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Long-term influences of introduced deer on the composition and structure of New Zealand *Nothofagus* forests

Sean W. Husheer[a,*], David A. Coomes[b], Alastair W. Robertson[a]

[a]*Ecology Group, Institute of Natural Resources, Massey University, Private Bag 11222, Palmerston North, New Zealand*
[b]*Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EA, UK*

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Abstract

New Zealand's *Nothofagus* (southern beech) forests evolved in the absence of mammalian herbivores. The deliberate introduction of deer in the 19th century caused a rapid decline in the abundance of palatable understorey herbs and shrubs, but the longer-term consequences of deer herbivory remain poorly understood. This study uses data from permanent plots established in two separate surveys in northern and southern Kaimanawa Forest Park, central North Island, New Zealand to relate the impacts of two post-irruptive populations of deer to two decades of change in forest composition and canopy species regeneration. Plots were established on randomly located transects in *Nothofagus* forest between 1979 and 1982. Some were re-measured in 1987/1988, and all were re-measured between 1998 and 2000. Our objective was to gain a better understanding of the long-term effects of deer on *Nothofagus* forests. In the northern forests dominated by *Nothofagus fusca*, *N. menziesii* and *Weinmannia racemosa*, there was an expansion in the stem densities (stems $\geq$20 mm diameter at breast height) of highly unpalatable species of small trees. Numbers of unpalatable *Pseudowintera colorata* stems increased on north-facing slopes. The unpalatable *Neomyrtus pedunculatus* and *Leucopogon fasciculatus* increased in number at many sites. Analysis of seedling densities indicated that two palatable species (*W. racemosa* and *Griselinia littoralis*) were failing to recruit into the >75 cm height class. In the southern Kaimanawa forests of *N. solandri* var. *cliffortioides*, understorey composition shifted towards browse-tolerant herbs. This is consistent with deer influencing the competitive interactions of herb and shrub communities, but storm-induced disturbances dominated tree demographics in the southern Kaimanawa, making the effects of deer difficult to ascertain. It is possible, but less likely, that factors other than deer, such as other herbivores and normal successional processes, are responsible for the changes in forest structure and composition that were observed in this study. There is some evidence that deer were affecting gap-phase regeneration of *Nothofagus*, but not strongly enough to prevent recruitment on a large scale. We believe that there is sufficient evidence of deer browsing shifting the composition of Kaimanawa Forest Park *Nothofagus* forests for managers to justify increased deer control.

Keywords: Herbivory; Forest composition; Deer; *Nothofagus*

1. Introduction

Deer were introduced into New Zealand in the 19th century and are now considered a serious threat to conservation of forests administered by the Department of Conservation (Holloway, 1993; Nugent and

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[*] Corresponding author. Present address: Department of Conservation, Private Bag, Turangi, New Zealand.
Fax: +64-7-386-7086.
E-mail address: shusheer@doc.govt.nz (S.W. Husheer).

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Fraser, 1993). It was soon noticed that deer were reducing the density of understorey vegetation in some forests and altering composition by preferentially browsing certain species (Walsh, 1892; Cockayne, 1926; Caughley, 1983). New Zealand forests evolved with avian and invertebrate herbivores, in the absence of mammalian herbivores until approximately 150 years ago (Greenwood and Atkinson, 1977). Invertebrate and avian herbivores have different feeding characteristics than mammalian herbivores, particularly ruminants, so introduced deer imposed a novel selective pressure. Avian herbivores have no teeth, simple stomachs, and probably quite different feeding behaviour that exerts unique selective pressures on plants (Cooper et al., 1993). Many of these avian herbivores became extinct several hundred years ago, soon after the arrival of Polynesians to New Zealand (Fleming, 1969). Since this time, vertebrate herbivory would have been relatively unimportant until the introduction into New Zealand of the brushtail possum (*Trichosurus vulpecula*) in 1837 and deer in 1861 (Logan and Harris, 1967).

The short-term effects of deer invasion are well documented, but the ongoing effects on forest dynamics in the post-irruptive phase of colonisation are still poorly understood (Rogers and Leathwick, 1997; Lee, 1998; Forsyth et al., 2001; Nugent et al., 2001). To understand ongoing impacts of deer, it is important to know if forests have been shifted into an alternative state by deer browsing, from which further directional change is unlikely to occur, or whether deer browsing may continue to induce further shifts in vegetation composition. There are three main reasons for the ongoing lack of understanding about long-term changes: firstly, deer only browse on the lowest 2 m tier of forests so their impact on overstorey composition may take decades to become apparent in the structurally dominant trees; secondly, it is difficult to partition deer browsing from the effects of other agents of change such as spatially complex disturbance events and other herbivores (Coomes et al., in press); thirdly, reduction in seedling densities may not result in reduced adult density if browsing simply replaces some of the mortality that would have occurred anyway by the process of self-thinning (Westoby, 1984). Many studies have investigated the influences of deer in temperate forests of the northern hemisphere, where ungulate herbivores have been present for hundreds of thousands of years (e.g. Gill, 1992; Gonzalez-Hernandez and Silva-Pando, 1996; Hobbs, 1996; Reimoser and Gossow, 1996; Motta, 1996; Duncan et al., 1998). Most forest stands in the northern hemisphere regenerated in the presence of deer, so the influence of deer herbivory on forest composition can be difficult to ascertain. In contrast, New Zealand's *Nothofagus* (southern beech) forests provide an opportunity to understand the influence of mammalian herbivory on temperate forest composition because invasion was so recent that directional responses of forests to introduced deer might still be occurring (Veblen and Stewart, 1982). Because of the long-time scale over which deer impacts act, long-term monitoring of forest structure and composition provides an important method of observing the impacts of invasive organisms (Wiser et al., 1998), and forms the basis of this study.

This study examines the influence of introduced deer on long-term shifts in under- and overstorey composition in *Nothofagus fusca*, *N. menziesii* and *N. solandri* var. *cliffortioides* forest vegetation in the Kaimanawa Ecological District, central North Island, New Zealand (Fig. 1). Red deer (*Cervus elaphus*) reached a high population density throughout Kaimanawa Forest Park by 1930 after dispersing from liberations in 1896 at nearby Tongariro to the west, and in 1883 at Matapiro to the south-east (Elder, 1962). Similar patterns were observed following deer introductions in other parts of New Zealand, where deer numbers typically reached irruptive peaks within two to three decades of establishment (Challies, 1985). Sika deer (*Cervus nippon*) were liberated in Kaimanawa Forest Park in 1905 (Davidson, 1973), but colonised the study area much more slowly (Elder, 1962). They only colonised northern Kaimanawa Forest Park in the 1950s (Davidson, 1973) and southern Kaimanawa Forest Park during the 1980s. Sika deer are thought to have the ability to browse more intensively than red deer because of a different digestive morphology (Fraser, 1996). In Japan, sika deer eat unpalatable plants and litterfall when preferred food sources are not available (Hiroshi and Koichi, 2001). Reproductive rates of both deer species were initially high until carrying capacity was exceeded and deer numbers crashed, or were reduced through intensive commercial and government-funded hunting (Caughley, 1983). Recreational-, and ground- and aerial-based

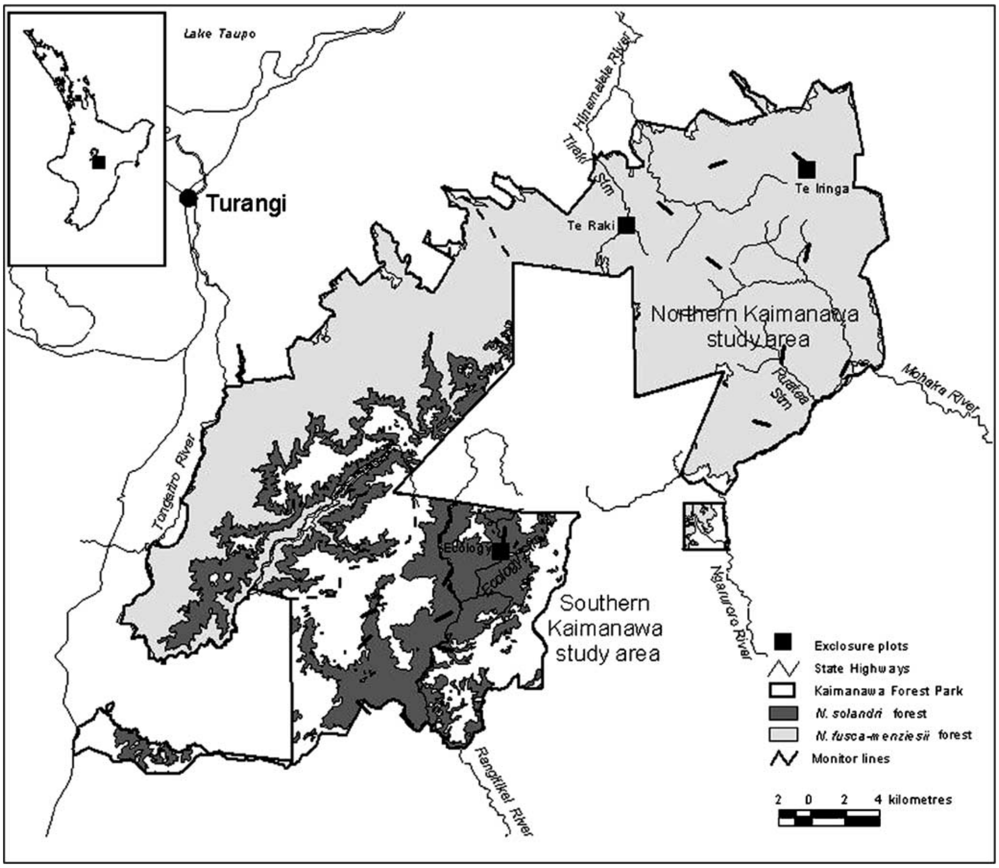

Fig. 1. Northern and southern Kaimanawa Forest Park study areas showing exclosure plots and random permanent plot monitoring lines.

commercial hunting is the most commonly used management technique chosen to control deer in New Zealand (Parkes et al., 1997). During the period of this study, deer management in Kaimanawa Forest Park was restricted to recreational hunting.

Common New Zealand tree species have been classified by a number of authors for their palatability to deer, using a variety of methods including observed signs of browse, changes in abundance following deer colonisation and studies of deer diet (McKelvey, 1959; Wallis and James, 1972; Jane and Pracy, 1974; Veblen and Stewart, 1980, 1982; Allen et al., 1984; Wardle, 1984; Stewart and Harrison, 1987; Stewart et al., 1987; Nugent and Challies, 1988; Stewart and Burrows, 1989; Nugent et al., 1997; Fraser and Speedy, 1997). A general consensus has now been reached on most species. We reviewed these studies and arbitrarily classified each species into unpalatable, moderately palatable, palatable and highly palatable classes, and this has been used in this study to determine an overall classification, based on subjectively assessed common agreement (Table 1). We hypothesised that under the presence of intense deer browsing, seedlings and saplings of palatable species such as *Coprosma tenuifolia*, *Weinmannia racemosa* and *Griselinia littoralis* are generally expected to decline in abundance, followed in turn by moderately palatable species such as *Nothofagus* spp. (Nugent et al., 1997).

We also hypothesised that unpalatable woody species such as *Leucopogon fasciculatus*, *Neomyrtus pedunculatus*, *Phyllocladus alpinus* and *Pseudowintera colorata* would increase significantly in abundance due to competitive release, along with unpalatable ferns, and browse-tolerant grasses and herbs with prostrate growth.

Table 1
Results of a literature search on common species found in northern and southern Kaimanawa Forest Park[a]

Species	Source[b]													
	1	2	3	4	5	6	7	8	9	10	11	12	13	This study
Carpodetus serratus					P	MP			HP	HP	HP	P	HP	HP
Coprosma linariifolia													MP	MP
Coprosma microcarpa	P			P									MP	P
Coprosma pseudocuneata							MP						UP	MP
Coprosma "taylorae"	P			P			MP					UP	MP	MP
Coprosma tenuifolia	P			P		HP								P
Griselinia littoralis					P		HP	P	HP	HP	HP	P	HP	HP
Leucopogon fasciculatus			UP			UP							UP	UP
Neomyrtus pedunculatus	UP						UP		UP	UP		UP	UP	UP
Nothofagus fusca		MP					MP						MP	MP
N. menziesii		MP					MP		MP				MP	MP
Nothofagus solandri							MP					MP	MP	MP
Phyllocladus alpinus							UP							UP
Pseudowintera colorata	UP					UP	UP	UP	UP	UP		UP	UP	UP
Weinmannia racemosa	P	HP			P	P	P		MP	HP	MP	P	HP	P

[a] Species were subjectively rated as highly palatable (HP), palatable (P), moderately palatable (MP) and unpalatable (UP). For this study, a consensus of these ratings was used to assign a palatability score to each species based on the most common ratings of previous studies.

[b] Sources: 1, McKelvey (1959); 2, Wallis and James (1972); 3, Jane and Pracy (1974); 4, Veblen and Stewart (1980); 5, Veblen and Stewart (1982); 6, Allen et al. (1984); 7, Wardle (1984); 8, Stewart and Harrison (1987); 9, Stewart et al. (1987); 10, Nugent and Challies (1988); 11, Stewart and Burrows (1989); 12, Nugent et al. (1997); 13, Fraser and Speedy (1997).

2. Methods

2.1. Study site description

Kaimanawa Forest Park is located within the Kaimanawa Mountains, which form the bulk of the Kaimanawa Ecological District, and are made up of a series of ranges running north-east to south-west in the central North Island of New Zealand (39° south, 176° east). Altitudes vary from a low point of 560 m in the north to the high point of 1727 m in the south. Geology in the northern and southern study areas is predominantly Jurassic folded greywacke with a schist belt in the north. Terraces and flats are common in valley bottoms. Soils are derived from a combination of the greywacke bedrock or volcanic ash and ignimbrite flows from Taupo eruptions over the last millennia.

Forests in Kaimanawa Forest Park are dominated by the genus *Nothofagus*: silver (*N. menziesii*), red (*N. fusca*), and mountain (*N. solandri* var. *cliffortioides*) beech. All three species have relatively fast seedling growth in high light conditions and are important colonists after disturbance (Wardle, 1970a). At some sites in Kaimanawa Forest Park, beech forests have been replaced by *Chionochloa*- and *Poa*-dominated grasslands with *Leptospermum scoparium*, probably due to repeated Polynesian fires (McGlone, 1989). *Nothofagus* is able to grow on drier and more exposed sites than many New Zealand trees but seedlings compete relatively poorly with more shade-tolerant species (Wardle, 1970b). Consequently, at higher altitude and drier sites, *Nothofagus* dominates. At lower altitudes the genus gives way to more competitive hardwoods such as *W. racemosa*. In areas of low fertility, poor drainage, low moisture or areas of recent forest disturbance, *Nothofagus* may dominate (Wardle, 1991).

The northern study site is co-dominated by *N. fusca* and *N. menziesii* with *N. solandri* at higher altitudes. *N. menziesii* is the main species from about 1100 m altitude to the crests of the ridges, while *N. fusca* dominates below 1100 m, with *N. menziesii* often forming a sub-canopy. At lower levels, *Carpodetus serratus*, *G. littoralis* and *Raukaua simplex* form an open sub-canopy with occasional *Podocarpus hallii* and sometimes *W. racemosa*. The shrub layer is dominated by *Myrsine divaricata*, *Neomyrtus pedunculata*, *P. colorata* and *Coprosma microcarpa*, *Coprosma* "taylorae", *C. tenuifolia*, and *C. foetidissima*.

In the southern Kaimanawa study area, *N. solandri* is the dominant tree species over large areas, especially between 1100 m and the upper timberline, which varies between 1375 and 1430 m. The understorey has few woody species and these include *C.* "taylorae" and *Gaultheria antipoda*. *Coprosma linariifolia* and *C. microcarpa* are also important below 1100 m, but are replaced by *C. pseudocuneata*, *P. alpinus* and *P. hallii* higher up. The southern area has high relief (valley bottoms 800–1000 m; ridgetops 1500–1700 m) and is steep (mean plot slope 34°). Mean plot altitude is 1117 m in the south and 843 m in the north and is less steep (18°). Nomenclature follows Parsons et al. (1995) and Edgar and Connor (2000). *C.* "taylorae" is referred to in Eagle (1986).

2.2. Permanent plot establishment and re-measurement

Detailed data were collected for overstorey, understorey and environmental variables from 57 20 m × 20 m permanent plots in northern Kaimanawa Forest Park, that were established between January 1979 and January 1980. The methods used to establish these plots follow a protocol used to establish over 5000 permanent plots in New Zealand (Allen, 1993). Forty of the more eastern plots were re-measured between November 1987 and January 1988. All 57 were re-measured once again between July and December 1998. In the southern Kaimanawa, 35 permanent plots were established between November 1981 and January 1982 and were re-measured between November 1999 and March 2000, using the same protocols used in the northern survey. Plots were systematically located (at 200 m intervals from line origins except for the first plot which was 40 m from origin) on randomly located transect lines that ran from streams or valley floors to the nearest ridgetop (Fig. 1). There were eleven transects in the northern study area and eight in the south.

2.3. Paired exclosure plot establishment and re-measurement

Three pairs of 20 m × 20 m plots (one of the pair fenced to exclude deer) were established at two sites in the north and one in the south (Fig. 1). The Te Raki Stream paired exclosure (altitude 760 m, aspect 300°, and slope 5°) was in mixed *N. fusca* and *N. menziesii* forest. It was established in May 1985, and re-measured in March 1993 and August 1998. Most trees at Te Raki are *N. menziesii* with some *N. fusca*, *W. racemosa*, *N. pedunculatus* and *P. colorata* stems. The Te Iringa exclosure (established in April 1983 and re-measured in February 1991 and August 1996; altitude 1000 m, aspect 70°, slope 20°) is in *N. menziesii* forest with some *G. littoralis*, *R. simplex*, *P. colorata* and *M. divaricata* stems in the sub-canopy. The Ecology Stream exclosure (established in October 1983 and re-measured in June 1991, March 1996, and January 2000; altitude 1020 m, aspect 300°, slope 20°) had an overstorey almost completely dominated by *N. solandri* (>98% of basal area) with 13 stems of *P. alpinus*, *G. littoralis*, and *M. divaricata* found in the two plots at this site.

2.4. Plot measurement procedure

Identical methods were used for all measurements of permanent and paired exclosure plots following Allen (1992, 1993). In each 20 m × 20 m plot, the species of all trees over 20 mm diameter at breast height (DBH = 1.35 m) were identified, tags were nailed into stems and the diameter over bark at breast height measured. Epiphytes over 20 mm DBH, rooted below breast height, were measured and recorded. In the original southern Kaimanawa survey, all dead trees were included in the measurement, but in other surveys only live trees were measured. All saplings (<20 mm DBH, >135 cm high) were counted and species identified. Circular understorey subplots ($n = 24$; 49 cm radius) were systematically located according to Allen (1993) within each plot. All woody seedlings >15 cm high were identified by species and counted in four height classes (15–45, 46–75, 76–105, 106–135 cm) in each of the sub-plots. The presence of small seedlings (<15 cm high) in sub-plots was also recorded and their species identified. Herbaceous plants were only identified in the <15 cm height tier. Altitude was estimated to the nearest 5 m using map references; slope was estimated with a Suunto inclinometer to the nearest 5° and aspect to the nearest 5° using a compass. For analysis, aspect was converted to degrees from true north. Plots were not established at two sites in the southern study area where plot slope was >60°.

2.5. Data analysis

Upon re-measurement in 1998, errors and omissions were found for 1979/1980 and 1987/1988 understorey and tree tag data from the northern Kaimanawa. No herbarium specimens were collected so corrections could not be made to understorey species identifications. Consequently, only data from easily recognised species in the understorey in these two surveys are reported here (*N. menziesii*, *N. fusca*, *W. racemosa* and *G. littoralis*). Secondly, calculation of recruitment and mortality was limited to the southern Kaimanawa where the fates of individual trees were followed more reliably than in the north.

Basal area is a good descriptor of canopy structure because it serves as an indicator of site occupancy with a clear link to regeneration in *Nothofagus* forests (Wardle, 1970b). Basal areas and density of stems per hectare were calculated in SYSTAT (SPSS, 2000) before statistical analysis was undertaken. Recruitment and mortality rates for southern Kaimanawa *N. solandri* were calculated according to McCune and Cottam (1985) using PC-Diam (Hall, 1994).

$$\text{Recruitment} = (1 + B_x)^{1/x} - 1, \qquad (1)$$

where B_x is the proportion of new stems for period x.

$$\text{Mortality} = 1 - (1 - Q_x)^{1/x}, \qquad (2)$$

where Q_x is the proportion of dead stems for period x.

An audit re-measurement of four randomly selected plots from the 35 plots in the southern Kaimanawa that were re-measured in 1999/2000 showed that field standards for overstorey re-measurement and understorey species identification were high. Audits of mean diameter measurements were within 4% of survey measurements and there was 96% agreement of species identifications. Counts of seedlings and saplings were more variable (43.6% more seedlings and 10.9% more saplings in the audit than in the original measurement). We assumed that error was not biased and thus was included as random error in statistical tests. Where possible, statistical tests on understorey data used frequency presence data and not seedling counts.

Statistical comparisons of univariate data were made with student *t*-tests (e.g. change in stem density over time) or step-wise regressions (e.g. relationship between stem density and environmental variables). Multivariate comparisons were made using general linear models in SYSTAT 10 (SPSS, 2000) and with canonical correspondence analysis (CCA) in CANOCO 4.0 (Ter Braak and Smilauer, 1998). An automatic forward selection procedure was used in CCA to test for the effect of time between surveys, altitude, aspect and slope on overstorey species composition of stand dominants (>100 mm DBH) in northern and southern Kaimanawa and vascular understorey composition in southern Kaimanawa. Because randomly located permanent plots were repeatedly measured and we expected large spatial variation because of variability in deer impacts and normal successional processes, plots were treated as blocks to reduce unexplained variation in analysis. Abundance values (stems/ha) were used for overstorey analysis and in the understorey importance values were calculated from the relative occurrence of vascular plants (<135 cm high) in 24 sub-plots in each plot. The presence of uncommon species can have a large influence on CCA results so these were down-weighted in analysis using an option in CANOCO.

3. Results

3.1. Changes in stand basal area and tree abundance in northern Kaimanawa

In the northern Kaimanawa *N. fusca* and *N. menziesii* forests, there was no significant difference in plot basal area between 1979/1980 (63.3 m^2/ha) and 1998 (63.7 m^2/ha; *paired* $t = 0.160$, d.f. $= 56$, $P = 0.874$). Total tree stem density ($\geq$20 mm DBH) for all northern Kaimanawa plots increased from 1347.8 stems/ha in 1979/1980 to 2340.4 stems/ha in 1998 (*paired* $t = 5.965$, d.f. $= 56$, $P < 0.001$). A series of paired *t*-tests showed that this overall increase in abundance was mainly due to increases in unpalatable and browse-resistant small trees (20–100 mm DBH), but these only had a small effect on stand basal area. No correction was made for multiple comparison of species so interpretation of these results needs to be made with caution for species with marginally significant differences in abundance between years. The palatable *C. serratus* and the unpalatable *L. fasciculatus*, *N. pedunculatus*, and *P. colorata* increased significantly in abundance in the 20–100 mm DBH size class; in the same size class the highly palatable *C. tenuifolia* and *W. racemosa* decreased significantly in abundance (Table 2). Although there was no significant change of the highly palatable *G. littoralis* in this size class, this species decreased in abundance in the >100 mm size class between 1979/1980 (23.7 stems/ha) and 1998 (15.4 stems/ha; *paired* $t = 2.595$, d.f. $= 56$, $P = 0.012$), while *C. serratus* increased in abundance between 1979/1980 (39.5 stems/ha) and 1998 (66.5 stems/ha; *paired* $t = 3.153$, d.f. $= 56$, $P = 0.003$). Increases in the abundance of *P. colorata*, *N. pedunculatus* and *L. fasciculatus* were influenced by recruitment into plots, where they were not found in the initial measurement as well as by increases in density in plots where they were initially found. Decreases in *C. tenuifolia*, *W. racemosa* and *C. serratus* were influenced by these species disappearing from some plots. Paired *t*-tests showed no significant difference in abundance of other overstorey species at the 95% level of confidence in the 20–100 mm or the >100 mm size classes. Of the species that had densities >100 stems/ha, *N. menziesii*, *N. fusca*, *C.* "taylorae" and *C. pseudocuneata* are the only species without significant changes in abundance.

Multiple regression, using a forward stepwise procedure, showed that changes in the abundance of unpalatable *P. colorata* was significantly related to aspect (Fig. 2, d.f. $= 2, 44$; $r^2 = 0.336$, $P = 0.014$), while changes in density of unpalatable *N. pedunculatus* (d.f. $= 1, 33$; $F = 4.9$, $P = 0.035$) was positively related to altitude. Changes in the abundance of the palatable *W. racemosa* were negatively related to altitude (d.f. $= 7, 1$, $F = 6.8$, $P = 0.048$). CCA showed no significant shifts in species composition using data from all size classes (trees >20 mm DBH) with time ($P = 0.055$) or aspect ($P = 0.635$), but there were significant effects of altitude ($P = 0.005$) and slope ($P = 0.005$). *G. littoralis*, *N. pedunculatus*, *P. colorata* and *W. racemosa* had highly significant changes in abundance detected in univariate analysis and were also most strongly influenced by environmental variables and time in CCA. These three species had >15% of their CCA scores explained by time and

Table 2
Mean density of stems (stems/ha) in the 20–100 mm diameter size class from 57 plots in northern Kaimanawa recorded in 1979/1980 (initial) and 1998 (final) surveys, and from 35 plots in southern Kaimanawa 1981/1982 (initial) and 1999/2000 (final) surveys[a]

Species	Palatability	Initial tree density	*N* initial	Final tree density	*N* final	*T*-value	*P*-value
Northern Kaimanawa							
C. serratus	Highly palatable	28.5 ± 8.0	24	46.1 ± 12.0	27	2.196	0.032
C. tenuifolia	Palatable	6.6 ± 3.4	7	2.6 ± 1.8	3	2.260	0.028
W. racemosa	Palatable	75.4 ± 23.1	19	48.2 ± 16.4	12	3.360	0.001
N. menziesii	Moderately palatable	148.2 ± 44.8	41	296.5 ± 93.3	45	1.636	0.108
N. fusca	Moderately palatable	44.3 ± 19.5	21	58.8 ± 16.1	21	0.744	0.460
P. colorata	Unpalatable	511.0 ± 120.3	41	1088.6 ± 201.8	46	5.424	<0.001
N. pedunculatus	Unpalatable	97.4 ± 21.4	30	335.1 ± 65.5	32	4.558	<0.001
L. fasciculatus	Unpalatable	3.1 ± 1.9	3	12.7 ± 4.8	11	2.543	0.014
All other species		94.3 ± 19.1	57	81.1 ± 13.9	57	0.787	0.435
Southern Kaimanawa							
G. littoralis	Highly palatable	70.7 ± 27.7	13	45.0 ± 16.8	13	2.038	0.049
C. microcarpa	Palatable	21.4 ± 8.9	12	49.3 ± 17.7	12	2.039	0.049
N. solandri	Moderately palatable	925.0 ± 169.7	35	1465.0 ± 285.1	34	2.384	0.023
C. pseudocuneata	Moderately palatable	249.3 ± 75.1	19	267.1 ± 84.0	19	0.302	0.764
C. linariifolia	Moderately palatable	67.1 ± 27.9	11	127.9 ± 46.4	11	2.161	0.038
C. "taylorae"	Moderately palatable	372.9 ± 110.9	28	327.9 ± 90.3	25	0.988	0.330
P. alpinus	Unpalatable	146.4 ± 41.5	25	208.6 ± 56.4	25	2.650	0.012
All other species		298.6 ± 67.5	35	255.7 ± 44.3	35	0.964	0.342

[a] For each species the palatability rating and number of plots where it occurred in respective surveys (*N*) are given. Changes in density are tested with paired *t*-tests. Data are displayed by palatability rating for species with significant changes (*P*-value <0.05) or species that had stem densities in the initial or final survey of >100 stems/ha.

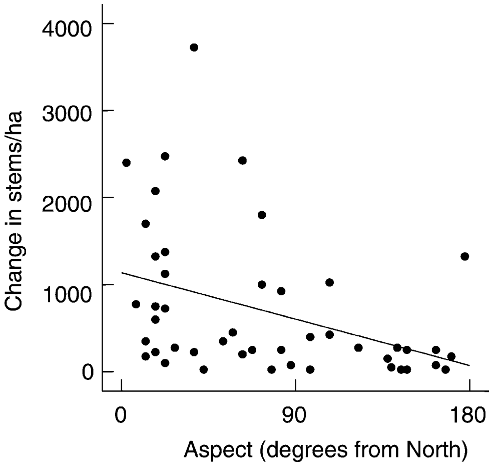

Fig. 2. The relationship between the change in tree stem density of *P. colorata* and plot aspect from 47 plots in northern Kaimanawa, where the species was present as a tree in the 1979/1980 or 1998 surveys. The line of best fit, calculated in linear regression, is change = 1135.977 − 5.924 × aspect ($r^2 = 0.007$, $P = 0.007$).

environmental variables, whereas all other species had <15% of variation explained. Although *C. serratus*, *C. tenuifolia* and *L. fasciculatus* had moderately significant changes in abundance detected by univariate tests, they had <15% of variation explained by time and environmental variables.

3.2. Changes in stand basal area and tree abundance in southern Kaimanawa

In the southern Kaimanawa, overstorey dead trees contributed considerably to basal area in 1981/1982 (5.9 m^2/ha of a total of 31.7 m^2/ha for live and dead stems combined). There was a significant increase in the mean overall basal area (all tree species) between the 1981/1982 and 1999/2000 surveys from 25.8 to 29.2 m^2/ha (*paired* $t = 3.593$, d.f. $= 34$, $P = 0.001$). Most of this increase was due to increases in the basal area of *N. solandri* (Table 3). *C. linariifolia*, *C. microcarpa* and *G. littoralis* also increased in basal area between 1981/1982 and 1999/2000, but contributed little to total increases. The abundance of *C. linariifolia*, *C. microcarpa*, *N. solandri* and *P. alpinus* trees (20–100 mm DBH size class) increased significantly between surveys, whereas *G. littoralis* tree abundance decreased significantly in this size class (Table 2). Changes in the abundance of *C. linariifolia*, *C. microcarpa* and *P. alpinus* were in part due to increases in the number of plots these species were found in (2, 4 and 5 additional plots for each species, respectively). These statistical tests need to be treated with caution because their *P*-values were all moderately significant and were not corrected for multiple comparisons. No other significant changes in abundance were detected in the southern Kaimanawa overstorey in the 20–100 mm or the >100 mm size classes between surveys. *N. solandri* showed considerable recruitment into the smaller size classes (<220 mm = 1.9% recruitment), particularly the smallest size class (<70 mm = 2.5% recruitment; Table 4). In comparison, annual mortality rates were nearly half that of recruitment at 1% overall, and remained between 0.7 and 3.0% through all age classes.

A stepwise multiple regression showed no significant relationship between *N. solandri* stem density and *N. solandri* mortality at the 400 m^2 plot scale (d.f. $= 1, 27$; $F = 2.867$, $P = 0.122$). The same multiple regression showed that *N. solandri* mortality decreased with plot altitude ($F = 24.381$, $P = 0.004$; Fig. 3) and plot basal area ($F = 9.344$, $P < 0.001$).

CCA showed no significant shifts in tree species composition in the overstorey with time ($P = 0.170$)

Table 3
Basal area (m^2/ha ± S.E.M.) of tree species which exhibited significant changes over time (*P*-value <0.05) in 35 plots in southern Kaimanawa[a]

Species	Tree basal area (m^2/ha) 1981/1982	Tree basal area (m^2/ha) 1999/2000	*T*-value	*P*-value
N. solandri	22.45 ± 1.99	25.60 ± 2.07	2.926	0.006
G. littoralis	1.46 ± 0.43	1.82 ± 0.50	2.140	0.040
C. microcarpa	0.01 ± 0.005	0.034 ± 011	2.781	0.009
All other species	0.706 ± 0.218	0.375 ± 0.065	1.711	0.096

[a] Statistics from paired *t*-tests are displayed.

Table 4
N. solandri tree recruitment and mortality between 1981/1982 and 1999/2000 surveys by DBH size classes in 35 plots, southern Kaimanawa

Class (mm)	New/ha ± S.E.M.	%New	%New per annum	Dead/ha ± S.E.M.	%Mortality	%Mortality per annum
20–69	889.3 ± 196.3	55.0	2.5	197.1 ± 33.0	12.2	0.7
70–119	77.1 ± 25.4	21.2	1.1	122.1 ± 44.0	33.6	2.3
120–169	7.1 ± 4.0	4.5	0.2	36.4 ± 11.6	23.1	1.5
170–219	2.1 ± 1.2	2.2	0.1	15.0 ± 4.2	15.3	0.9
220–269				7.9 ± 2.2	15.9	1.0
270–319				5.7 ± 2.1	15.4	0.9
320–369				9.3 ± 2.5	37.1	2.6
370–419				5.0 ± 1.7	23.3	1.5
420–469				3.6 ± 1.5	29.4	1.9
470–519				3.6 ± 1.8	41.7	3.0
>520				1.4 ± 1.0	33.3	2.2
Total	975.7 ± 211.3	40.8	1.9	407.1 ± 73.4	17.0	1.0

or any significant effects of altitude ($P = 0.430$), aspect ($P = 0.655$) or slope ($P = 0.115$).

3.3. Changes in seedling abundance

Visual inspection of the height-class distributions in northern Kaimanawa of palatable *W. racemosa* and highly palatable *G. littoralis* showed distinct gaps in the regeneration of taller seedlings (>45 cm high), whereas the moderately palatable *N. fusca* and *N. menziesii* showed no distinct gaps (Fig. 4). Seedling abundance of *N. fusca* increased by approximately 15 times and *N. menziesii* by three times in the northern Kaimanawa study area (Table 5). These increases in seedling density were not related to changes in plot basal area (classified as low, ≤ 25 m^2/ha; medium, 25–50 m^2/ha; or high, ≥ 50 m^2/ha), plot aspect (closer to true north or south) or altitude (classified into low, ≤ 900 m; or high, >900 m). Changes in the abundance of *N. fusca* were significantly related to plot aspect (Table 5; Wilks' lambda = 0.847, $F = 3.348$; d.f. = 2, 37; $P = 0.048$), but no other exploratory tests of the effect of altitude or basal area produced significant results.

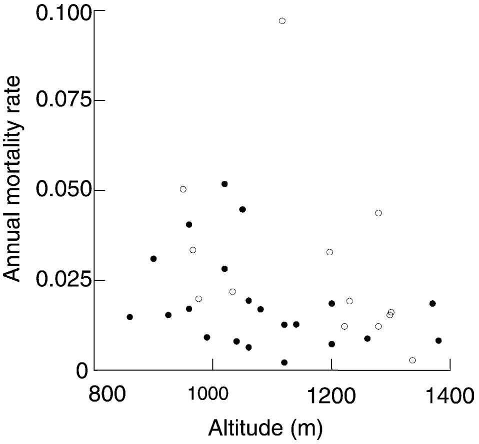

Fig. 3. The relationship between *N. solandri* mortality rate (proportion of tree deaths/annum) and altitude (m) in 35 20 m × 20 m low ((○) <25 m^2/ha) and high basal area ((●) ≥25 m^2/ha) plots from southern Kaimanawa.

There was no overall change in *N. solandri* seedling abundance in the southern Kaimanawa between 1981/1982 (8603 seedlings/ha) and 1999/2000 surveys (6634 seedlings/ha; *paired* $t = 1.202$, d.f. = 34, $P = 0.238$). This overall pattern of a decline of 2500 seedlings/ha masked considerable variation among plots as is shown by the high standard deviation of 9900 seedlings/ha. Seedling density tended to increase in plots at high altitude and decrease in plots at lower altitude (Fig. 5).

3.4. Exclosure plots

Little difference in seedling (15–135 cm high) abundance was apparent between three paired fenced and unfenced plots in the first 10 years after establishment in 1983 and 1985 (Fig. 6). By the 1996/1998 remeasurements, fenced plots had greater densities of

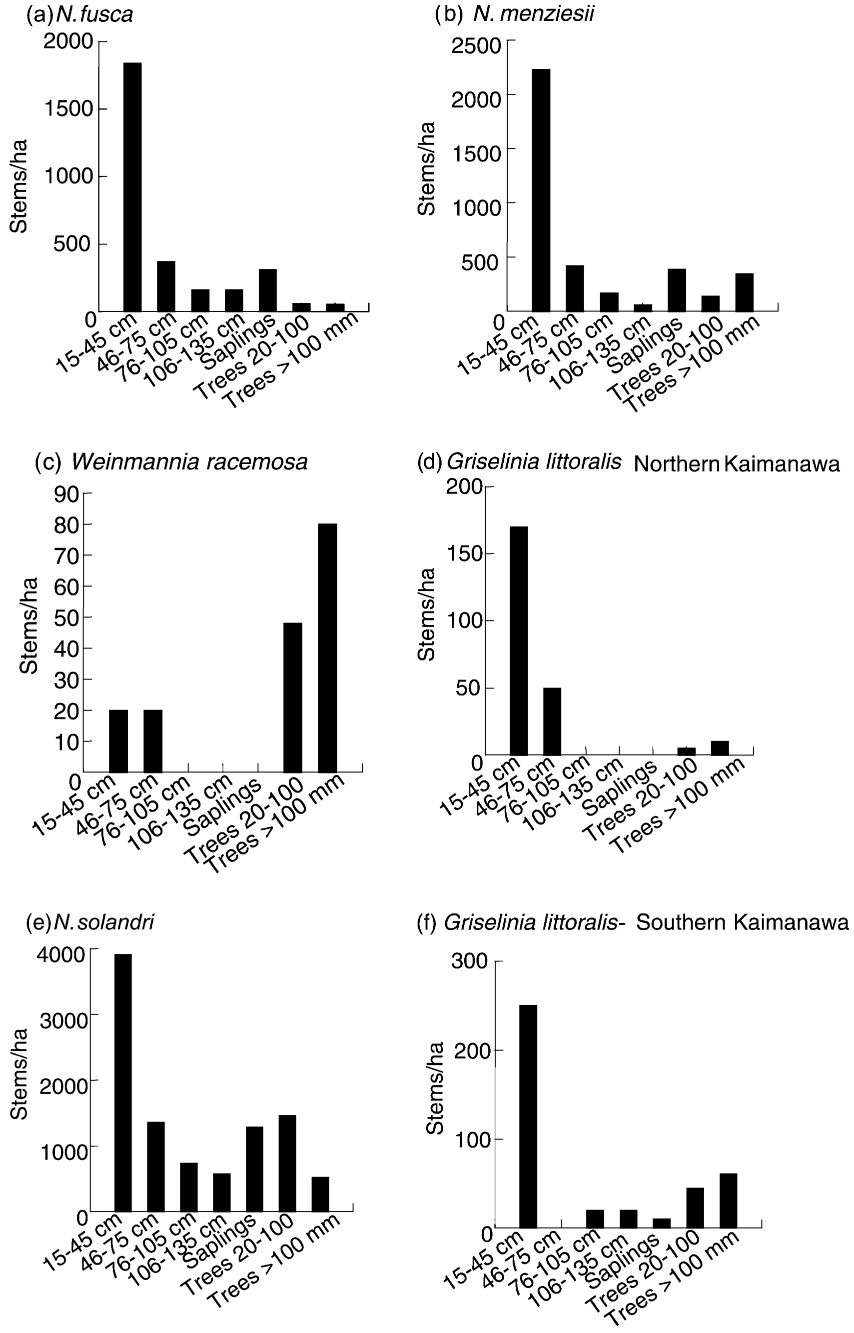

Fig. 4. Mean numbers of seedlings (height classes of 15–45, 46–75, 76–105, 106–135 cm), saplings (>135 cm high and less than 20 mm DBH), small trees (20–100 mm DBH) and large trees (>100 mm DBH) of: (a) *N. fusca*, (b) *N. menziesii*, (c) *W. racemosa*, (d) *G. littoralis* in northern Kaimanawa, 1998, and (e) *N. solandri* and (f) *G. littoralis* in southern Kaimanawa, 1999/2000.

Table 5

Mean (±S.E.M.) numbers/ha of *N. fusca* and *N. menziesii* seedlings (stems within 15–135 cm height class) in 1979/1980, 1987/1988 and 1998 surveys from 40 plots in northern Kaimanawa, tested using repeated measures ANOVA[a]

Species	1979/1980	1987/1988	1998	Wilks' Lamda	d.f.	*F*-value	*P*-value
N. menziesii	14 ± 14	1764 ± 555	3000 ± 675	0.663	2, 38	9.643	<0.001
N. fusca	83 ± 51	2111 ± 733	2181 ± 517	0.667	2, 38	9.476	<0.001
N. fusca (north aspect)	0	3301 ± 1605	1275 ± 461				
N. fusca (south aspect)	145 ± 87	1232 ± 4432	2850 ± 812				

[a] Means for density of *N. fusca* seedlings for north (17 plots) and south (23 plots) aspects are also presented.

Nothofagus seedlings, while there was little or no change in adjacent unfenced plots. By 1996 at Te Raki, *N. fusca* seedling abundance in the fenced plot had increased moderately to >1000 seedlings/ha and *N. menziesii* increased to >1500 seedlings/ha. By 1998 in the Te Iringa fenced plot *N. menziesii* densities had increased to >10,000 seedlings/ha, while density of *N. solandri* had increased to >40,000 seedlings/ha in the Ecology Stream fenced plot by 1998.

Some of the changes in seedling numbers could have arisen from the chance creation of canopy gaps in fenced plots, but not in neighbouring unfenced plots. Plot basal area in the Ecology Stream exclosure declined from 73.5 m^2/ha in 1983 to 41.9 m^2/ha in 2000, whereas the paired unfenced plot increased from 48.9 to 51.9 m^2/ha. At Te Iringa, basal area increased in both the exclosure (93.6–99.5 m^2/ha) and unfenced (69.2–74.1 m^2/ha) plots between 1983 and 2000. At Te Raki Stream, basal area in the exclosure plot declined substantially from 101.1 m^2/ha in 1985 to 58.1 m^2/ha in 1998 after one large *N. fusca* tree died (basal area 40.5 m^2/ha) between plot establishment and the first re-measurement in 1993. There was an increase in basal area in the unfenced plot from 72.3 m^2/ha in 1985 to 78.8 m^2/ha in 1998.

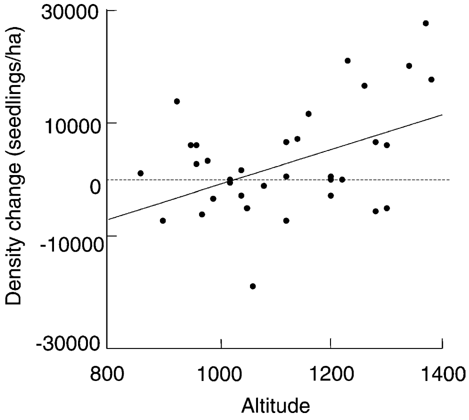

Fig. 5. The relationship between changes in *N. solandri* seedling (15–135 cm high) abundance between 1981/1982 and 1999/2000 and plot altitude in 35 plots in southern Kaimanawa. A line of best fit from linear regression is: change in seedling density = 32.7 × altitude − 34559.7; $r^2 = 0.189$, $P = 0.009$.

3.5. Analysis of understorey community composition in the southern Kaimanawa

CCA (Table 6, Fig. 7) showed significant changes in understorey species composition, shifting away from woody species towards herbaceous species and ferns

Table 6

CCA on vascular understorey species composition from 35 permanent plots established in 1981/1982 and re-measured in 1999/2000 in southern Kaimanawa[a]

Variable	Lambda marginal	Lambda conditional	*F*-value	*P*-value
Year	0.07	0.07	2.64	0.005
Slope	0.04	0.04	1.69	0.030
Year–aspect–altitude	0.04	0.04	1.24	0.655
Aspect	0.03	0.02	1.00	0.465
Year–aspect	0.02	0.03	1.21	0.155
Altitude	0.02	0.03	0.80	0.525
Year–altitude	0.02	0.03	1.48	0.035
Year–slope	0.02	0.02	0.74	0.775

[a] Importance values for each plot were calculated using frequency occurrence in 24 sub-plots. Factors of time, altitude aspect and slope (and their interactions) are displayed in order of their inclusion in the forward selection procedure. The variance each factor explains (lambda marginal), the additional variance explained at the time each factor was included (lambda conditional) and the significance of the variable at that time (*P*-value) are shown. Eigenvalue analysis showed that the first four axes explained 36.6, 34.4, 18.3 and 10.7%, respectively.

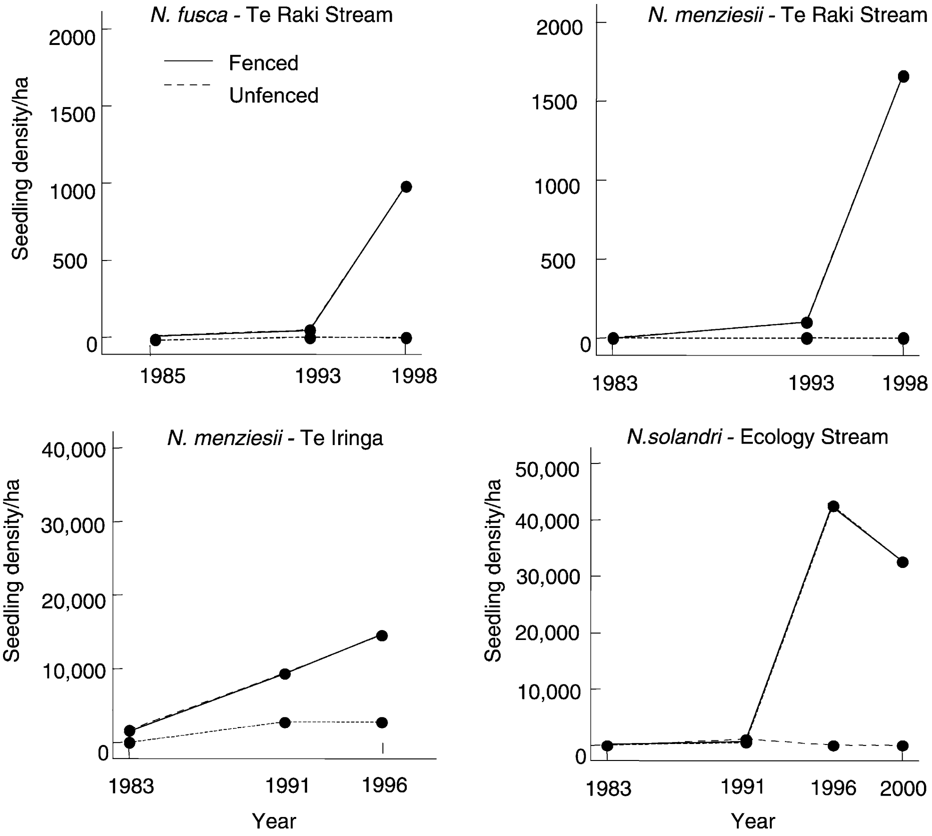

Fig. 6. *Nothofagus* seedling (15–135 cm high) abundance in three paired exclosure plots, Kaimanawa Forest Park.

(many of which can form prostrate ‘mats’). The shrubs and small tree species that became less common included *Coprosma* spp., *Cyathodes fraseri*, *Cyathodes juniperina*, *Dracophyllum recurvum*, *Fuchsia excorticata*, *G. antipoda*, *L. scoparium*, *N. pedunculatus*, *Olearia furfuracea* and *Olearia nummularifolia*, and the other species in decline included the fern *Sticherus cunninghamii*, the climber *Rubus cissoides*, and *Lycopodium* species. The herbaceous species that increased their dominance, and had >15% variation in their CCA scores explained by environmental variables, included *Chiloglottis cornuta*, *Corybas trilobus*, *Epilobium pedunculare*, *Gnaphalium ruahinicum*, *Hydrocotyle moschata*, *Lagenifera pinnatifida*, *Lagenifera strangulata* and *Sagina procumbens* and the increases in fern species included *Grammitis billardieri*, *Histiopteris incisa* and *Hymenophyllum* species. A rush (*Juncus novaezelandiae*) also increased its dominance. When prostrate and rosette-forming herbaceous plants such as *Epilobium*, *Hydrocotyle*, *Lagenifera* and *Viola cunninghamii* are in high abundance they tend to form mat-like turfs. *Caladenia lyallii*, *Coprosma pseudocuneata*, *C. foetidissima* and *N. solandri* increased their importance over time with increasing site slope and decreasing altitude and all had >15% variation in their CCA scores explained by environmental variables.

4. Discussion

Our study has shown significant temporal changes in the abundance of smaller trees (20–100 mm DBH) in Kaimanawa Forest Park and changes in understorey composition in southern Kaimanawa Forest Park. Despite these changes there was no evidence from ordination analysis of an overall change in overstorey composition. Previous studies throughout New

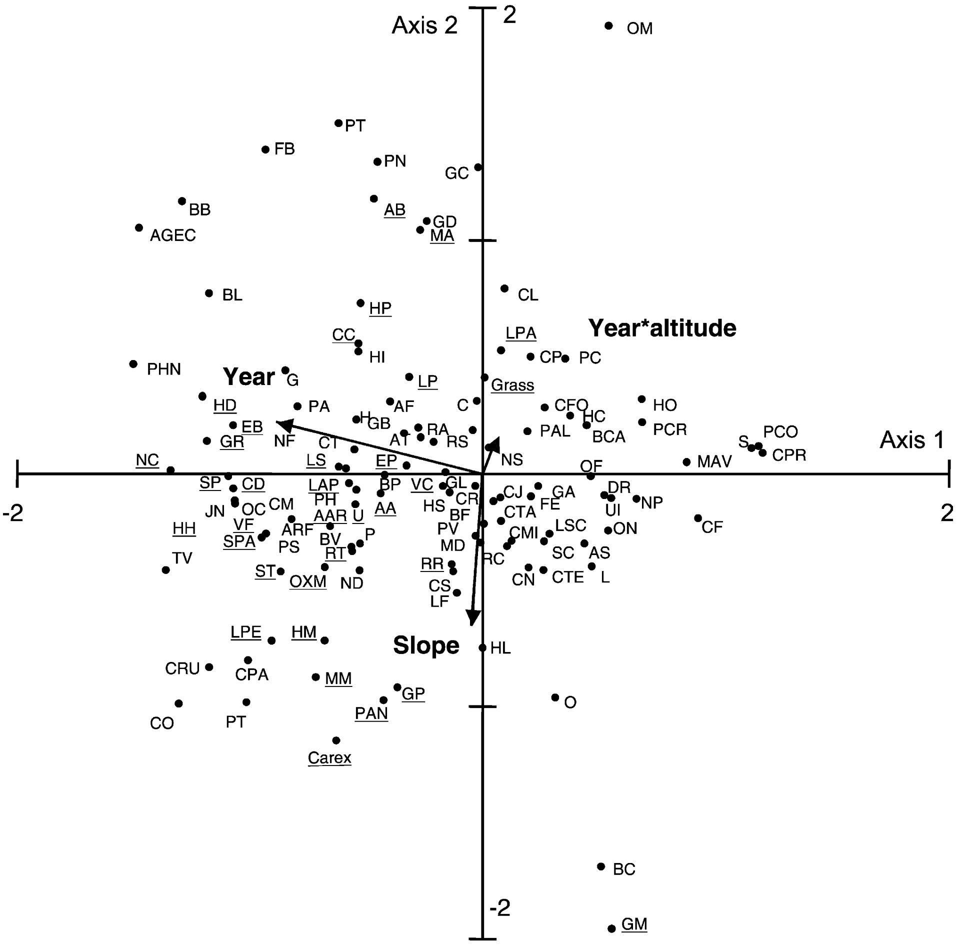

Fig. 7. CCA of southern Kaimanawa understorey composition. Significant environmental factors are displayed. Axis 1 explained 36.6% of total variation and axis 2 explained 34.4%. Species positions are shown using abbreviations (names in Appendix A). Turf-forming species are underlined.

Zealand indicated that there would have been a substantial shift in understorey composition within a decade of deer reaching an irruptive peak in Kaimanawa Forest Park (e.g. Jane and Pracy, 1974; Stewart and Burrows, 1989). These historical shifts favouring unpalatable seedling regeneration now seem to have been translated into shifts in the abundance of small trees. If this trend continues it is likely that the composition of stand dominants will be affected in the future. Although there are several alternative explanations for the changes observed in this study, including normal successional processes or browsing by invasive brushtail possums, ongoing browsing by introduced deer is the single most plausible explanation. Four main lines of evidence support an explanation of deer-induced forest modification in Kaimanawa Forest Park. Firstly, there was a general trend for the stem density of small trees of deer-unpalatable species to increase while deer-palatable species decreased in density. Secondly, there was structural evidence of very little regeneration of the most palatable subcanopy and canopy species. Thirdly, three paired deer exclosure plots showed increases in *Nothofagus* seedling abundance in fenced plots while unfenced plots had low seedling abundance. Finally, there was evidence of a shift in southern Kaimanawa understorey composition towards herbaceous, turf-forming species.

Unpalatable trees capable of forming a sub-canopy such as *N. pedunculatus* and *P. colorata* increased in abundance by between two and four times between the northern Kaimanawa 1979/1980 and 1998 surveys. Increases of *P. colorata* tended to be associated with warmer, north-facing sites which might be more favoured by deer as well as having increased light availability. There was some evidence that *C. serratus* also increased in abundance. Although this species is palatable to deer it has a divaricating growth form that makes it tolerant to browsing as deer may find its small leaves protected by numerous branches. In contrast, seedlings of the palatable *G. littoralis* and *W. racemosa* did not appear to be recruited into the >75 cm height tier. There were signs that lack of regeneration was affecting the abundance of these species as small trees.

CCA failed to show any shift towards a browse-resistant community in the overstorey, even though some individual unpalatable species increased in dominance as small trees while some palatable species declined. In the future this apparent imbalance may be translated through to compositional changes in stand dominants, but this is not yet apparent. This could be because only some sites are vulnerable to deer impacts and therefore large shifts in composition at all sites cannot be expected. Without data on deer abundance at individual plot sites or deer abundance trends over time and with season, it is not possible to show this conclusively. Compositional shifts could occur at a subset of vulnerable sites, to a set of key species, and not be detected by ordinations. CCA might not detect these types of changes if most species in most plots do not change in abundance, and if key species that do change in abundance do not occur at the same sites.

Levels of productivity may affect plant competitive interactions and responses of some species to herbivory (Van der Wal et al., 2000). In New Zealand, palatable woody plants tend to be small tree species limited to more productive low-altitude, high-fertility sites (Coomes et al., in press) and tend to have high nitrogen and low lignin concentrations in their foliage. *W. racemosa* is a notable exception to this generalisation (Forsyth et al., 2001). This may mean that highly productive sites with fast-growing plants are most vulnerable to modification by ungulates, as well as being more attractive to deer because of the high levels of nutrients at these sites. Thus, if deer are affecting forest regeneration then the problem is likely to be more serious at sites on the potentially more productive lower slopes and river terraces, such as the Ecology Stream exclosure site where conspicuous regeneration occurred once deer were excluded (Fig. 8). Such findings are reported by McShea and Rappole (2000) in the USA and Smale et al. (1995) in New Zealand.

The three exclosure plots showed that once deer browse was removed, all three *Nothofagus* species present increased in abundance through increased growth or survivorship. This suggests that deer could affect the regeneration of *Nothofagus* species in northern and southern Kaimanawa Forest Park as has been found in other exclosure plot studies in *Nothofagus* forests (Wardle, 1984). If this occurs at sites critical

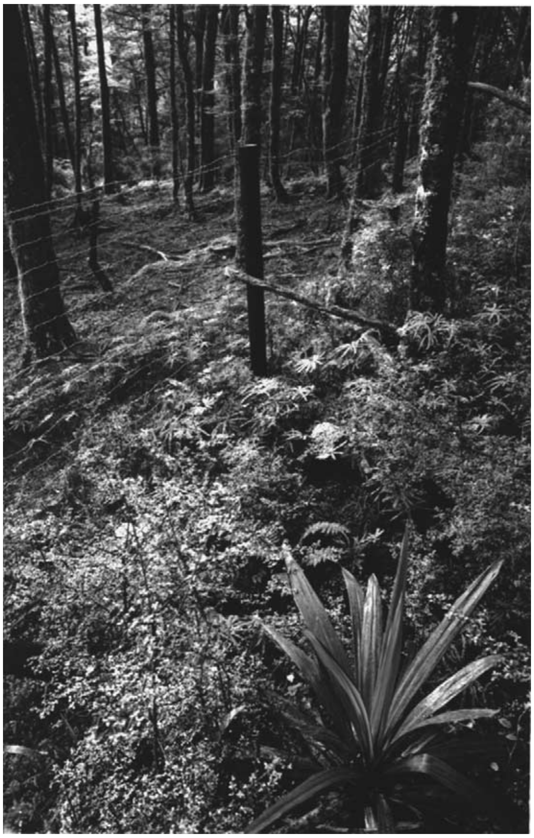

Fig. 8. Ecology Stream deer exclosure site showing little regeneration outside the fenced plot, but conspicuous regeneration of *Cordyline indivisa*, *N. solandri*, *G. littoralis* and *C.* “taylorae” inside the fence.

for canopy regeneration, canopies could shift away from beech dominance towards shrubs and small trees that are resistant to deer browse (such as *L. fasciculatus*, *N. pedunculatus*, *P. alpinus* and *P. colorata*). This evidence of deer impact was confounded by disturbance (measured through changes in basal area) which differed between fenced and unfenced plots, and a lowering of seedling abundance between 1996 and 2000 at Ecology Stream. Lowered basal area is usually associated with increased nutrient and light availability and so lowering of basal area is likely to increase seedling growth. *Nothofagus* seedling abundance increased significantly between surveys in the northern Kaimanawa, but without replicated exclosures and longer-term monitoring it is not possible to determine if this increasing abundance is sufficient to maintain a forest canopy at all sites. Overall, *N. fusca* seedlings increased in abundance in the northern Kaimanawa over the study but were at approximately half the abundance on north aspects compared to south aspects in the 1998 survey. This may be because deer have higher browsing impact on the north-facing sites or because of competitive exclusion from plants better suited to these warmer sites. Because of the high spatial variation in seedling abundance it is most likely that some sites have sufficient seedling regeneration to maintain a canopy while others do not. This might be related to high spatial and seasonal variation in deer abundance at a stand scale. Evidence for deer-induced regeneration failure is also found in South American *Nothofagus* forests; Veblen et al. (1989) showed that red deer introduced between 1911 and 1936 were impeding the regeneration of *Nothofagus dombeyi* in Argentina.

The low basal area, conspicuous tree-fall, and high proportion of standing dead trees recorded in the 1981/1982 southern Kaimanawa survey show that a large disturbance event, probably a tropical cyclone, is likely to have occurred in the study area less than two decades prior to plot establishment. In this area, there was little evidence of density-dependent tree mortality despite evidence of disturbance and recruitment into the 20–120 mm size classes. Deer-induced mortality could be replacing natural stand thinning processes, but this is impossible to determine without replicated exclosure plots. There was evidence of increased tree mortality at lower altitude sites, and stands of lower basal area in the southern Kaimanawa. It would be expected that canopy opening through disturbance would increase opportunities for regeneration, but in fact there was a decrease in *N. solandri* seedling abundance at low-altitude sites. This may exacerbate any canopy replacement problem associated with increased tree mortality at these sites.

In southern Kaimanawa, CCA shows evidence of compositional shifts in the understorey in the last two decades, away from shrubs and towards unpalatable ferns and browse-resistant herbaceous species capable of forming turf communities. The most plausible explanation for this is that ongoing deer browsing is capable of replacing palatable shrub species with browse-tolerant herbaceous turf communities in Kaimanawa Forest Park. In nearby Urewera National Park, an exclosure plot study demonstrated deer-induced compositional shifts from palatable to unpalatable shrub species (Allen et al., 1984) as did Wardle et al. (2001) at other New Zealand exclosure plots. Our study is the first to show clear compositional shifts from shrubs to herbaceous species across extensive areas of New Zealand forest. These turf species, while being palatable to deer, are often tolerant of browse due to their prostrate growth form which allows them to be grazed to a low, dense turf. Instead of increases in turf communities being a response to herbivory, it is possible that this is a response to increasing basal area and overstorey tree abundance following storm damage prior to plot establishment. Although it seems unlikely that increased competition for nutrients and light associated with increasing basal area would favour turf-forming herbs (Fredericksen et al., 1999), this possibility cannot be dismissed without further evidence from stands from which deer are excluded for a number of years following a canopy disturbance event.

Deer-induced compositional shifts might be largely irreversible, even after deer are removed, if slower-growing, unpalatable or browse-tolerant species are able to gain an advantage once the faster growing palatable species are removed (Wardle et al., 2001). Our permanent plot data suggests that shifts towards unpalatable or browse-tolerant species have occurred in the northern Kaimanawa *N. fusca* and *N. menziesii* forest, and that the induction of a vegetative turf has occurred in the southern Kaimanawa *N. solandri* forest. If this turf does impede woody seedling establishment, then compositional shifts may not be completely reversible at these sites, even in the absence of deer browse. In contrast, our exclosure plot data showed recovery in *Nothofagus* seedling growth and abundance once deer browse was removed, in comparison to adjacent unfenced plots. Closer examination of the data showed that tree deaths in two of the exclosures potentially confounded this interpretation of recovery following deer exclusion. In the long term, deer might shift successional pathways by removing otherwise competitive indigenous plants and encourage the establishment of unpalatable species. If deer browse prevents regeneration of some species for long enough, local seed sources may be eliminated and this could prevent their re-establishment. As the seed sources of important food plants for deer, such as *G. littoralis* (Nugent and Challies, 1988; Nugent, 1990) are removed through lack of regeneration, food availability for deer might decline. The consequences of this on forest impacts are difficult to predict. Deer impacts might increase as deer switch to more unpalatable food sources. Alternatively, impacts might decrease if deer populations decline considerably.

Long-term data on plant population and community changes are an essential resource for conservation management, but the interpretation of such data is speculative because the information is not derived from experimental manipulation. Other possible causes of compositional and structural change are successional processes and the impacts of other introduced herbivores such as brushtail possums. Nevertheless, we believe that deer browse is the main factor influencing structural and compositional shifts observed in this study. Successional processes are likely to favour palatable species that in New Zealand, and sometimes in other temperate hardwood forests, tend to be large-leaved and adapted to low light environments, or fast-growing species that are more competitive in gaps (Grime, 1979; Coomes et al., in press). In our study, fast-growing and larger-leaved palatable species declined in abundance. The dietary preferences of arboreal brushtail possums mean that they are also unlikely to explain the compositional changes observed in this study (Owen and Norton, 1994).

In conclusion, our study found evidence of ongoing tree abundance and structural changes in the northern Kaimanawa overstorey consistent with deer affecting the regeneration of palatable species. Less-palatable species appear unaffected, or to be increasing in abundance. There is some evidence in the southern Kaimanawa of compositional shifts away from shrubs to herbaceous plants in the understorey. While exclosure plots showed that deer were likely to be reducing *Nothofagus* seedling abundance, there was no evidence in this study that this had yet affected the stand dominants. Our findings could have been strengthened if we had access to information on deer abundance and site productivity. Future monitoring studies of this type should use replicated exclosures and collect serial information on soil fertility, water availability, light availability and deer abundance to show the relationship between these important environmental variables and changes in species composition through time. Individually tagging seedlings and saplings would also be worthwhile, compared to the counts used in this study, as they also provide information on seedling growth, mortality and recruitment as well as probably more accurate measures of abundance.

If the changes observed in this study reflect the impact of two post-irruptive introduced deer populations and not natural forest succession following disturbance, then Kaimanawa Forest Park conservation managers will need to implement intensive deer control to reduce deer impacts. With time, compositional changes may become increasingly irreversible if deer have shifted competitive balances between plants, altered successional pathways and ecosystem processes, or eliminated seed sources.

Acknowledgements

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Appendix A

AGEC: *Wahlenbergia pygmaea*, *Gentiana bellidifolia*, *Euphrasia cuneata*, *Coprosma cheesemanii*, *Coriaria pteridoides*
AA: *Acaena anserinifolia*
AAR: *Anisotome aromatica*
AB: *Anaphalioides bellidioides*
AF: *Astelia fragrans*
ARF: *Aristotelia fruticosa*
AS: *Aristotelia serrata*
AT: *Asplenium terrestre*
BB: *Brachyglottis bidwillii*
BC: *Blechnum chambersii*
BCA: *Blechnum capense*
BF: *Blechnum fluviatile*
BL: *Brachyglottis lagopus*
BP: *Blechnum penna-marina*
BV: *Blechnum vulcanicum*
C: *Celmisia* spp.
CC: *C. cornuta*
CD: *Cardamine debilis*
CF: *C. fraseri*
CFO: *Coprosma foetidissima*
CJ: *C. juniperina*
CL: *C. lyallii*
CM: *Corybas macranthus*
CMI: *C. microcarpa*
CN: *C. linariifolia*
CO: *Corybas orbiculatus*
CP: *C. pseudocuneata*
CPA: *Clematis paniculata*
CPR: *Coprosma propinqua*
CR: *Coprosma rhamnoides*
CRU: *Coprosma rugosa*
CS: *C. serratus*
CT: *C. trilobus*
CTA: *C.* “taylorae”
CTE: *C. tenuifolia*
DR: *D. recurvum*
EB: *Epilobium brunnescens*
EP: *E. pedunculare*
FB: *Forstera bidwillii*
FE: *F. excorticata*
G: *Gentiana* spp.
GA: *G. antipoda*
GB: *G. billardieri*
GC: *Gaultheria colensoi*
GD: *Gaultheria depressa*
GL: *G. littoralis*
GM: *Geranium microphyllum*
GP: *Galium propinquim*
GR: *G. ruahinicum*
H: *Hymenophyllum* spp.
HC: *Hebe corriganii*
HD: *Hydrocotyle dissecta*
HI: *H. incisa*
HL: *Helichrysum lanceolatum*
HM: *H. moschata*
HO: *Hebe odora*
HP: *Hieracium pilosella*
HS: *Hebe stricta*
JN: *J. novaezelandiae*
L: *Lycopodium* spp.
LAP: *L. pinnatifida*
LF: *L. fasciculatus*
LP: *Luzula picta*
LPA: *Luzula parviflora*
LPE: *Lagenifera petiolata*
LS: *L. strangulata*
LSC: *L. scoparium*
MA: *Muehlenbeckia axillaris*
MAV: *Microlaena avenacea*
MD: *M. divaricata*
MM: *Mycelis muralis*
NC: *Nertera ciliata*
ND: *Nertera dichondrifolia*
NF: *N. fusca*
NP: *N. pedunculatus*
NS: *Nothofagus solandri*
OC: *Ophioglossum coriaceum*
OF: *O. furfuracea*
OM: *Ourisia macrophylla*
ON: *O. nummularifolia*
OXM: *Oxalis magellanica*
P: *Pterostylis* spp.
PA: *Pseudopanax arboreus*
PAL: *P. alpinus*
PAN: *Pratia angulata*
PC: *P. colorata*
PCO: *Pseudopanax colensoi*
PCR: *Pseudopanax crassifolius*
PH: *P. hallii*
PHN: *P. hallii* × *nivalis*
PN: *Podocarpus nivalis*
PS: *Paesia scaberula*
PT: *Pittosporum tenuifolium*
PV: *Polystichum vestitum*
RA: *Raukaua anomalus*
RC: *R. cissoides*
RR: *Ranunculus reflexus*
RS: *R. simplex*
RT: *Raoulia tenuicaulis*
S: *Senela* spp.
SC: *S. cunninghamii*
SP: *S. procumbens*
SPA: *Stellaria parviflora*
ST: *Schizeilema trifoliolatum*
TV: *Trichomanes venosum*
U: *Uncinia* spp.
UI: *Urtica incisa*
VC: *V. cunninghamii*

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