/Co	N.S
Controls	3.75 ± 1.63	Ex vs T	N.S
Mainland island terrace plots (T)	1.25 ± 0.15	Co vs T	0.1
Mainland island steep plots (S)	2.38 ± 0.47	T vs S	0.1

TABLE 8: Average density ± standard error in seedling (15-140cm) tier for all plots including statistical comparisons.

Plot	Av. density (seedlings/m2)	Statistical comparison	P <
Exclosures (Ex)	4.48 ±1.8	Ex/Co	N.S
Controls	2.77 ±1.7	Ex vs T	0.05
Mainland island terrace plots (T)	0.32 ± 0.09	Co vs T	0.05
Mainland island steep plots (S)	0.464 ± 0.264	T vs S	N.S

Figure 1: Density of saplings and trees (2-10 cm dbh) by species for Tataweka site

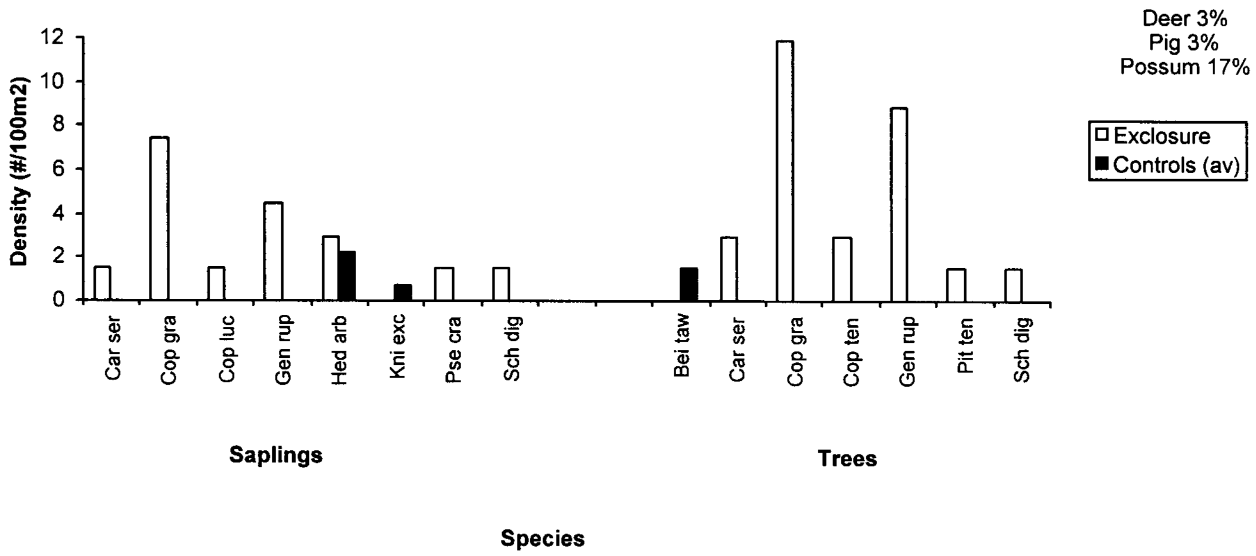


Figure 2: Density of saplings and trees (2-10 cm dbh) by species for Ngahiramai site

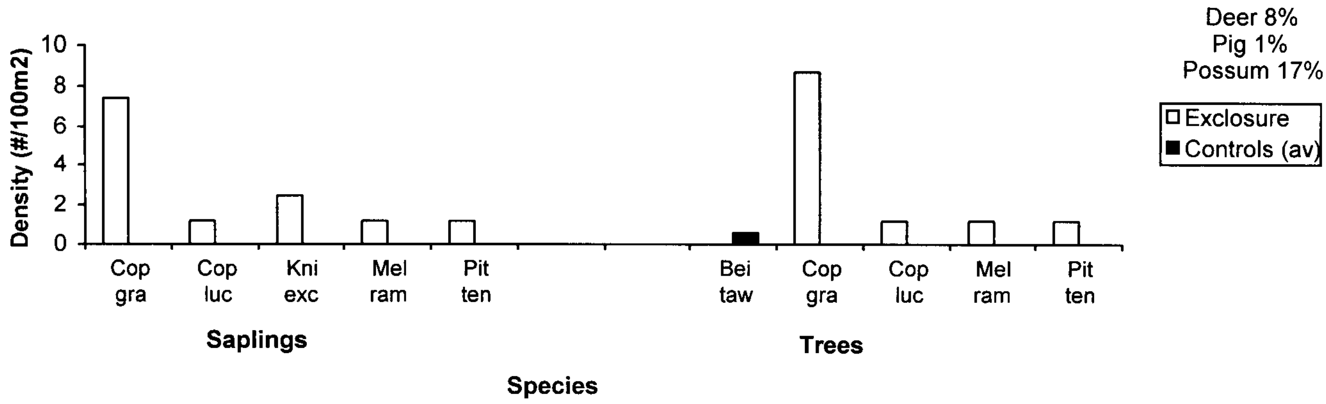


Figure 3: Density of saplings and trees (2-10 cm dbh) by species for Horomanga site

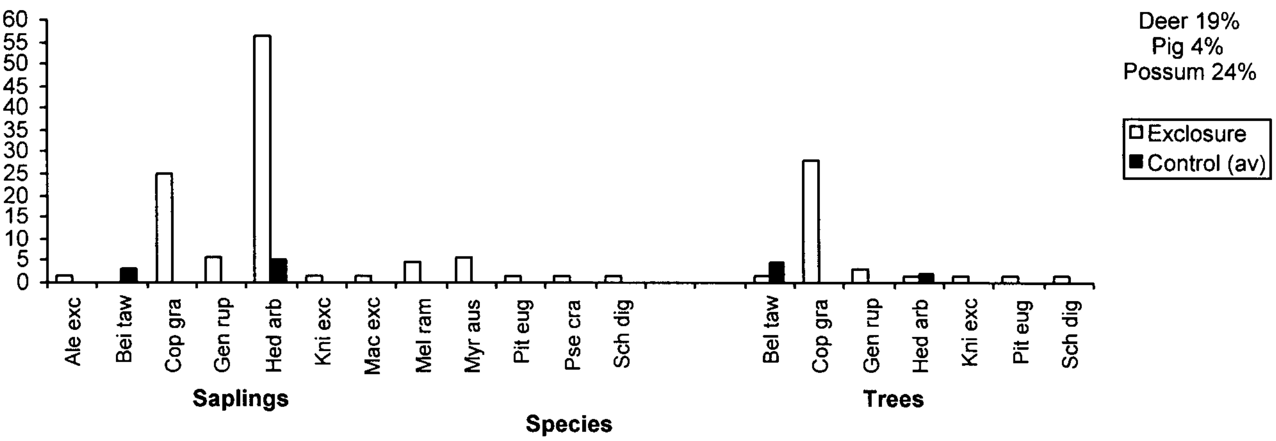


Figure 4: Density of saplings and trees (2-10 cm dbh) by species for Central Waikare site

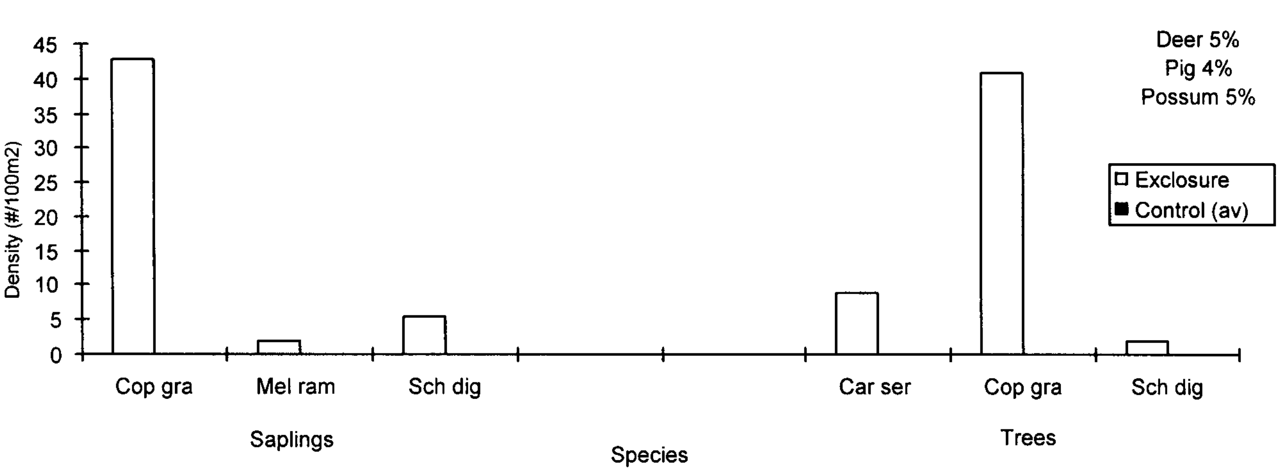


Figure 5: Density of saplings and trees (2-10 cm dbh) by species for Waihua site

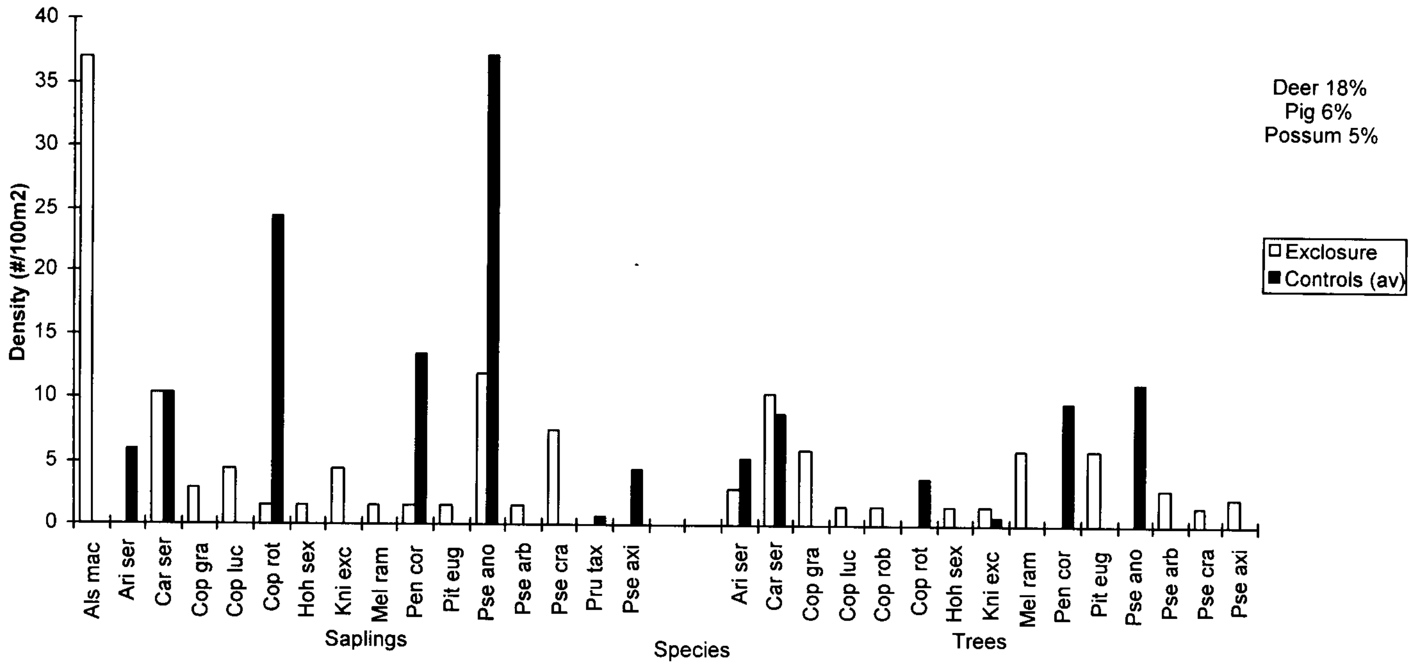


Figure 6: Average density of saplings by species over all exclosure and control sites

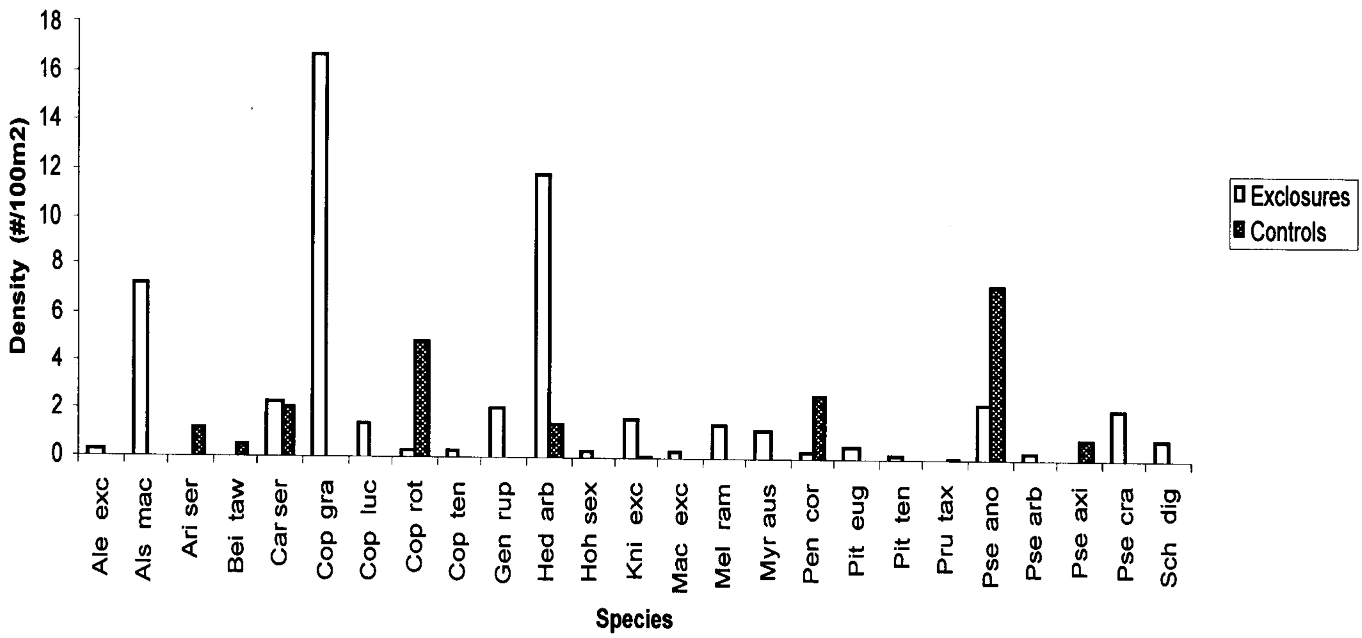


Figure 7: Average density of trees (2-10cm dbh) by species over all exclosure and control sites

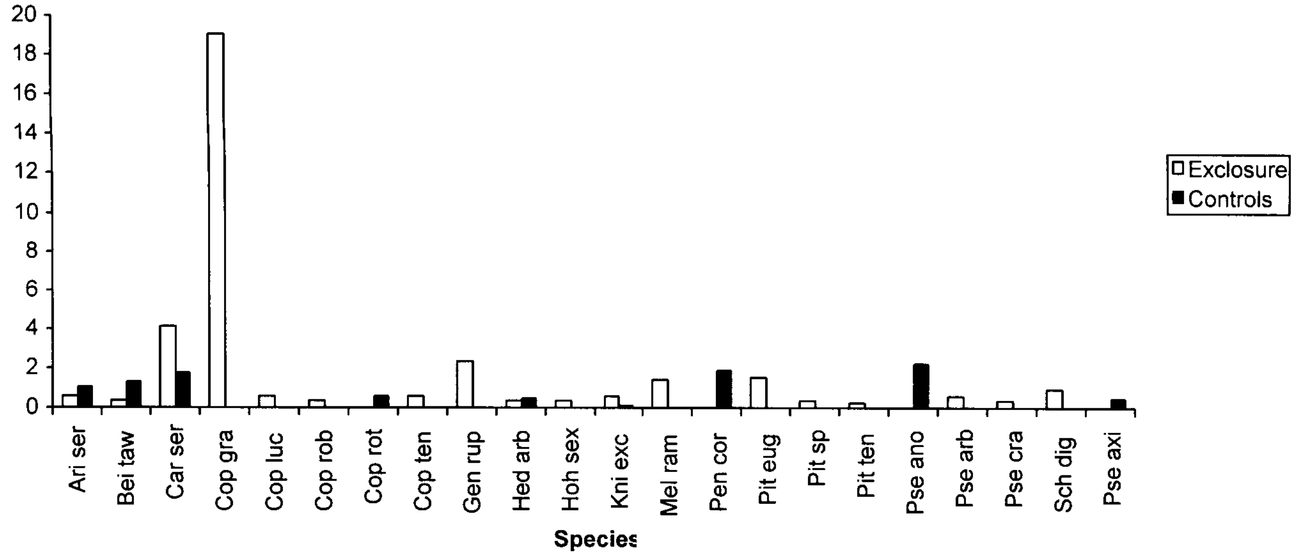


Figure 8: Average density of saplings and trees (2-10 cm dbh) for 'mainland island terrace and steep ridge face plots

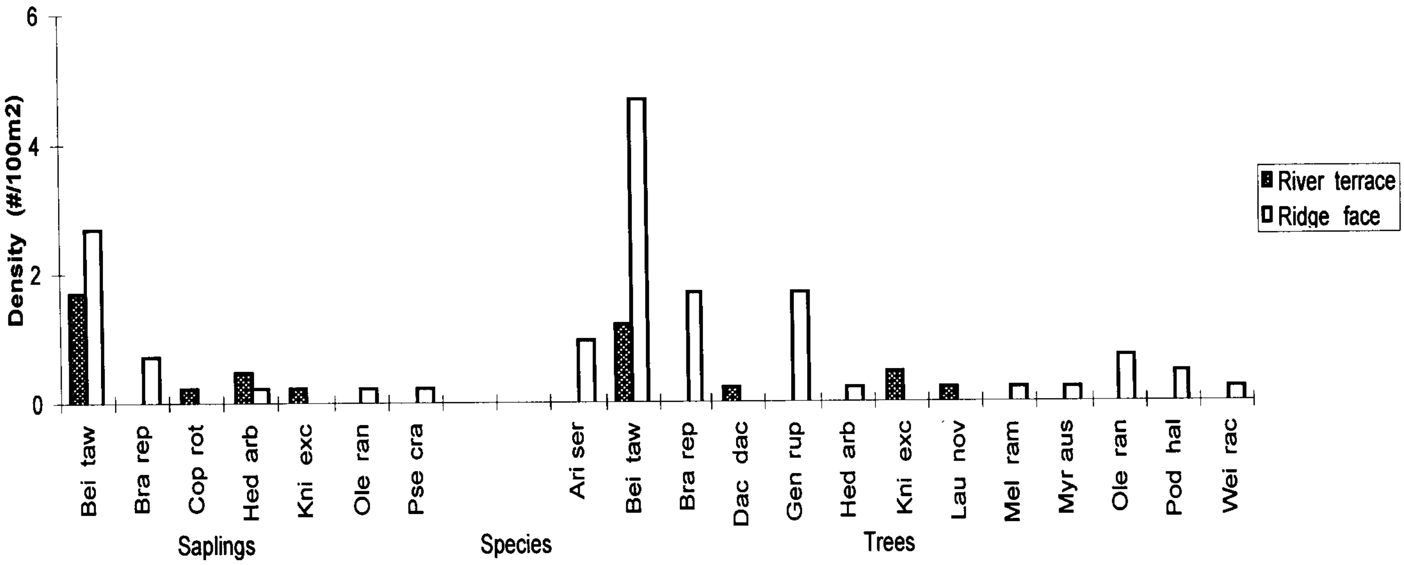


Figure 9: Average density of seedlings (0-15 cm) by species over all exclosure and control sites

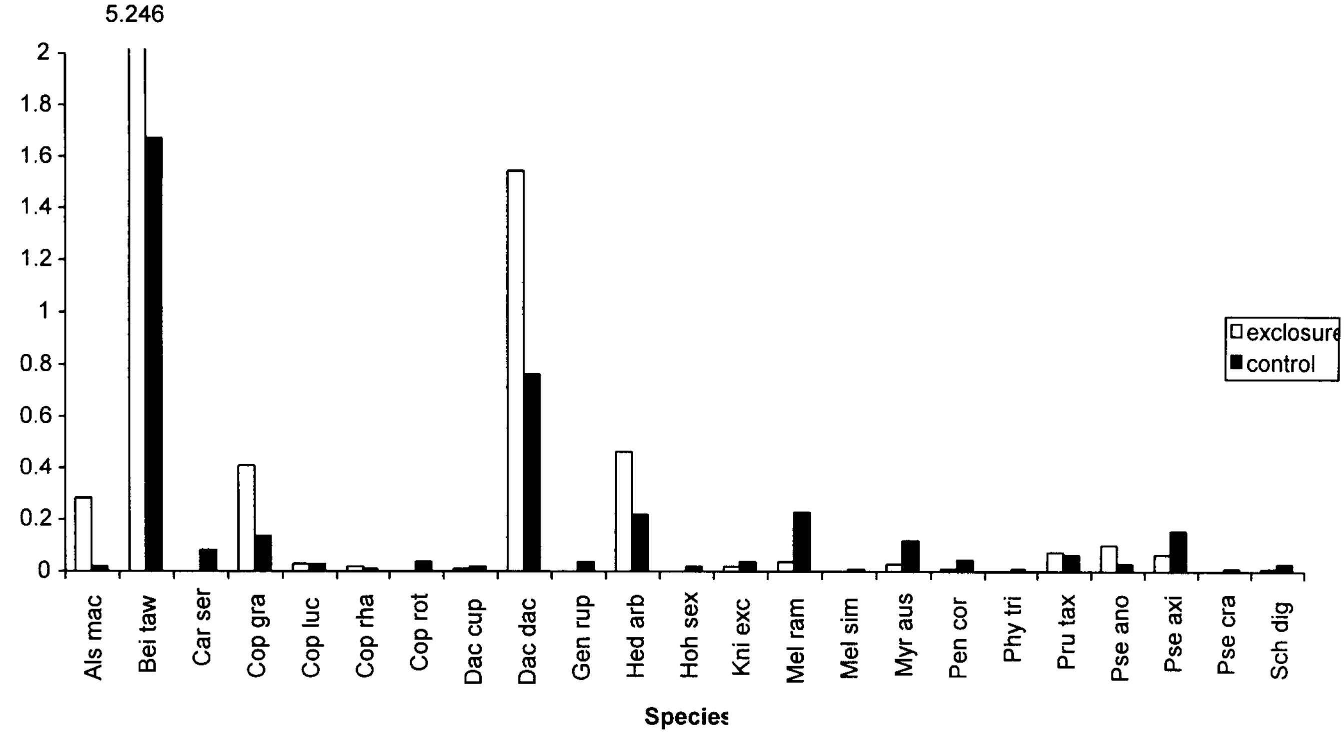


Figure 10: Average density of seedlings (15-140 cm) by species over all exclosure and control sites

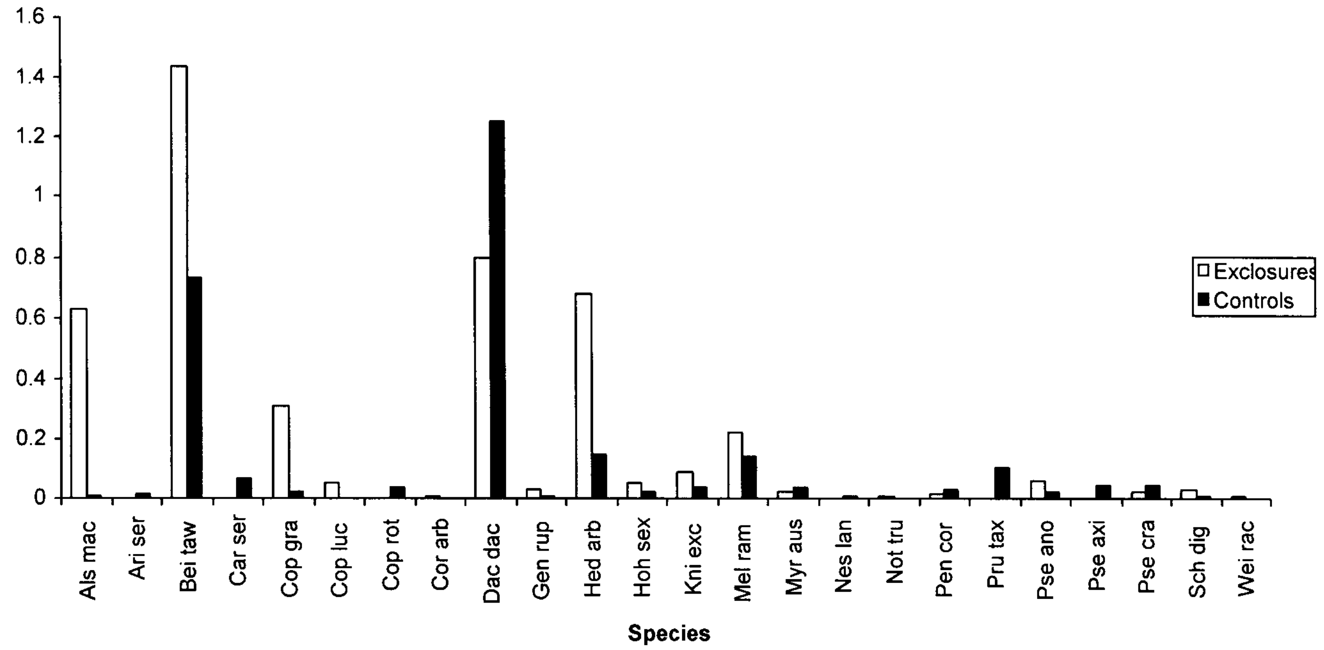


Figure 11: Average seedling (0-15cm) density for mainland island low-altitude flat slope and high-altitude steep slope sites

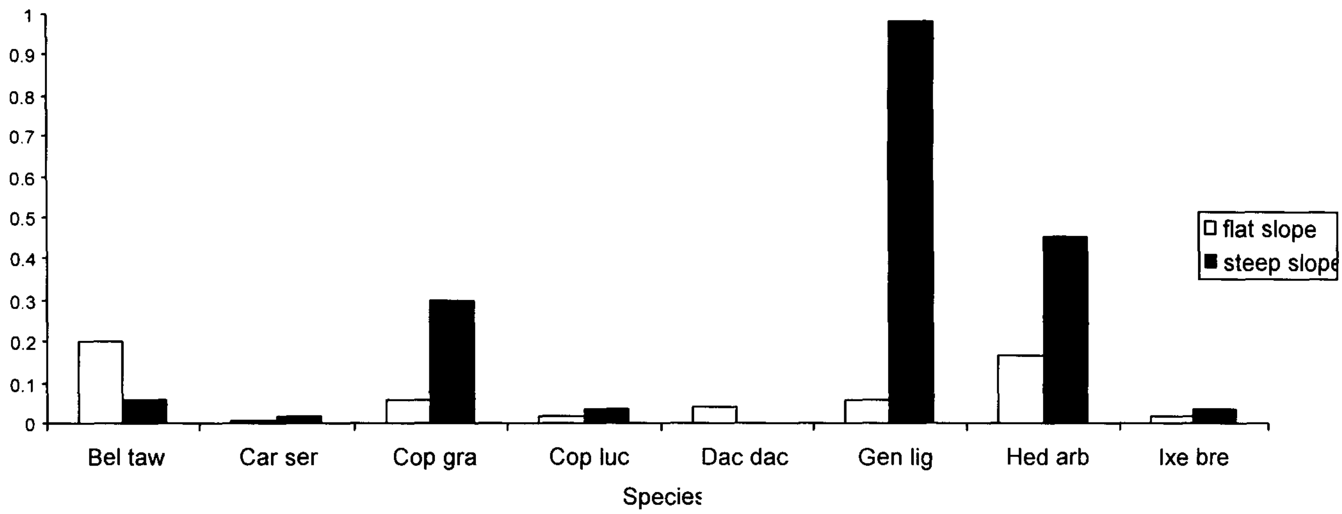


Figure 12: Average seedling (16-140 cm) density for mainland island low--altitude flat slope and high-altitude steep slope sites

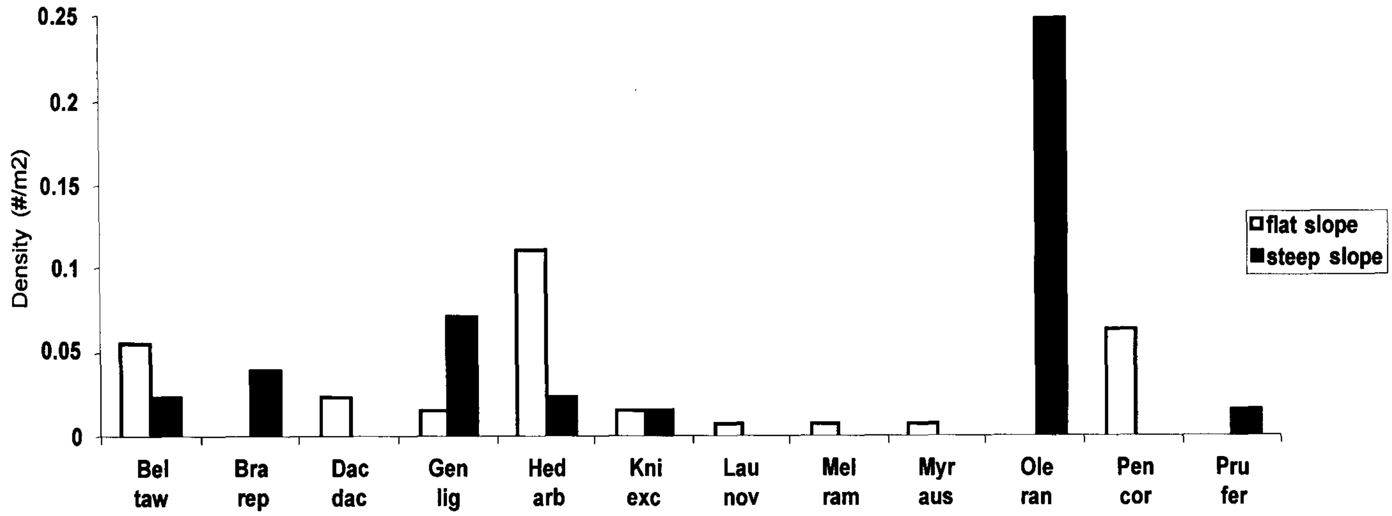


Figure 13: Proportions of non woody species occurring within exclosure and control plots (% occurrence within seedling plots)

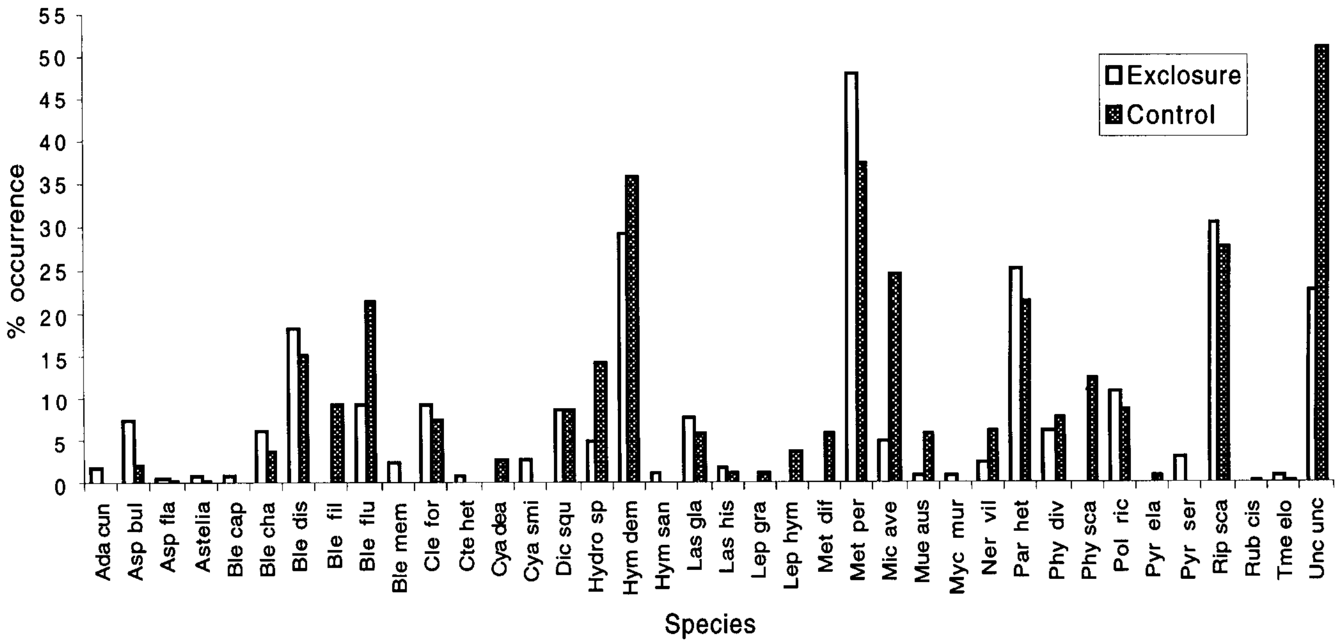


Figure 14: Proportions of non-woody species within 1 m^2 seedling plots for river terrace mainland island plots

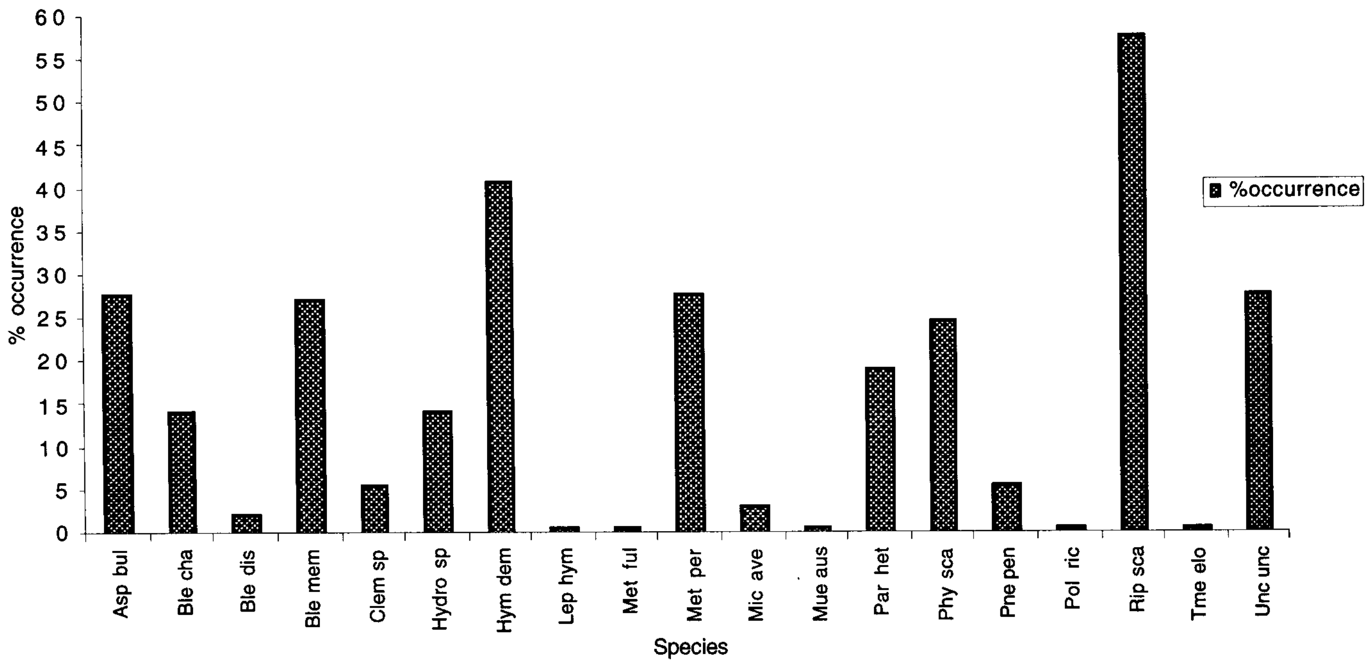


Figure 15: Proportions of non woody species within 1 m2 seedling subplots for steep slope ridge face mainland island plots

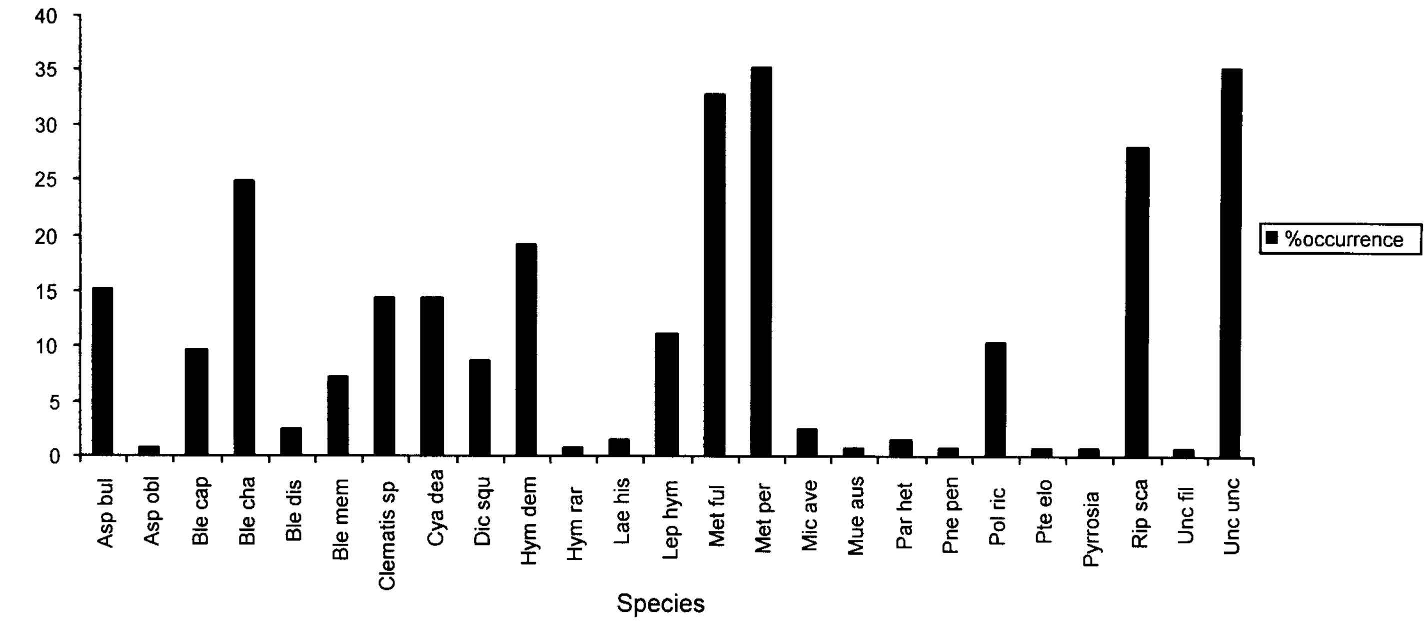
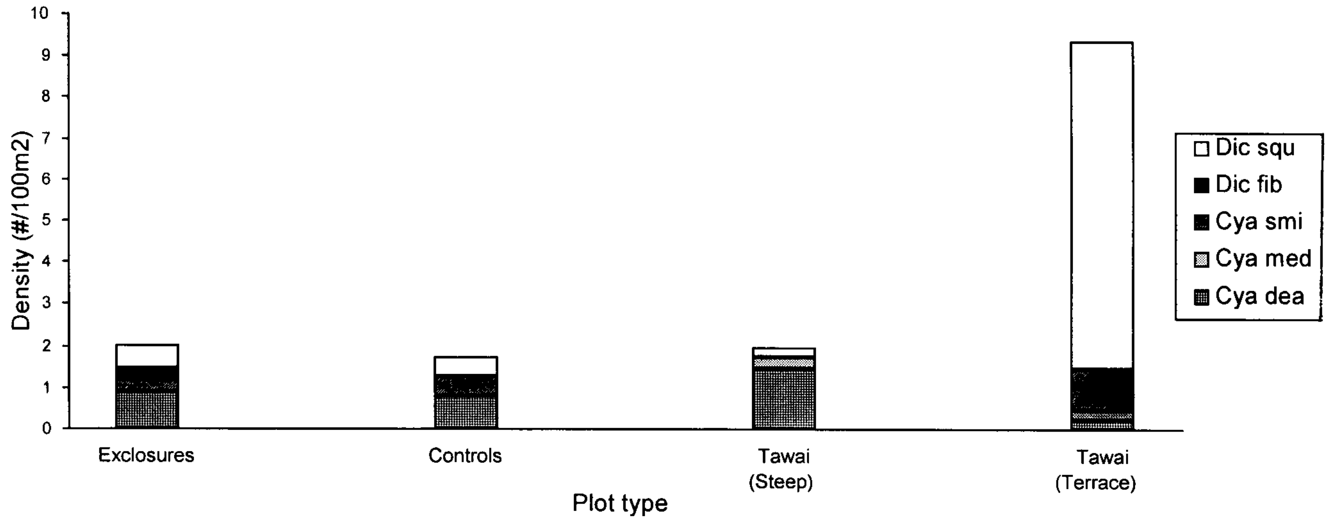


Figure 16: Tree fern density by species across all plot types



8. Appendices

8.1 DESCRIPTION OF PHYSICAL FACTORS OF PLOT SITES

a. Exclosure/control sites.

Site	Year established	Altitude	Aspect	Slope	Plot size
Tataweka	1963	530m	310°	4°	9.0x9.0m
Ngahiramai	1963	260m	215°	9°	9.0x7.5m
Horomanga	1961	300m	250°	26°	9.0X7.5m
Central Waikare	1966	300m	95°	4°	7.5x7.5m
Waihua	1968	400m	60°	0°	9.0X7.5m

b. Mainland Island river terrace plots

Altitude	Aspect	Slope	Size
210m	210°	6°	9x9m
200m	360°	6°	9x9m
215m	270°	4°	9x9m
220m	95°	20°	9x9m
205m	270°	9°	9x9m

c. Mainland Island steep slope plots

Altitude	Aspect	Slope	Size
485m	40°	44°	9x9m
485m	270°	40°	9x9m
560m	65°	38°	9x9m
560m	260°	37°	9x9m
560m	320°	20°	9x9m

8.2 WOODY SPECIES

Abbreviation	Scientific name	Common Maori / European name
Ale exc	*Alectryon excelsus*	titoki
Als mac	*Alseuosmia macrophylla*	
Ari ser	*Aristotelia serrata*	makomako/wineberry
Bel taw	*Beilschmiedia tawa*	tawa
Bra rep	*Brachyglottis repanda*	rangiora
Car ser	*Carpodetus serratus*	putaputaweta
Cop rha	*Coprosma rhamnoides*	
Cop rot	*Coprosma rotundifolia*	
Cop luc	*Coprosma lucida*	karamu
Cop gra	*Coprosma grandifolia*	kanono
Cop ten	*Coprosma tenuifolia*	
Cop rob	*Coprosma robusta*	karamu
Cor arb	*Coriaria arborea*	tutu
Dac cup	*Dacrydium cupressinum*	rimu
Dac dac	*Dacrycarpus dacrydioides*	kahikatea
Gen rup	*Geniostoma ruprestre var ligustrifolium*	hangehange
Hed arb	*Hedycarya arborea*	porokaiwhiri/pigeonwood
Hoh sex	*Hoheria sexstylosa*	long leaved lacebark
Ixe bre	*Ixerba brexioides*	tawari
Kni exc	*Knightia excelsa*	rewarewa/NZ honeysuckle
Lau nov	*Laurelia novae-zelandiae*	pukatea
Mac exc	*Macropiper excelsum*	kawakawa
Mel sim	*Melicope simplex*	
Mel ram	*Melicytus ramiflorus*	mahoe/whitey wood
Myr aus	*Myrsine australis*	mapou
Nes lan	*Nestegis lanceolata*	white maire
Not tru	*Nothofagus truncata*	hard beech
Ole ran	*Olearia rani*	heketara
Pen cor	*Pennantia corymbosa*	kaikomako
Phy tri	*Phyllocladus trichomanoides*	tanekaha/celery pine
Pit eug	*Pittosporum eugenioides*	tarata/lemonwood
Pit ten	*Pittosporum tenuifolium*	kohuhu
Pod hal	*Podocarpus hallii*	Hall's totara
Pru tax	*Prumnopitys taxifolia*	matai
Pru fer	*Prumnopitys ferruginea*	miro
Pse ano	*Pseudopanax anomalus*	
Pse cra	*Pseudopanax crassifolius*	horoeka/lancewood
Pse axi	*Pseudowintera axillaris*	horopito
Pse arb	*Pseudopanax arboreus*	whauwhaupaku/five finger
Sch dig	*Schefflera digitata*	pate
Wei rac	*Weinmannia racemosa*	kamahi

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