

Changes to the forests of Egmont National Park 1977-2001

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ABSTRACT

Data from 47 forest plots (20 m × 20 m) in Egmont National Park, New Zealand, were used to assess changes in seedling and tree species composition. Forty-two of these plots were re-measured between 1977 and 2001. During this time intensive feral goat (*Caprus hircus*) culling lowered browsing pressure on palatable plant species, and increases were expected in the seedling- and sapling-densities of species preferentially selected in the diet of feral goats. In the understorey (stems < 2 cm diameter at breast height—DBH), the feral-goat-selected sub-canopy hardwoods *Coprosma grandifolia*, *C. tenuifolia*, *Geniostoma rupestre* and *Schefflera digitata* increased in density between establishment and re-measurement surveys. Densities of feral-goat-selected seedlings were also higher when compared to other New Zealand forests with ungulate populations present. These results demonstrate the benefits of successful feral-goat culling in Egmont National Park. In the overstorey (> 2 cm DBH), there was a decline in the stem density of *Myrsine salicina*, *Pseudowintera axillaris*, and *Weinmannia racemosa*, while *Hedycarya arborea* increased in density. There has been little change in tree size class structure and species composition in Egmont National Park in the past two decades, but it is likely that fast-growing palatable species such as *Coprosma grandifolia*, *Griselinia littoralis*, *Pseudopanax colensoi*, *Raukaua simplex* and *Weinmannia racemosa* will continue to benefit from ongoing feral goat culling and eventually increase their importance in the overstorey. Possum (*Trichosurus vulpecula*) culling did not appear to arrest the decline in tree density of *W. racemosa*, supporting a view that possum populations need to be culled in the early stage of their colonisation rather than when extensive tree decline has already occurred.

Keywords: Goats, *Capra hircus*, brushtail possum, *Trichosurus vulpecula*, long-term plots, herbivory, tree species, forest composition, Egmont National Park, Taranaki, New Zealand

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1. Introduction and objectives

Feral goats (*Capra hircus*) have been present in Egmont National Park (34 169 ha) for a century. They have probably altered forest species composition and ecosystem-level processes by preferentially browsing on plant species with poor chemical and morphological defences against mammalian browsers (Bond et al. 2004; Wardle et al. 2004). Since 1925 government-funded culling has been undertaken to lower feral goat population densities and reduce their adverse effects on forest regeneration. See Forsyth et al. (2003) for details of feral goat culling in Egmont National Park. Culling effort peaked in the early 1980s, by which time goat densities had been reduced to c. 10% of habitat carrying capacity and of former population density. *Coprosma grandifolia*, *Griselinia littoralis* and *Weinmannia racemosa* are palatable to feral goats in Egmont National Park (Forsyth 2002; Mitchell 1987a, b). A series of 20 m × 20 m permanent vegetation monitoring plots ($n = 47$) were established between 1977 and 1982. To monitor an expected density increase in the species preferentially selected in the diet of feral goats, 42 of these plots were re-measured between 1999 and 2001.

Many plant species¹ occurring in Egmont National Park (e.g. *Libocedrus bidwillii*, *Metrosideros robusta*, *Podocarpus hallii*, and *Weinmannia racemosa*) are also likely to be vulnerable to browsing by brushtail possums (*Trichosurus vulpecula*). Previous research has shown that forests composed of these tree species may be vulnerable to large scale dieback following colonisation by possums (Pekelharing & Batcheler 1990; Rogers & Leathwick 1997; Allen et al. 2002; Bellingham et al. 1999). In 1994 brushtail possum culling was implemented in Egmont National Park to reduce possum population density and alleviate browsing pressure on vulnerable trees such as *M. robusta*, *P. hallii*, and *W. racemosa* (Stronge 1996). If responses to possum culling have been rapid there may already be evidence of reductions in the mortality of mature trees palatable to possums, such as *W. racemosa*. The aim of the present study was to relate changes in the forest vegetation of Egmont National Park between 1977 and 2001 to the browsing effects of feral goats and brushtail possums. The specific objectives were to assess changes in forest structure and composition in relation to potential or likely impacts of feral goats and brushtail possums. A second objective was to provide direction on how to conduct future monitoring in Egmont National Park.

¹ Nomenclature for plants follows Parsons et al. (1995). *Coprosma taylorae* is described by Jane (2005). *Raukaua edgerleyi* and *Raukaua simplex* are described by Mitchell et al. (1997).

2. Methods

2.1 STUDY SITE

Egmont National Park forests grow on soils derived from andesitic bedrock and ashfall derived from Mt Taranaki (formerly known as Mt Egmont). Rainfall varies between 1500 mm on lower slopes and 8000 mm at higher altitudes. Forests occur from low altitude farmland at c. 100 m a.s.l. to dense *Olearia colensoi* shrublands at c. 1300 m a.s.l. Groundcover is dominated by bryophytes (e.g. *Dicranoloma* spp., *Ptychomnion* spp.), ferns (*Asplenium* spp., *Blechnum* spp.) and monocotyledons (e.g. *Microlaena* spp., *Uncinia* spp.). Tree ferns (*Cyathea* spp., *Dicksonia* spp.), shrubs and trees dominate the understorey and sub-canopy (e.g. *Pseudowintera colorata*, *Coprosma grandifolia*). *Weinmannia racemosa*, and *Beilschmiedia tawa* dominate the canopy tier. With increasing altitude, canopy-emergent trees such as *Dacrydium cupressinum* and *Metrosideros robusta* are replaced by *Podocarpus hallii*. The vegetation is fully described by Clarkson (1985, 1986).

2.2 SAMPLING STRATEGY AND PLOT MEASUREMENT PROCEDURES

This study used data from a network of 47 (20 m × 20 m) forest plots established by the New Zealand Forest Service during three surveys between February and April 1977 ($n = 33$), between January and April 1979 ($n = 6$) and in February 1982 ($n = 8$). A thorough data correction exercise was undertaken prior to analysis (Hurst & Husheer 2004). Data from 38 plots measured in 1985 were included where available (uncorrected electronic data from 38 plots, and understorey data from 8 plots). Plot selection followed a random stratified sampling procedure. Forests in Egmont National Park were split into wedge shaped sectors, and plots were randomly assigned to a sector, a random distance from the sector's boundary, randomly on the right or left of the nearest waterway and a random distance from the waterway. Plots established at high altitude and in the Kaitake Range were situated at mid points on faecal pellet monitoring lines as described by Russell (1981). Faecal pellet lines were fixed length (1000 m) transects, and were located using a restricted random process. Lines started in creek beds and traversed an area on predetermined compass bearings. Mean plot altitude (\pm SD) is 626 ± 237 m a.s.l. and varies from 160 m to 1120 m a.s.l. Forty-two of the plots were re-measured between February 1999 and April 2001 by the Department of Conservation (DOC) to assess the response of vegetation to ongoing culling of feral goats.

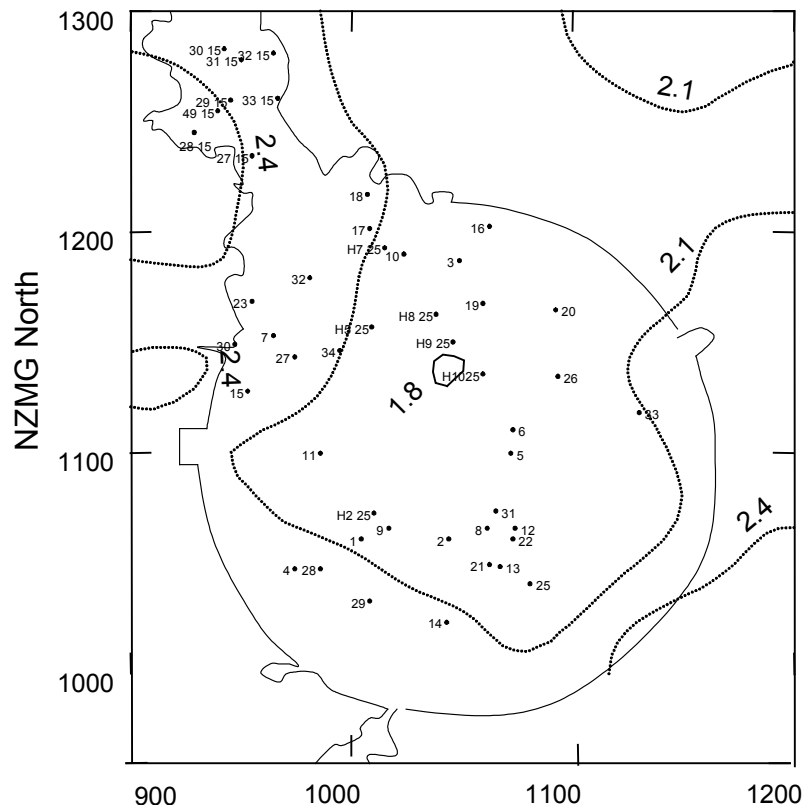
The methods used to establish these plots follow a protocol used to establish over 5000 permanent plots in New Zealand (Allen 1993). Permanent 20 m × 20 m plot measurement procedures generally follow Allen (1992, 1993). All trees (stems ≥ 20 mm diameter at breast height—DBH) were tagged, identified to species and the diameter over bark at breast height measured. All saplings (individual plants, but not multiple stems, > 135 cm high) were counted and species identified in 20 m × 20 m plots in the final survey. Definitions of maximum DBH of saplings and

minimum DBH of trees varied between surveys (e.g. stems > 1 cm DBH in 1976–77 versus > 3 cm DBH in 2000 and 2001). Prior to analysis raw data was checked and reconciled so that a consistent cut-off of 2 cm DBH was used. Twenty-four understory subplots (49 cm radius) were systematically located within each 20 m × 20 m plot at 5 m spacings as described by Payton et al. (2004). All woody seedlings (15–135 cm high) were identified to species level and counted in four height classes (15–45 cm, 46–75 cm, 76–105 cm, and 106–135 cm) in each of the subplots. During the establishment surveys only woody species were recorded in seedling plots, but both woody and herbaceous species were measured in the final survey. Herbaceous species have not been included in analysis. For the purpose of some analyses seedling data was pooled into one height class (15–135 cm). The presence of all small seedlings (< 15 cm high) was also recorded and species identified. The presence of herbaceous plants was only recorded in the < 15 cm height tier.

2.3 ARE PLOTS REPRESENTATIVE?

Examination of locations of plots suggest that plots may be more concentrated in the northwest of Egmont National Park (Fig. 1). In contrast, more rigorous graphical comparisons of differences between the locations of Egmont National Park permanent plots and those selected from a uniform random distribution show that plot location is generally representative (Fig. 2). There is no evidence that plots are clustered in any particular area or that sites that were selected deviate from a fully random selection, even though a stratified random sampling approach was taken to select plot sites. This confirms that plots are randomly selected, representative of Egmont National Park forests, and allows inferential statistical analysis to be undertaken.

Figure 1. Locations of permanent 20 m × 20 m plots established between February 1977 and February 1982 in Egmont National Park with a spatial simulation model of DCA axis 1 scores. (Park boundary as a solid line, dotted contours were generated from a spatial simulation model.)



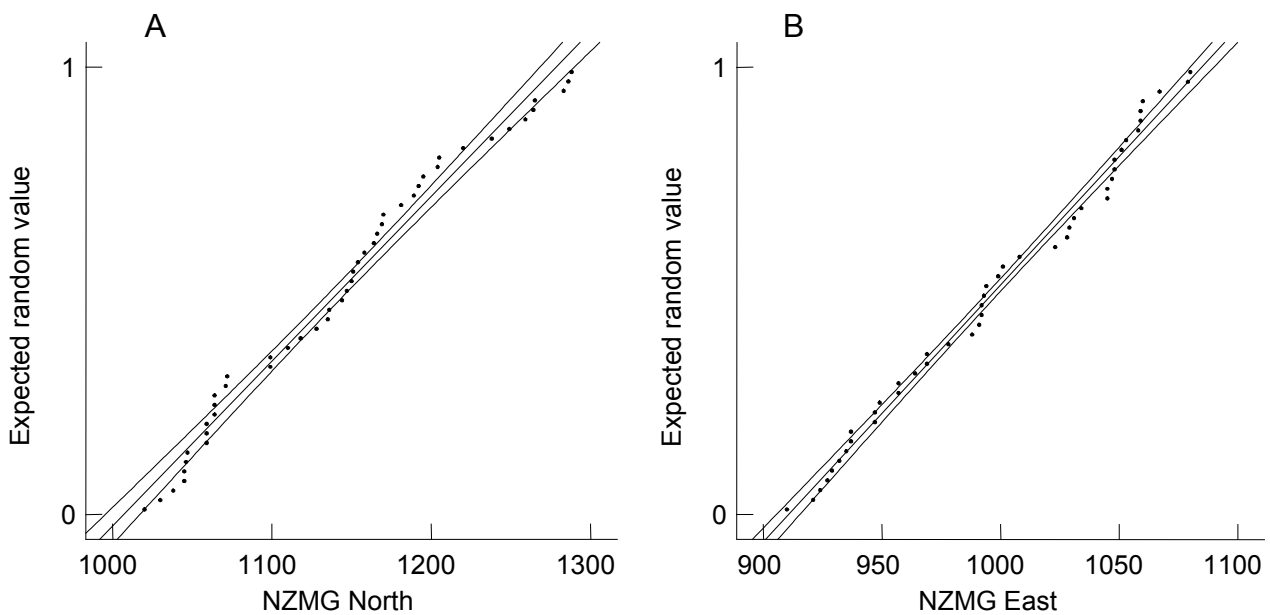


Figure 2. The relationship between expected values from a uniform random distribution and **A.** plot latitude, and **B.** plot longitude.

2.4 DATA INCLUDED IN ANALYSIS

Final analysis has used data from woody trees (≥ 2.0 cm DBH), seedlings (15–135 cm high) and saplings (135 cm high and < 2 cm DBH; woody species criteria of Poole & Adams 1994). Initially analysis was also undertaken on seedlings < 15 cm and those vascular plants in any survey with mean frequency of occurrence $> 5\%$. Standing dead trees were not recorded in the 1981 or 1995 surveys and are not included in analysis. Seedling data were comparable between all surveys in terms of height definitions but accuracy in species identification probably differed. Unfortunately there were too many discrepancies in species identification (particularly for non-woody species) among surveys for these data to be relied upon completely. For example, *Blechnum chambersii*, *Hymenophyllum demissum*, *Hymenophyllum sanguinolentum*, *Rhopalostylis sapida*, and various *Uncinia* spp. were common in the 1981, 1985 and 2000 surveys, but were absent from the 1977 and 1978 surveys.

Several plots were not 20 m \times 20 m in size, and this has been allowed for in analysis. In 1977 plot 31 was only 200 m², and in 2000 H8 25 was 200 m² and H1025 was 100 m². H1025 had 12 seedling subplots and four 5 m \times 5 m quadrats in 1978 and 2000. Plot 31 and H8 25 were also non-standard in 2000. Tree ferns (included in Poole & Adams 1994) were not counted as seedlings in 1977 and have been omitted from analysis. To allow for the possibility that some species may have been occasionally miss-identified only common species were included in analysis. These were species with a basal area greater than 1 m²/ha or a seedling or tree stem density > 100 stems/ha in 2000. Tree ferns and *Rhopalostylis sapida* were counted using different protocols between surveys, and these species were also excluded from analysis. Stems of *Freycinetia banksii* and *Ripogonum scandens* are inherently difficult to accurately count in the overstorey and so are only analysed as seedlings.

2.5 DATA ANALYSIS

Common species were rated as selected, not selected or avoided by feral goats (Table 1) according to a thorough literature review, with studies in Egmont National Park being given more weighting than other New Zealand studies. Plot values for mean stem or plant abundance were converted to means per ha using SYSTAT (SPSS 2000).

Species composition was summarised by calculating a Detrended Correspondence Analysis (DCA) scores for each plot using CANOCO (Ter Braak & Smilauer 1998). This process is able to reduce data from multiple species in multiple plots into four dimensions. For instance, density data from 30 species (considered as 30 dimensions) in 20 plots can be reduced to four dimensions providing four DCA values for each plot and for each species. Plots with high DCA scores will have a greater number and density of species with high DCA scores.

To compare species density data with environmental data (i.e. plot altitude, aspect, year of survey and their interactions) Canonical Correspondence Analysis (CCA) was employed in CANOCO. This analysis procedure uses an approach similar to multiple regression to relate environmental gradients to species and plot scores produced using a DCA type approach. Statistical tests were then undertaken in CANOCO using an iterative randomisation procedure to test for significance of the effects of environmental variables on plot and species scores. SYSTAT (SPSS 2000) was used to undertake all other statistical tests including a series of paired *t*-tests, a spatial simulation model of plot locations and plot DCA scores. The simulation model used establishment DCA axis 1 tree stem data and took a multivariate normal approach to spatial data summarisation.

3. Results

3.1 UNDERSTOREY

The seedling density of *Coprosma grandifolia*, a species preferentially selected by feral goats, increased threefold between plot establishment (1977–82) and re-measurement (1999–2001; Table 1). Two other species not preferentially selected by goats (*Elaeocarpus dentatus* and *Myrsine salicina*) also substantially increased in density. Only these three species changed significantly in density and there was no overall change in seedling density between surveys. It is possible that species misidentification contributed to these results.

Sapling densities of the feral goat selected *Coprosma grandifolia*, *C. tenuifolia*, *Gentostoma rupestre*, and *Schefflera digitata* increased significantly in density by more than twenty-fold (Table 2). The only other common species to increase significantly in density as a sapling was a three-fold increase in *Hedycarya arborea*, a species not preferentially selected by feral goats. CCA showed that there were significant changes in understorey species composition between surveys and that these changes varied with altitude and aspect (Table 3). CCA results show that species with high CCA axis 1 scores tended to increase in

TABLE 1. RESULTS OF LITERATURE SEARCHES* ON PALATABILITY TO FERAL GOATS AND BRUSHTAIL POSSUMS OF COMMON SPECIES AT EGMONT NATIONAL PARK.†

SPECIES	POSSUM‡	SEEDLING DENSITY (plants/ha)				TREE DENSITY (stems/ha)			
		ESTABLISHMENT	RE-MEASURE	df = 41	P [§]	ESTABLISHMENT	RE-MEASURE	df = 41	P [§]
Selected by feral goats[§]									
<i>Carpodetus serratus</i>	Eaten [‡]	154 ± 75	132 ± 53	0.380	0.706	146 ± 49	109 ± 29	1.514	0.138
<i>Coprosma grandifolia</i>	Eaten [‡]	355 ± 132	966 ± 326	2.082	0.044	106 ± 29	115 ± 37	0.308	0.759
<i>Coprosma lucida</i>	Eaten [‡]	177 ± 90	132 ± 84	0.550	0.585	12 ± 7	14 ± 10	0.321	0.750
<i>Coprosma robusta</i>		106 ± 52	13 ± 13	1.747	0.088	6 ± 5	2 ± 1	0.813	0.421
<i>Coprosma tenuifolia</i>		4279 ± 2161	1236 ± 299	1.356	0.183	148 ± 39	95 ± 25	1.966	0.056
<i>Geniostoma rupestre</i>	Eaten [‡]	177 ± 93	688 ± 360	1.603	0.117	15 ± 10	17 ± 11	0.779	0.440
<i>Griselinia littoralis</i>	Eaten [‡]	1478 ± 548	1786 ± 690	1.166	0.251	86 ± 25	70 ± 17	1.465	0.150
<i>Hebe stricta</i>		12 ± 12	132 ± 132	0.893	0.377	<1	<1		
<i>Melicytus ramiflorus</i>	Eaten [‡]	95 ± 42	159 ± 69	0.682	0.499	212 ± 57	194 ± 51	1.058	0.296
<i>Pseudopanax arboreus</i>	Eaten [‡]	12 ± 12	0	1.000	0.323	0	0		
<i>Pseudopanax colensoi</i>	Eaten [‡]	355 ± 159	556 ± 490	0.300	0.766	3 ± 2	1 ± 1	1.302	0.200
<i>Pseudopanax crassifolius</i>	Eaten [‡]	686 ± 336	357 ± 169	1.728	0.091	32 ± 16	24 ± 10	1.118	0.270
<i>Raukawa simplex</i>	Eaten [‡]	59 ± 39	489 ± 209	1.355	0.183	9 ± 8	5 ± 2	0.477	0.636
<i>Schefflera digitata</i>	Eaten [‡]	236 ± 77	251 ± 143	0.104	0.918	57 ± 39	110 ± 50	1.302	0.200
<i>Weinmannia racemosa</i>	Eaten [‡]	556 ± 210	701 ± 270	0.484	0.631	1025 ± 182	719 ± 133	3.955	<0.001
Total (selected spp.)		8735 ± 19183	7598 ± 1283	0.424	0.673	1857 ± 203	1475 ± 148	2.767	0.008
Not selected by feral goats^{1, 5, 6}									
<i>Coprosma</i> "taylorae"		95 ± 59	185 ± 96	1.851	0.071	10 ± 6	13 ± 8	0.215	0.831
<i>Elaeocarpus dentatus</i>	Eaten [‡]	0	172 ± 77	2.237	0.031	6 ± 2	12 ± 6	0.976	0.335
<i>Elaeocarpus hookerianus</i>	Eaten [‡]	<1	<1			2 ± 1	4 ± 3	1.000	0.323
<i>Freycinetia banksii</i>		1312 ± 679	714 ± 213	1.191	0.240	<1	<1		
<i>Hedycarya arborea</i>	Eaten [‡]	2246 ± 827	1468 ± 344	1.301	0.201	166 ± 40	226 ± 61	2.032	0.049
<i>Macropiper excelsum</i>		378 ± 273	93 ± 60	1.291	0.204	42 ± 28	8 ± 5	1.455	0.153
<i>Metrosideros diffusa</i>	Eaten [‡]	24 ± 24	106 ± 69	1.062	0.294	<1	<1		
<i>Metrosideros robusta</i>	Eaten [‡]	12 ± 12	198 ± 113	1.615	0.114	4 ± 3	5 ± 4	0.298	0.767
<i>Myrsine divaricata</i>		12 ± 12	0			2 ± 2	2 ± 2	0.198	0.844
<i>Myrsine salicina</i>	Eaten [‡]	177 ± 166	1372 ± 458	2.743	0.009	272 ± 62	202 ± 50	2.420	0.020
<i>Pennantia corymbosa</i>	Eaten [‡]	118 ± 65	159 ± 93	0.443	0.660	17 ± 11	17 ± 7	0.144	0.886
<i>Prumnopitys ferruginea</i>	Eaten [‡]	189 ± 62	238 ± 83	0.771	0.445	8 ± 6	14 ± 7	1.502	0.141
Total (not selected spp.)		4563 ± 1119	4705 ± 761	0.170	0.866	529 ± 71	502 ± 71	0.623	0.537
Avoided by feral goats^{2, 5}									
<i>Alseuosmia macrophylla</i>		544 ± 203	499 ± 272	0.449	0.656	0	0		
<i>Beilschmiedia tawa</i>	Eaten [‡]	319 ± 119	251 ± 109	1.667	0.103	59 ± 23	65 ± 24	0.692	0.493
<i>Dacrydium cupressinum</i>		59 ± 35	0	1.704	0.096	11 ± 5	10 ± 5	1.432	0.160
<i>Dysoxylum spectabile</i>	Eaten [‡]	12 ± 12	0	1.000	0.323	6 ± 6	11 ± 11	0.866	0.392
<i>Hebe corriganii</i>		319 ± 167	0	1.646	0.107	3 ± 2	7 ± 7	0.679	0.501
<i>Knightia excelsa</i>		626 ± 417	172 ± 75	1.004	0.321	15 ± 5	14 ± 5	0.255	0.800
<i>Laurelia novaezelandiae</i>	Eaten [‡]	154 ± 67	423 ± 209	1.320	0.194	73 ± 38	84 ± 40	1.068	0.292
<i>Nestegis cunninghamii</i>		47 ± 37	159 ± 79	1.546	0.130	7 ± 3	8 ± 4	0.298	0.767
<i>Podocarpus ballii</i>	Eaten [‡]	461 ± 177	406 ± 187	1.470	0.149	89 ± 28	77 ± 24	0.933	0.356
<i>Pseudowintera axillaris</i>		236 ± 101	185 ± 86	0.385	0.703	18 ± 10	32 ± 14	2.125	0.040
<i>Pseudowintera colorata</i>		6643 ± 1451	6461 ± 1585	0.427	0.672	607 ± 217	854 ± 288	0.837	0.408
<i>Rhopalostylis sapida</i>	Eaten [‡]	35 ± 26	159 ± 112	1.355	0.183	<1	<1		
Total (avoided spp.)		9456 ± 1546	8715 ± 1573	0.934	0.356	888 ± 216	1162 ± 291	0.876	0.386
Total for all common species		22754 ± 3271	18783 ± 2229	1.394	0.170	3272 ± 331	3135 ± 299	0.505	0.616
Shannon–Weiner diversity						1.16 ± 0.09	1.460 ± 0.09	3.750	0.001
Common species basal area						72 ± 6	74 ± 6	0.197	0.845

* Literature search: ¹ Asher (1979); ² Mitchell (1987); ³ Nugent et al. (2000); ⁴ Payton (2000); ⁵ Forsyth et al. (2002); ⁶ Husheer et al. (2003).

† *Cyathea smithii* and *Dicksonia squarrosa* are not included in analysis because they were not counted as seedlings or saplings in 1977 or as trees in any survey.

‡ Also displayed are results of a literature search on species recorded in the diet of possums, and mean (± SEM) seedling and tree stem densities from establishment (1977–81) and re-measurement surveys (2000).

§ Statistically significant *P* values (≤0.05) are in **bold**.

density as seedlings with time, while seedling species with high axis 2 scores tended to have higher densities at lower altitudes (Fig. 3). This reinforces univariate analysis results, because *C. grandifolia* seedling density increased at many sites and *Raukaua simplex* increased more in density between surveys with increasing altitude. Associations containing these species increased with time compared to plant associations containing seedlings of *Beilschmiedia tawa*, *C. tenuifolia* and *Pseudowintera axillaris*. Results also confirm that species such as *P. colorata*, *Podocarpus hallii*, and *Raukaua simplex*, tended to be more important at higher altitudes and more northerly aspects, while *Laurelia novaezelandiae*, *Macropiper excelsum*, *B. tawa*, and *Pseudowintera axillaris* tend to have higher densities at lower altitudes.

3.2 OVERSTOREY

There was a 30% decline in the stem density of *Weinmannia racemosa* between establishment and re-measurement surveys (Table 1), which contributed to an overall decline in the density of tree species selected by feral goats. *Hedycarya arborea* increased in density, while *Myrsine salicina* and *Pseudowintera*

TABLE 2. MEAN (\pm SEM) SAPLING DENSITIES OF COMMON SPECIES (> 100 per ha in 2000) FROM ESTABLISHMENT (1977–81) AND RE-MEASUREMENT SURVEYS (2000), WITH BONFERONI CORRECTED RESULTS FROM A SERIES OF PAIRED *t*-TESTS.

SPECIES	ESTABLISHMENT	RE-MEASURE	df = 41	<i>P</i> *
<i>Coprosma grandifolia</i>	71 \pm 35	1875 \pm 422	4.295	0.001
<i>Coprosma lucida</i>	5 \pm 5	536 \pm 292	1.839	0.657
<i>Coprosma tenuifolia</i>	96 \pm 46	2872 \pm 606	4.662	<0.001
<i>Gentostoma rupestre</i>	15 \pm 15	997 \pm 359	2.800	0.072
<i>Hedycarya arborea</i>	757 \pm 287	2113 \pm 396	3.825	0.004
<i>Myrsine salicina</i>	379 \pm 239	1190 \pm 359	1.959	0.513
<i>Pseudopanax colensoi</i>	1 \pm 1	967 \pm 497	1.944	0.531
<i>Pseudowintera colorata</i>	1823 \pm 974	3869 \pm 997	1.629	0.999
<i>Schefflera digitata</i>	8 \pm 6	1161 \pm 411	2.823	0.063

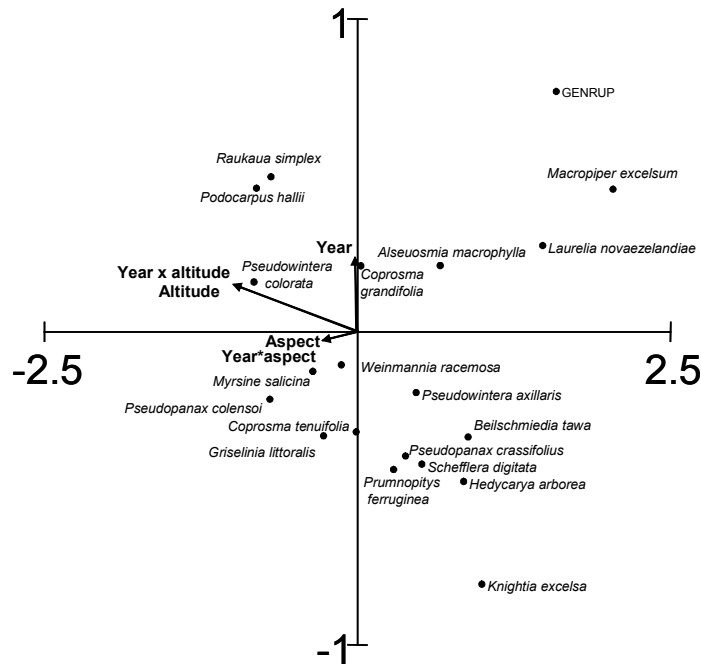
* *P* values which were statistically significant (≤ 0.05) prior to Bonferoni correction are in **bold**.

TABLE 3. RESULTS FROM A STEPWISE CCA PROCEDURE OF EFFECTS OF TIME, ALTITUDE, ASPECT, SLOPE, AND THEIR INTERACTIONS ON SEEDLING (15–135 cm high) SPECIES COMPOSITION BETWEEN 1977 AND 2000 AT 42 SITES (see Fig. 3).

EFFECT	LAMBDA MARGINAL	LAMBDA CONDITIONAL	<i>F</i>	<i>P</i> *
Altitude	0.63	0.63	10.34	0.005
Slope	0.25	0.23	3.85	0.005
Year	0.13	0.12	2.12	0.005
Year \times altitude	0.63	0.10	1.65	0.030
Year \times slope	0.25	0.08	1.53	0.115
Aspect	0.13	0.08	1.40	0.080
Year \times aspect	0.13	0.06	1.00	0.450

* *P* values denote the probability that effects were statistically significant.

Figure 3. The relationship between seedling species composition and environmental variables and their interactions. Analysis uses a CCA of seedling density data from 20 m × 20 m plots established between 1977 and 1981 and re-measured in 1985 and 2000–2001 in Egmont National Park. Vectors of environmental factors with significant effects on species composition are displayed. Only species with weight in CCA > 20 000 are displayed. Eigenvalues for axes 1, 2, 3, and 4 are 0.644, 0.223, 0.173, and 0.103 respectively.



axillaris declined. While total tree stem density for common species did not change significantly, there was an increase in tree diversity between surveys, perhaps due to an increase in the number of species correctly identified in the re-measure survey. CCA showed that there were significant changes in overstorey species composition between surveys and that these changes varied with altitude and aspect (Fig. 4; Table 4). A tree association including feral-goat-selected species (*Coprosma grandifolia*, *Griselinia littoralis* and *Raukaua simplex*) appeared to become more important over time, particularly at lower altitudes and aspects, even though these species did not increase significantly as individual stems.

Figure 4. The relationship between tree species composition and environmental variables and their interactions. The CCA diagram is of tree species composition from 20 m × 20 m plots established in 1977 and 1981 and re-measured in 1985 and 2000–2001 in Egmont National Park. Significant environmental factors are displayed. Importance values are calculated from tree stem density data. Only species with weight in CCA > 20 000 are displayed. Eigenvalues for axis 1, 2, 3, and 4 are 0.671, 0.331, 0.195, and 0.105 respectively.

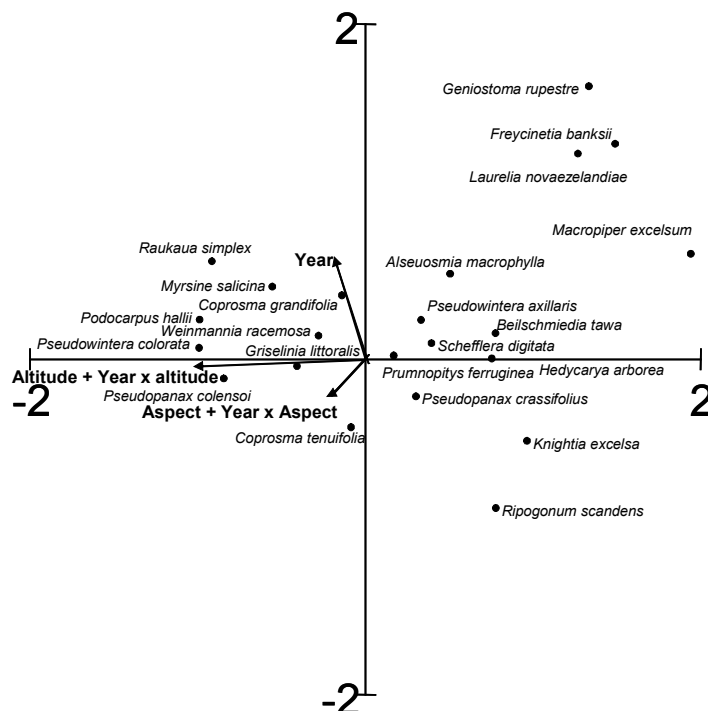
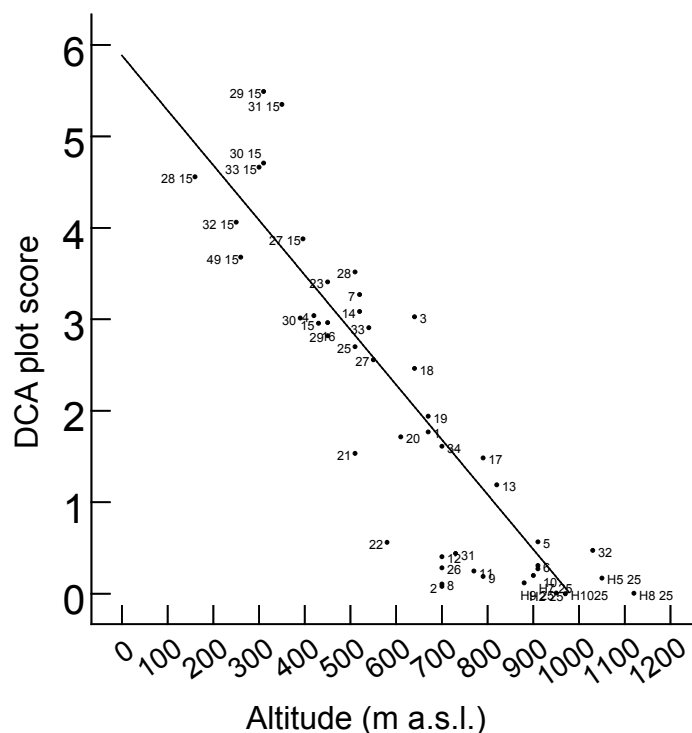


TABLE 4. RESULTS OF A STEPWISE CCA PROCEDURE OF EFFECTS OF TIME, ALTITUDE, ASPECT, SLOPE, AND THEIR INTERACTIONS ON TREE (≥ 2.0 cm DBH) SPECIES COMPOSITION BETWEEN 1977 AND 2000 AT 42 SITES (see Fig. 4).

EFFECT	LAMBDA MARGINAL	LAMBDA CONDITIONAL	F	P
Year \times altitude	0.66	0.66	9.61	0.01
Altitude	0.66	0.13	2.10	0.01
Slope	0.26	0.25	3.79	0.01
Year \times slope	0.26	0.10	1.44	0.13
Year	0.20	0.18	2.71	0.01
Aspect	0.12	0.08	1.29	0.15
Year \times aspect	0.11	0.08	1.22	0.20

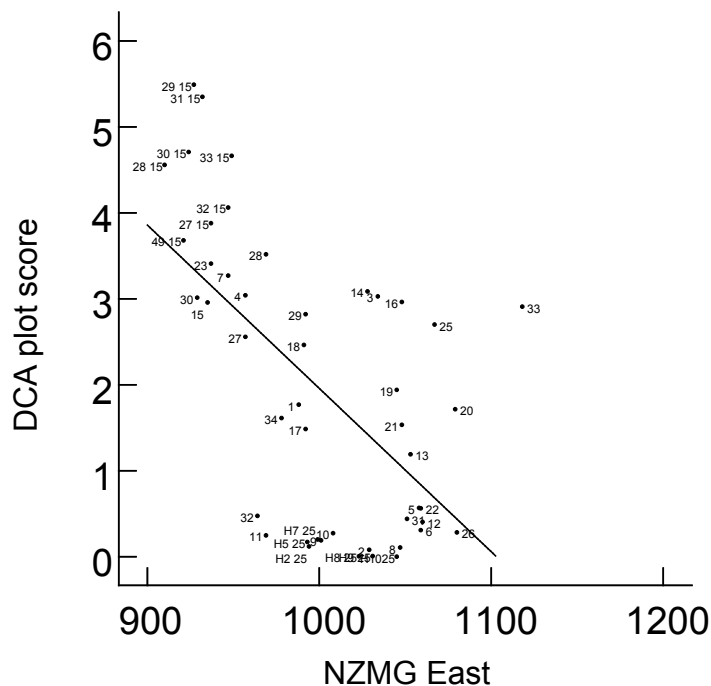
DCA was used to summarise tree species composition without including the constraints of environmental data as in CCA (Figs 5 and 6). DCA scores were then related to altitude, aspect, slope and longitude using a multiple regression to ensure that the effects of these environmental variables had been properly accounted for in CCA. Altitude and latitude had significant effects on tree species DCA scores (Figs 7 and 8). Linear regression confirmed that DCA scores declined with increasing altitude and latitude.

Figure 5. The relationship between tree species composition and altitude. DCA axis 1 plot tree scores against plot altitude with fitted regression line calculated in linear regression: $DCA\ score = 5.884 - altitude \times 0.006 - 1.613$ ($r^2 = 0.784$; $F = 163.672$, $df = 1, 45$, $P < 0.001$) is displayed.



Posthoc power analysis was used to determine the number of plots that would have been required for *t*-tests to detect significant differences of 10% change between initial and final surveys in mean densities of selected, not selected and avoided seedlings at Type I $P = 0.05$ and Type II $P = 0.20$. These sample sizes were 7460, 1760, and 2040 respectively. This large sample size was required because of the massive variability in plant density among plots shown by high

Figure 6. DCA axis 1 plot tree scores against NZMG east reference with fitted regression line calculated in linear regression:
 $DCA\ score = 20.957 - latitude \times 0.019 - 1.613$
 $(r^2 = 0.365, F = 25.871, df = 1, 45, P < 0.001)$.



SEM values. The numbers of 20 m × 20 m plots required to detect a doubling in final densities for selected, not selected and avoided seedlings were 42, 48, and 38 plots respectively. This compares favourably with the current number of plots in the Egmont National Park permanent plot system ($n = 47$).

Figure 7. Statistical (DCA) summary of tree species composition from tree species density data from establishment (1977–82) measurement of permanent 20 m × 20 m plots. Species located close together on the graph were commonly found in the same plots at Egmont National Park. Eigenvalue analysis showed that most variation in species composition was explained by DCA axis 1 (14.2%) followed by axis 2, 3, and 4 (20.7%, 25.0%, and 28.4% cumulatively). Only species with weight in DCA > 20 000 are displayed.

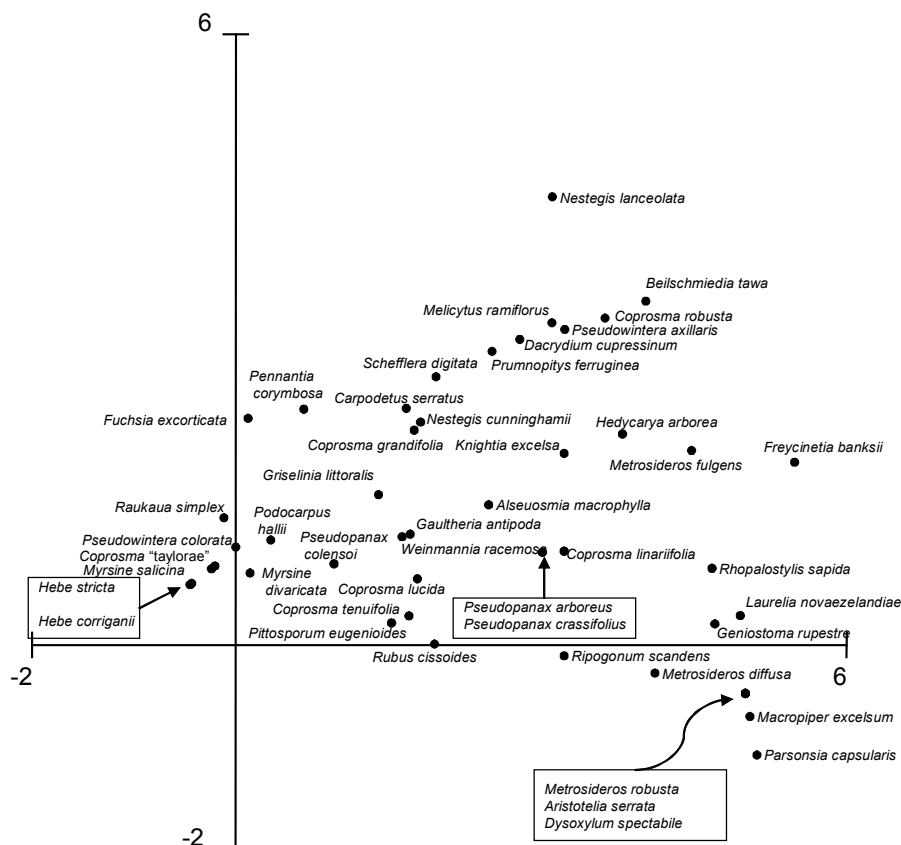
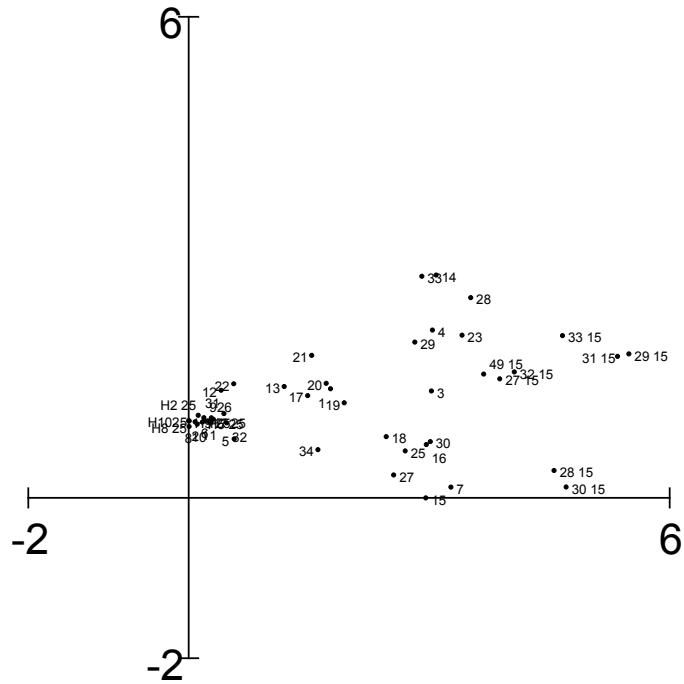


Figure 8. DCA values for individual plots, obtained during the analysis that is displayed in Fig. 7.



3.3 SIZE CLASS STRUCTURE

There was no significant difference in size class structure between surveys for the 12 most common tree species (> 100 stems/ha; Table 5). A Kruskal-Wallis one-way analysis of variance non-parametric test showed that no common woody species in the overstorey showed statistically significant differences in size class structures ($P > 0.388$) for 15–75, 75–135, and > 135 cm high size classes.

TABLE 5. SIGN TEST PROBABILITIES FROM A SERIES OF TESTS ON COMMON SPECIES (> 100 stems/ha) COMPARING THE DISTRIBUTION OF SIZE CLASS STRUCTURES BETWEEN ESTABLISHMENT AND RE-MEASUREMENT. (This is a test of the null hypothesis that data come from different distributions.)

SPECIES	<i>P</i>
<i>Carpodetus serratus</i>	1.000
<i>Coprosma grandifolia</i>	1.000
<i>Coprosma tenuifolia</i>	1.000
<i>Griselinia littoralis</i>	0.754
<i>Hedycarya arborea</i>	0.219
<i>Melicytus ramiflorus</i>	0.039
<i>Metrosideros robusta</i>	1.000
<i>Myrsine salicina</i>	1.000
<i>Podocarpus hallii</i>	0.039
<i>Pseudowintera colorata</i>	0.125
<i>Schefflera digitata</i>	1.000
<i>Weinmannia racemosa</i>	0.815

4. Discussion

4.1 RESPONSE OF EGMONT NATIONAL PARK FORESTS TO FERAL GOAT CULLING

During the two-decade span of this study there were high seedling densities of species preferentially selected in the diet of feral goats. In comparison, other New Zealand forests where ungulate browsers are present had much lower densities. Seedling densities of *Carpodetus serratus*, *Coprosma grandifolia*, *C. lucida*, *C. tenuifolia*, *Geniostoma robusta*, *Griselinia littoralis*, *Pseudopanax colensoi*, *Schefflera digitata*, and *Weinmannia racemosa* all exceeded 100 stems/ha, and in some instances exceeded the >1000 stems/ha found in Egmont National Park. In the Arawhata, Kaipo, and Rotoiti Valleys, and in Aorangi, Lake Sumner, Kaimanawa, Kaweka, Pureora, Rangataua, Tararua, Urewera, and Waitutu Forests many of these species were absent in recent surveys or had seedling densities <100 stems/ha (Allen et al. 1984; Bellingham & Allan 2003; Husheer et al. 2003; Husheer in press; Husheer 2005; Husheer & Frampton 2005; Husheer et al. 2006). This suggests that ongoing culling of feral goats had already resulted in successful regeneration of palatable species prior to establishment of plots in Egmont National Park. In comparison, other forests, some of which have had intensive feral goat and red deer (*Cervus elaphus*) culling since the 1960s, have seedling densities of palatable plants so low that they are unlikely to be regenerating successfully. Egmont National Park differs in two main respects from other New Zealand forests where permanent plots are present. First, feral goat culling has been undertaken since 1925, making it the longest-running pest control operation in the world (Stronge 2000). Second, feral pigs and deer have been prevented from colonizing Egmont National Park. In other forests where ungulate culling has been less successful these benefits are usually not apparent outside ungulate exclusion plots.

In Egmont National Park there were pronounced (more than 20 ×) increases in the densities of saplings of *Coprosma grandifolia*, *C. tenuifolia*, *Geniostoma rupestre* and *Schefflera digitata* between plot establishment and re-measurement two decades later, but only two species increased in density as seedlings between establishment and final surveys. There was a three-fold increase in the density of *C. grandifolia* seedlings, while at higher altitudes there is some evidence that seedlings of *Raukaua simplex* increased in importance compared to other species. Lowered feral goat densities prior to the 1980s have probably allowed goat selected seedling densities to quickly increase to high levels, and continued culling thereafter allowed these species to grow through to the sapling tier. High densities of saplings may have prevented many seedlings from establishing and surviving through a process of competitive exclusion.

Compared to changes in the densities of seedlings and saplings of feral goat selected species, there has been no substantial change in tree population structure, density and species composition in Egmont National Park forests over the past three decades (Tables 1 and 5). In other New Zealand forests, enclosure plot studies have often shown that a group of tree species respond positively to the removal of ungulate herbivory (e.g. *C. grandifolia*, *G. littoralis*,

M. ramiflorus, *Pseudopanax arboreus*, *S. digitata*, and *W. racemosa*; Husheer in press). High standard error values show that there was a large variation in tree stem densities among plots, suggesting that at some plots palatable trees positively responded to reductions in feral goat density while at other plots there was no such response. Idiosyncratic differences between sites involving one or more as yet unidentified key factors may explain this large variation (Wardle et al. 2001). In some other New Zealand forests palatable species have shown more consistent responses following protection from ungulate browsing (e.g. Jane & Pracy 1974; Allen et al. 1984). This might be partly explained by the observation that few plots in Egmont National Park were located in stream beds or collapsed forest, where large increases in tree stem density of feral goat selected species have been observed (K. Mathews and P. Prip Stratford Area Office, DOC, pers. comm.). During the 1980s feral goats frequented stream beds, increasing the relative impact of goats in those areas (W. Reid and B. Fleury, pers. comm.). Forest sites were consistently selected for plot establishment and no plots were located in stream beds.

There are four alternate explanations for a lack of overall change in forest canopy composition in Egmont National Park. Firstly, although reductions in feral goat densities prior to plot establishment may have resulted in a large increase in the densities of selected species in the understorey, this may not yet have been translated into changes in the overstorey. Secondly, the observed response of fast growing species such as *Coprosma grandifolia* may have competitively excluded slower-growing species avoided by feral goats. Thirdly, the remaining feral goat population may have prevented seedling regeneration of slower-growing species browsed by goats. Finally, the direction of forest succession may have been permanently shifted by ongoing feral goat browsing towards a stable alternate state prior to the establishment of plots in 1976. The high seedling densities of selected species found in all surveys of this study and the high sapling densities in the re-measurement survey tend to support the first of these four explanations. Plant species preferentially selected by feral goats appear to have been close to their potential maximum densities as seedlings at most plots during the course of this study, and have increased as saplings through successful recruitment. With ongoing feral goat culling it should be anticipated that continued successful regeneration will result in compositional shifts favouring feral goat selected species in the forest overstorey.

4.2 RESPONSE OF EGMONT NATIONAL PARK FORESTS TO BRUSHTAIL POSSUM CULLING

Brush-tail possum browsing has afflicted regeneration of plant species such as *Dysoxylum spectabile*, *Fuchsia excorticata*, mistletoe (*Alepis flavida*, *Peraxilla colensoi*, *Peraxilla tetrapetala*, *Tupeia antarctica*) and *W. racemosa* in many New Zealand forests (Pekelharing et al. 1998; Payton 2000; Sessions et al. 2001; Nugent et al. 2002; Sweetapple et al. 2005). Culling of possums can curb declines in the condition of these and other possum palatable species (Norton 2000), but in Egmont National Park, the possum palatable *W. racemosa* continued to decrease in tree density despite possum culling in 1994, while the unpalatable *Pseudowintera axillaris* increased in tree density. A similar pattern has been

observed in Pureora Forest Park, despite over two decades of possum culling there. In that forest *W. racemosa* declined, while less palatable species such as *Beilschmiedia tawa* and *Prumnopitys ferruginea* increased in density as trees (Husheer in press).

There was also little change in tree basal area between surveys in Egmont National Park, which would have been expected if the Egmont forests were in the late stage of stand development with ongoing self-thinning. It is possible that growth of mature trees was so low that it was balanced by loss of small stems, which generally contribute very little to total basal area in comparison to larger trees. Results are more consistent with factors other than natural stand succession, such as brushtail possum induced mortality, leading to reductions in *Weinmannia racemosa* stem density. It appears that mortality of *W. racemosa* was concentrated in smaller size classes, which is consistent with normal stand development. If brushtail possum browsing is responsible for *W. racemosa* decline, then recent brushtail possum culling may reduce any further decline of *W. racemosa*. This should become apparent if permanent plots are re-measured within the next decade. Unlike other forests where ungulate browsers have not been removed, recruitment of common palatable species such as *W. racemosa* is likely to be sufficient to maintain present tree densities in Egmont National Park. If the ongoing effects of brushtail possums were responsible for the decline in *W. racemosa*, and not natural disturbance or stand dynamics, then these results suggest that the effects of brushtail possums may not be reversible in Egmont National Park within a decade. In the absence of a study on forest responses to brushtail possum culling with proper replication using multiple treatment and non-treatment areas over several decades this conclusion will remain speculative. Although *W. racemosa* establishes primarily on elevated micro-sites such as tree fern trunks and fallen trees following the creation of small canopy gaps, continuous vegetative regeneration is also important (Veblen & Stewart 1980, Stewart & Veblen 1982; Allen & Rose 1983). To reliably relate the effects of introduced herbivores on changes in *W. racemosa* density this combination of regeneration mechanisms needs to be considered when selecting measurement protocols. Unfortunately, data used in this and previous studies does not provide reliable information on seedling, sapling or tree mortality for *W. racemosa*, identify substrates which seedlings grew on or differentiate between vegetative and non-vegetative reproduction. Nevertheless, results from this and previous studies on the effects of possums and ungulates (red deer and feral goats) on *W. racemosa* populations allow two general conclusions to be drawn, which have implications for conservation management. Firstly, adult trees of possum palatable species such as *W. racemosa* appear better able to tolerate possum browsing, compared to the low tolerance of seedlings to ungulate browsing (Nugent et al. 1997, 2001). Ungulate densities may need to be nearly zero before regeneration of palatable plants can be assured, but at least some large individuals of possum palatable species such as *W. racemosa* survive for many decades following colonisation of possums (e.g. Nugent et al. 1997; Husheer et al. 2003; Husheer & Frampton 2005). This is because feral goats and other ungulates are able to prevent regeneration of whole cohorts of palatable seedlings and saplings, while possums tend to harvest a proportion of foliage of mature trees such as *W. racemosa*. Secondly, a lack of positive response by *W. racemosa* populations following possum culling in this and other studies

supports the recommendation of Pekelharing & Batcheler (1990) that possums need to be culled in their initial stages of colonisation, before damage occurs to forests. An emerging research conclusion is that the effects of brushtail possums on palatable plants can be halted, but are generally not reversed following culling (e.g. Pekelharing & Batcheler 1990; Smale et al. 1995; Payton et al. 1997; Ulrich & Brady 2005; but see Sweetapple et al. 2002). Simply put, possum culling will not quickly restore communities of dead and dying trees. Therefore, the many possum culling operations undertaken to restore *W. racemosa* forest vegetation in New Zealand may have little or no immediate benefit where ungulates are present in moderate or high densities, or where possums have already killed or induced an irreversible decline in populations of *W. racemosa* and other palatable trees. It is likely that some forest ecosystems benefit from possum culling, while others do not because of increased resilience to browsing of some plant populations in some regions (Sweetapple & Nugent 1999). Habitats with resilient vegetation will only be identified following properly replicated studies of responses to possum culling of key parameters such as soil chemistry, forest composition and structure, foliar biomass, tree mortality, and litterfall and invertebrate biomass.

4.3 RECOMMENDATIONS FOR FUTURE MONITORING

Comparisons of plot location data with a uniform random distribution showed that plots are likely to be representative of Egmont National Park forests. *Posthoc* power analysis also clearly shows that there is a sufficient number of recently re-measured plots ($n = 42$) to detect a doubling in feral goat selected, not selected and avoided seedling densities. A massive and unrealistic number of plots would have been required to clearly show changes in seedling density of species that had only moderate (but variable) changes since 1976. These results show that the Egmont permanent plot system is a very valuable monitoring resource, and is likely to detect compositional shifts occurring in the future. Plots should be maintained and re-measured within a decade to ensure that the value of this resource is not lost. When re-measurement of plots occurs recommendations for data quality improvement of Hurst & Husheer (2004) should be implemented.

There is little point in augmenting the existing system with additional randomly selected plots. Instead, consideration needs to be given to the specific monitoring requirements to answer current and future management questions. There are three main possible strategies for future feral goat culling in Egmont National Park: reduced culling with a tolerance of increased feral goat densities; ongoing feral goat culling maintaining current densities; and eradication of goats in Egmont National Park. This study has shown that holding goat populations to low densities has led to substantial increases in densities of feral goat selected plants as seedlings and saplings, which makes lower levels of culling difficult to justify. A lower-intensity culling strategy involves too high a risk to be recommended. If left unchecked feral goat populations could quickly return to high densities, denuding forest understories of species such as *Coprosma grandifolia* and *W. racemosa*, thereby requiring a large culling effort to reduce feral goat densities again. Therefore a key question for monitoring becomes: will the large expenditure required to completely remove feral goats from Egmont

National Park be justified with a positive response from feral-goat-selected plants? To answer this question recently developed paired exclosure-plot monitoring techniques could be employed (Husheer & Robertson 2005; Deverell 2006). This does not need to be expensive. To detect differences in seedling growth between fenced and unfenced plots may only require tagging of ten seedlings, and ten pairs of small exclosures (c. 10 m²), or it may be that a more innovative and research-based approach to monitoring is justified. For example, White et al. (2003) used a functional response model to predict the relationship between trembling aspen regeneration (*Populus tremuloides*) and elk (*Cervus elaphus*) herbivory. They used information on elk density, habitat use and predation risk in relation to browsing of aspen and aspen density. Such an approach might be used in Egmont National Park to determine the relationship between seedling survival and feral goat density. Data on demographics of feral-goat-selected species (e.g. length of time that *C. grandifolia* is at risk of death from feral goat browsing) and goat habitat-use would be required.

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