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Suppression of regeneration in New Zealand mountain beech forests is dependent on species of introduced deer

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Abstract

We compared the impacts on forest regeneration of introduced sika (*Cervus nippon*) and red (*Cervus elaphus*) deer in New Zealand. Plot data were used to compare mountain beech (*Nothofagus solandri* var. *cliffortioides*) regeneration between a region with sika deer, and four regions without sika deer. All regions surveyed had red deer present. In the region where sika deer had been present for more than a decade, there was evidence of poor mountain beech seedling regeneration. In the four regions without sika deer, there was evidence of a strong regenerative response at stands with low occupancy by trees. When compared to larger deer species, sika deer have a digestive morphology allowing greater dietary versatility, which may result in them impeding forest regeneration where red deer do not. In contrast to mountain beech, some small-leaved shrub species may have been competitively advantaged by intensive browsing from sika deer. This is contra to a current view that small-leaved shrub species with interlacing branches were able to tolerate browsing from extinct ratite birds, but not introduced deer. Sika deer have been introduced into countries where other deer species are indigenous, such as Canada, Denmark, Great Britain, Czech Republic, Ireland and the United States of America. Because of their dietary advantage, sika deer may have a greater potential to impede forest regeneration and competitively exclude larger deer species, particularly at low basal area sites where impacts on tree regeneration are likely to be greatest.

Introduction

Linking disturbance and regeneration is a central theme in the study of forest dynamics (Pickett and White 1989) because many tree species rely on canopy tree death for regeneration. The regeneration process starts with density independent canopy tree mortality that lowers stand occupancy by trees and increases the availability of light and nutrients for seedlings, which in turn leads to regeneration in many tropical and temperate hardwood forests (e.g. Canham 1988; Peterson et al. 1990; Denslow et al. 1998). Stand occupancy is frequently measured by tree basal area, which is a measure of the area that trees cover and is related to tree biomass. The effects of herbivores are often strongly related to stand occupancy (Russel et al. 2001; Horsley et al.

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* *Nomenclature*: Nomenclature for New Zealand plants follows Parsons et al. (1995). *Coprosma tayloriae* is described by Jane (2005) and *Phyllocladus alpinus* referred to by Wilson and Galloway (1993).

2003). Despite this, few studies in temperate forests have considered the impacts of herbivores on canopy tree regeneration within a context of stand occupancy (but see Castleberry et al. 2000; Cornett et al. 2000; Husheer and Frampton 2005). This is a critical omission because herbivory may be concentrated at sites where canopy tree death has occurred (Peterson and Pickett 2000). At these sites resource availability is often higher, and nutrient- and light-demanding plants more common (Kelly 2002).

In New Zealand's widespread *Nothofagus* (southern beech) forests, previous studies on the impacts of red deer (*Cervus elaphus* L.), which were widely introduced into New Zealand in the 19th century (Challies 1985), have found that deer do not usually affect canopy replacement (e.g. James and Wallis 1969; Wardle 1984; Stewart and Harrison 1987; Stewart et al. 1987; Nugent 1988; but see also Conway 1949; Wardle 1962; Jane and Pracy 1974; Jane 1986). This may be because the influence of stand occupancy has not been specifically considered, even though beech species show prolific regeneration with lowered stand occupancy (Wardle and Guest 1977; Allen and Allan 1997). Alternatively, beech species may be resistant to mammalian herbivory after having evolved a small-leaved growth form, under the browsing influences of a suite of now extinct avian herbivore species including the deer-sized moa (*Diornis* spp.; Atkinson and Greenwood 1989; Diamond 1990). Hunting and habitat destruction from Polynesians, soon after their colonisation of New Zealand in the last 600 years, probably caused the extinction of most indigenous terrestrial avian herbivores (Holdaway and Jacomb 2000). This meant that there was minimal browsing from terrestrial vertebrates in beech forests from the time of these extinctions until the introduction of ungulates such as red deer. Sika deer (*Cervus nippon* Temm.) were liberated in the central North

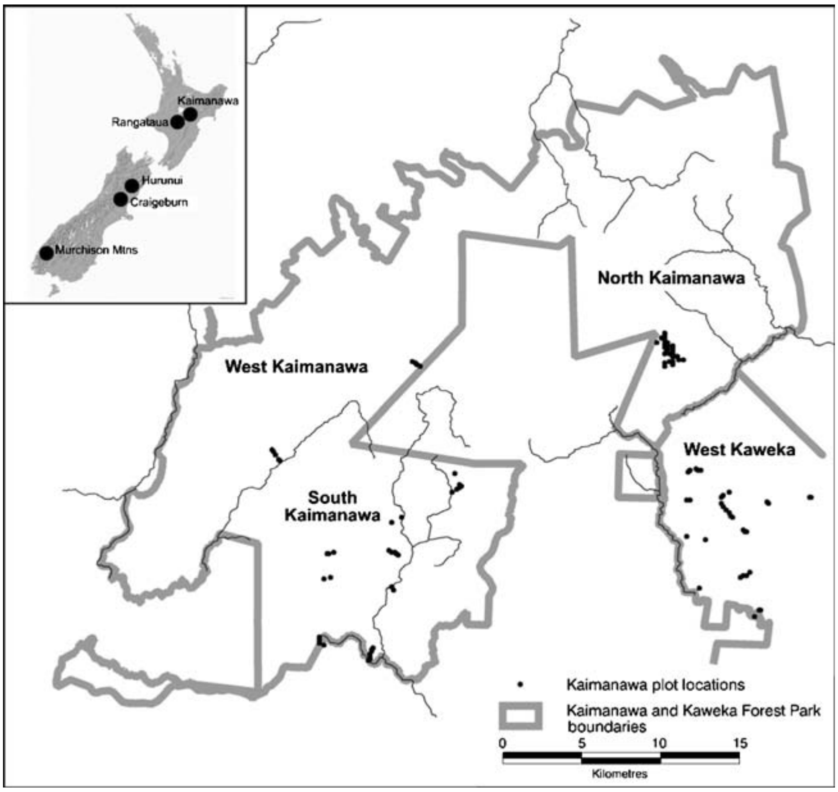

Figure 1. Map of randomly selected Kaimanawa transect locations. Inset are New Zealand's North and South Islands showing study areas in Kaimanawa ecological region, Rangataua Forest, Hurunui, Craigieburn, and Murchison Mountains.

Island in 1905 (Davidson 1979; Figure 1), but colonised more slowly than red deer (Elder 1956). Because of this slower rate of dispersal, there is a distinct history of colonisation of central North Island mountain beech (*Nothofagus solandri* var. *cliffortioides*) forests first by red deer, then by sika deer, followed by reduced abundance of red deer (Davidson and Fraser 1991).

Earlier New Zealand studies have often not differentiated between impacts of different species of introduced ungulate (e.g. Wardle et al. 2001; Bellingham and Allan 2003), although different species of ungulates may have different effects through either competition (Murray and Illius 2000) or facilitation (Arsenault and Owen-Smith 2002). Larger forest dwelling ungulates with relatively slow digestion, and large mouths, bodies and rumens, such as red deer, are better adapted to grazing plants high in cellulose such as grasses (Hanley 1997). In comparison, ungulates such as sika deer with different digestive morphology (Fraser 1996) and higher dietary versatility (Asada and Ochiai 1996) are better adapted to browsing small-leaved shrubs and plants high in chemicals such as monoterpenes and phenols that interfere with rumen microbial activity (Duncan et al. 1994). This is likely to allow a greater dietary concentration of plants with well-developed chemical and morphological defence strategies. This suggests that sika deer are likely to have higher impacts on tree and shrub species that are only moderately palatable to red deer such as mountain beech (Husheer et al. 2003). Observations of rumen contents from the central North Island show that beech species are nearly twice as common in the diet of sika deer as they are in red deer (Nugent et al. 2000). Previous studies in Japan have shown that where sika deer are present in large numbers for several decades, impacts on beech (*Fagus crenata*) forest regeneration can be strong (Takatsuki and Gorai 1994; Tsujino and Yumoto 2004). If impacts of sika deer over time are cumulative, New Zealand species that are palatable to sika deer such as broadleaf (*Griselinia littoralis*) and mountain beech might be more common in recently colonised areas. In areas with longer histories of colonisation by sika deer, divaricating shrubs with fewer leaves on their outer canopy and strong, acutely-angled branchlets, may become more common if their growth form is tolerant of browsing from terrestrial vertebrates (Atkinson and Greenwood 1989). There is also likely to be fine-scale variation in deer impacts independent of the colonisation history of deer due to factors such as plant species composition and habitat productivity. In New Zealand southern beech forests, the lowering of basal area following natural disturbance increases the availability of light and nutrients to seedlings and saplings (Allen et al. 1997) thereby increasing the nutrient content of those plants (Davis et al. 2003). If palatable plants such as mountain beech increase in abundance and growth in the browse tier at low basal area sites due to increased resource availability (Wardle 1984), this may attract deer to such sites. If deer are able to suppress regeneration of mountain beech then this is likely to be most pronounced at low basal area sites.

To contrast the impacts of sika and red deer on mountain beech regeneration, we first compare the abundance of mountain beech seedlings within a region containing both red and sika deer with four other regions where red but not sika deer are present. Second, we test whether the progressive sika deer colonisation of four areas in the region with sika deer has affected mountain beech seedling abundance and the frequency of occurrence of small-leaved trees and shrubs. If sika deer are able to suppress the regeneration of mountain beech, then browse-resistant trees should occur more frequently in areas where these plants were first released from competition from mountain beech, and least in areas where sika deer are not present. Finally, we consider the results from this study in a context of recent studies on the evolution of herbivory resistance in the New Zealand flora, and the implications for other regions around the world where sika deer have been introduced.

Methods

Sika deer study areas

In the Kaimanawa region of New Zealand (39° S, 176° E) one hundred and eight 20 m × 20 m survey plots were measured on 30 randomly located transect lines in mountain beech forest between January 1999 and April 2001. The plots were located in four contiguous areas that all had established populations of red deer by 1930 (Elder 1962), but with different histories of colonisation by sika deer. Northern Kaimanawa (29 plots, 8 transects, 1180–1380 m altitude) was the closest area to the sika liberation point, and sika deer became conspicuous there in the 1930s (Davidson 1973) following likely colonisation from their liberation point during the late 1920s. The Sika deer probably colonised the western Kaweka area (34 plots, 12 transects, 840–1360 m) in the 1940s and had displaced red deer at some sites there in the 1950s (Davidson and Fraser 1991). The western Kaimanawa area (10 plots, 2 transects, 700–1340 m) was probably colonised by sika deer through open grasslands and plantation forestry to the north of Kaimanawa Forest Park in the 1960s before being more commonly observed there in the early 1970s (Davidson 1973). In the southern Kaimanawa area (35 plots, 8 transects, 860–1380 m) sika deer only became dominant over red deer during the mid-1990s (pers. obs. SWH) and so probably colonised this area during the 1980s.

The Kaimanawa region consists of a series of ranges characterised by high relief, with often steep valley walls, valley bottoms often less than 500 m and a high point of 1727 m in the southern Kaimanawa. Soils are either derived from the predominantly sandstone bedrock or from ash from volcanic eruptions (ca. 1800 years BP, Wilson 1993). At the Boyd Airstrip, central Kaimanawa Forest Park, rainfall averages 2083 mm yr^{-1}, but it decreases further east in Kaweka Forest Park (1580 mm yr^{-1}).

Red deer regions and sampling approach

We found four surveys in the National Vegetation Surveys databank (Wiser et al. 2001) that were undertaken since 1998 in mountain beech forests throughout New Zealand, and where red but not sika deer were present. As in the Kaimanawa region, the surveys in these four regions were undertaken in unlogged southern beech dominated forest. The Craigieburn region is almost completely dominated by mountain beech occurring on sandstone bedrock derived soils (34 plots, 13 transects, 43° S 171° E, 1400 mm yr^{-1} rainfall, 800–1300 m altitude). In comparison, in the four other regions (Kaimanawa inclusive) mountain beech forms the treeline below 1400 m altitude but is replaced by red (*N. fusca*) and silver beech (*N. menziesii*) at lower altitudes. Rangataua Forest (13 plots, 5 transects, 39° S 175° E) occurs on a basalt lava flow on southern Mt. Ruapehu. Hurunui Valley has sandstone bedrock with steep, glacier formed valley sides (5 plots, 3 transects, 43° S 172° E), and the Murchison Mountains consist of glacier formed valleys with granite derived soils (16 plots, 6 transects, 45° S 167° E, 2400–4500 mm rainfall).

Plot measurement procedure

In all surveys, transects originated at randomly selected points on watercourses and terminated at the nearest highpoint or treeline, except for northern Kaimanawa where transect origins were at randomly located points and followed randomly selected compass bearings. On each transect, plots were established 40 m from transect origins and at 200 m intervals from the origin thereafter. Only large (>100 ha) areas of mountain beech dominated forest (determined by proportion of basal area) were sampled.

All eight surveys in this study used a protocol for 20 m × 20 m plot measurement described by Allen (1993). For the overstorey, species of all trees >30 mm diameter over bark at breast height (DBH measured at 135 cm) rooted within plots were identified, and their stem diameter measured. Mountain beech has periodic and variable seeding, often resulting in large numbers of small (<15 cm high) ephemeral seedlings (Wardle 1984). Therefore, we counted established seedlings (15–135 cm height tier) within 24 systematically located 0.49 m radius sub-plots within each plot. To determine woody species composition in the understorey, the presence of tree and shrub (distinguished using the criteria of Poole and Adams 1994) seedlings (15–135 cm tall) were recorded by species in these sub-plots.

Data analysis

Data for mountain beech seedling abundance in sub-plots was pooled for each plot and $\log_e$-

transformed to meet assumptions of ANOVA. Contrasts of seedling abundance between areas with and regions without sika deer were made using SYSTAT (SPSS 2000). Detrended correspondence analysis (DCA) in CANOCO 4.0 was used to produce plot ordination scores of understorey and overstorey composition (Ter Braak and Smilauer 1998) using frequency of occurrence of seedlings (15–135 cm) in 24 sub-plots and relative live tree basal area to calculate respective importance values. Understorey species composition is likely to be influenced by overstorey composition and site basal area, so we tested whether overstorey composition was comparable between regions and used basal area as a covariate in comparisons of seedling composition. First and second axis DCA scores, mean tree density, basal area, and understorey frequency of occurrence were compared using ANOVAs, with the Bonferroni correction for multiple comparisons (Sokal and Rohlf 1995). Because individual transects started in valley bottoms and ended at highpoints, or at treeline, there was a large variation in plot altitude within transects. Hypothesis tests among areas and regions used an error term of transects nested within areas or regions, to allow for this variation and avoid pseudoreplication at the plot level.

Results

Contrasts between regions with and without sika deer

Mountain beech seedling abundance was significantly higher in regions with no sika deer present ($\log_e + 1$; 22,025 seedlings ha^{-1}, 24 transects, 76 plots) compared to four areas in the Kaimanawa region where the deer were present (664 seedlings ha^{-1}; 29 transects, 108 plots; $F_{1,51} = 18.096$, $P < 0.001$). Basal area was used as a covariate, and had a significant effect ($F_{1,127} = 11.760$, $P = 0.001$) confirming that seedling abundance was affected by differences in basal area. In regions without sika deer there was a clear negative relationship between seedling abundance and plot basal area ($F_{1,74} = 31.124$, $R^2 = 0.296$, $P < 0.001$), particularly for data from Rangataua and Craigieburn (Figure 2). In contrast, the four Kaimanawa region areas showed no such relationship ($F_{1,106} = 0.276$, $R^2 = 0.003$, $P = 0.600$) demonstrating that seedling abundance at low basal area sites where sika deer are present are particularly low in comparison to similar sites with no sika deer (Figure 3). There was no significant difference in seedling abundance among the four regions with no sika deer ($F_{3,23} = 2.916$, $P = 0.056$) when basal area was included as a covariate, demonstrating that these regions had consistently higher seedling densities than the Kaimanawa region.

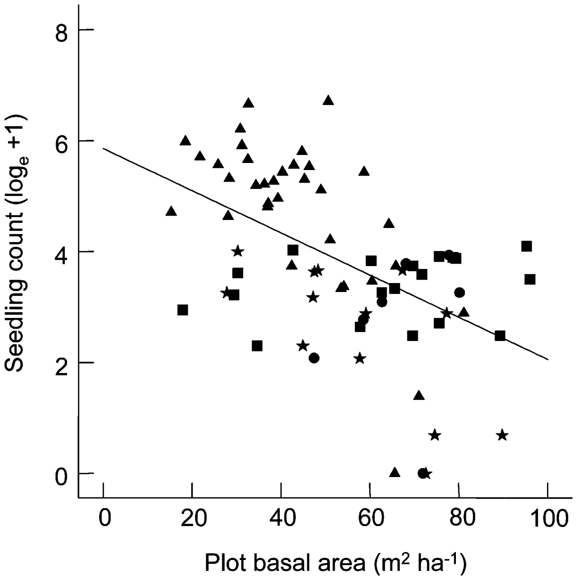

Figure 2. Relationship between the number of mountain beech seedlings ($\log_e + 1$) counted in twenty-four 0.75 m^2 sub-plots in each 20 m × 20 m plot and plot basal area (m^2 ha^{-1}) for 66 plots in four areas outside the Kaimanawa region where sika deer are not present. These areas are Craigieburn (▲), Hurunui (●), Murchison (■) and Rangataua (★). The regression equation is seedling count ($\log_e + 1$) = 5.814–0.037 × basal area.

The basal area of *G. littoralis* and celery pine (*Phyllocladus alpinus*) was higher in the Kaimanawa region, while mountain and silver beech and total basal area were higher in the four regions with no sika deer (Table 1). In contrast, first axis DCA scores calculated using relative basal area were not significantly different between the Kaimanawa region (mean score ± SE = 0.75 ± 0.03) and regions without sika deer (mean ± SE = 0.59 ± 0.02; $F_{1,52} = 3.002$, $P = 0.089$) showing that differences in basal area of

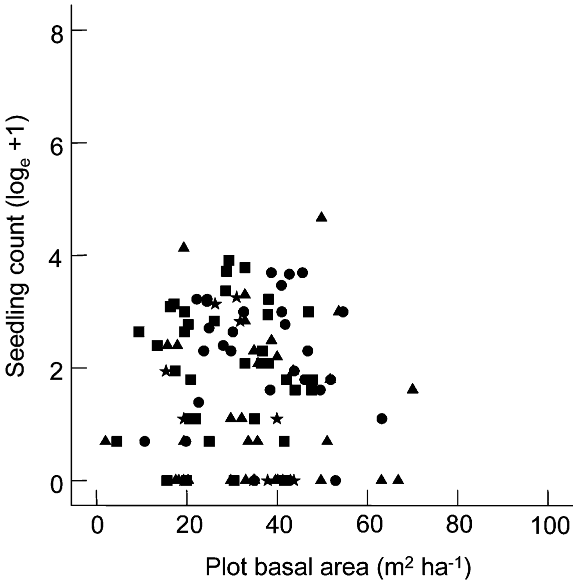

Figure 3. The relationship between the number of mountain beech seedlings ($\log_e + 1$) counted in twenty-four 0.75 m^2 subplots in each 20 m × 20 m plot and plot basal area (m^2 ha^{-1}) in the Kaimanawa region where sika deer are present. Data are from 108 plots in western Kaweka (▲), and northern (●), western (■) and southern Kaimanawa Forest Parks (★).

individual species did not have a large effect on differences in overall species composition. Tree abundance data were consistent with this result: apart from silver beech being more common in areas without sika deer, there was no overall difference in tree stem density for species with > 100 stems ha^{-1} between Kaimanawa and regions without sika deer.

Total tree and shrub seedling (15–135 cm tall) frequency of occurrence did not differ between Kaimanawa and regions without sika deer, but some individual species did differ in occurrence between the regions. Mountain beech had over twice the frequency of occurrence in regions without sika deer, which is consistent with seedling abundance comparisons of this species. Conversely, the occurrence of seedlings of the browse-resistant small-leaved shrubs *Coprosma tayloriae* and *Myrsine divaricata* was ca. five times higher in the Kaimanawa region compared to regions without sika deer. These differences led to significant differences in woody seedling composition, calculated using frequency of occurrence at plots with woody species present, between areas with sika deer (mean axis 1 DCA score ± SE = 2.51 ± 0.6) and regions without sika deer (mean axis 1 DCA score ± SE = 0.99 ± 0.8; $F_{1,49} = 53.745$, $P < 0.001$). When basal area was used as a covariate it did not have a significant effect on DCA scores for woody seedling frequencies of occurrence ($F_{1,115} = 0.521$, $P = 0.472$).

Contrasts among areas with different histories of sika deer colonisation

There was no significant difference in basal area among Kaimanawa areas for the stand dominants (*G. littoralis*, mountain and silver beech, and *P. alpinus*; Table 2). Differences in the abundance of the small-leaved trees *Coprosma pseudocuneata* and *P. alpinus* did not appear to be related to the history of colonisation by sika deer. There was no significant difference in mountain beech seedling density (stems ha^{-1}, $\log_e + 1$) among the four Kaimanawa areas when plot basal area (m^2 ha^{-1}) was used as a covariate ($F_{3,26} = 1.423$, $P = 0.259$) and therefore, no indication that the different colonisation history of the four areas influenced mountain beech seedling density.

Discussion

Mountain beech seedling abundance was high at low basal area sites, but only in the absence of sika deer. This confirms the importance of low basal area sites for mountain beech regeneration (Wardle 1970; Ogden et al. 1996), and is likely to be due to increasing nutrient and light availability following disturbance (Allen et al. 1997; Clinton et al. 2002). Where sika deer had colonised mountain beech seedling abundance was low at all plots, and did not increase with low basal area. Differences in the level of regeneration between areas with and without sika deer were so profound on a landscape scale that the impacts of sika deer appear to be the most plausible explanation for the suppressed mountain beech regeneration observed throughout the Kaimanawa region. Independent introductions of species into new ranges in a replicated manner are rare, so comparative studies such as ours are often the only possible approach to study introduced

Table 1. Means (±SE) of plot basal area, relative basal area (for species with basal area >1.0 m^2 ha^{-1}), tree stem density (for species with tree abundance >100 stems ha^{-1}) and frequency of occurrence of woody seedlings (for species with $>10\%$ occurrence in sub-plots) with Bonferroni adjusted *F*-tests.

	Without sika deer	With sika deer	*F*	*P*
Basal area (m^2 ha^{-1})				
Griselinia littoralis	0.1 ± 0.1	2.3 ± 0.3	16.913	<0.001
Silver beech	6.9 ± 1.7	0.4 ± 0.1	25.49	<0.001
Mountain beech	46.1 ± 2.2	26.6 ± 1.3	47.717	<0.001
Phyllocladus alpinus	0.2 ± 0.1	1.0 ± 0.1	8.455	0.020
All species	55.8 ± 2.5	33.1 ± 1.3	87.819	<0.001
Relative basal area (% of mean plot relative basal)				
G. littoralis	0.2 ± 0.1	8.0 ± 1.2	15.312	0.001
Silver beech	9.5 ± 2.0	3.0 ± 1.2	20.805	<0.001
Mountain beech	86.0 ± 2.3	78.4 ± 2.2	0.850	1.000
Phyllocladus alpinus	0.4 ± 0.2	3.4 ± 0.5	11.469	0.005
Tree density (stems ha^{-1}*)*				
C. tayloriae	58 ± 23	281 ± 46	0.725	1.000
Silver beech	257 ± 57	31 ± 12	16.36	<0.001
Mountain beech	1704 ± 152	1219 ± 113	0.27	1.000
P. alpinus	58 ± 23	244 ± 30	4.109	0.110
All species	2267 ± 168	2248 ± 139	4.281	0.095
Seedling frequency of occurrence in sub-plots (%)				
C. foetidissima	4 ± 1	12 ± 2	0.705	1.000
C. pseudocuneata	9 ± 2	16 ± 2	1.324	1.000
C. tayloriae	9 ± 3	33 ± 2	23.488	<0.001
M. divaricata	3 ± 1	16 ± 2	8.976	0.016
Mountain beech	57 ± 4	18 ± 2	47.599	<0.001
Mean of plot totals	113 ± 9	154 ± 9	0.335	1.000

All tests contrast four regions without sika deer with four areas within the Kaimanawa region where sika deer are present. Contrasts of seedling frequency of occurrence use plot basal area as a covariate.

organisms, but the causes of observed effects are never completely irrefutable unless alternate explanations can be ruled out (Oksanen 2001). There are three lines of reasoning that support a conclusion that sika deer are capable of suppressing mountain beech regeneration.

First, the morphology of sika deer provides this species with the potential to browse more intensively than red deer on seedlings of trees and shrubs (Fraser 1996; Hanley 1997) enabling them to maintain high reproductive rates, associated with better physiological condition, in depleted forest habitats (Asada and Ochiai 1996). This may allow sika deer to suppress mountain beech seedling regeneration where red deer would not, and to maintain higher population densities than red deer. Results from pellet frequency of occurrence surveys suggest that both red and sika deer populations can maintain high levels of abundance, but that red deer populations decline with commercial hunting pressure, or immediately following the colonisation of sika deer (Davidson 1973; Davidson and Fraser 1991). In the three Kaimanawa areas deer faecal pellet frequency of occurrence in 114 cm radius plots (an index of deer abundance, Riney 1957) was >30% between 1980 and 1988, and in 2004 was 33% despite ongoing hunting during that time. In Kaweka Forest Park, pellet frequency of occurrence was 11% in 1981 and 10% in 2000 (Husheer 2003). In contrast, in the Craigieburn and Murchison Mountain regions these indices of deer abundance were formerly high but declined following the initiation of commercial deer recovery operations in the 1970s (Craigieburn 1978 = 33%; 1983 = 17% Coomes et al. 2003; Murchison 1969 = 14%, 1977 = 4% Parkes et al. 1978). In the Rangataua region, where commercial hunting has not been allowed, pellet occurrence was more moderate in 2003 (16% Husheer, unpub. data). Using data from deer culling and pellet frequency of occurrence, Husheer and Robertson (2005) estimated that there were >16 deer km^{-2} in an area adjacent to

Table 2. Mean (±SE) basal area (for species with basal area >1 *m*^{2} ha^{-1}) and tree stem density (for stems >30 mm DBH and densities >100 stems ha^{-1}) from a total of 108 plots from western Kaweka, and northern, western and southern Kaimanawa Forest Parks.

Species	North Kaimanawa ($n=30$)	West Kaweka ($n=35$)	West Kaimanawa ($n=10$)	South Kaimanawa ($n=35$)	*F*	*P*
Sika dominance	≈1930s	≈1950s	≈1970s	≈1990s		
Basal area (m^2 *ha*$^{-1}$ *± SE)*						
Mountain beech	29.1 ± 3.0	30.8 ± 2.8	23.1 ± 4.3	24.72 ± 2.5	1.232	1.000
G. littoralis	1.5 ± 0.7	3.4 ± 0.7	1.7 ± 1.0	2.01 ± 0.6	0.751	1.000
Silver beech	1.3 ± 0.5	< 0.1 ± < 0.1	0	0	3.618	0.130
P. alpinus	0.9 ± 0.3	1. 1 ± 0.3	2.3 ± 0.4	0.8 ± 0.3	2.308	0.495
All 26 species	32.6 ± 2.8	36.0 ± 2.7	27.6 ± 4.0	27.7 ± 2.4	1.621	1.000
Tree stem density (stems ha^{-1} *± SE)*						
Mountain beech	1197.1 ± 257.0	644.4 ± 243.3	1785.0 ± 367.0	1529.4 ± 218.0	5.158	0.042
C. pseudocuneata	378.0 ± 49.8	21.7 ± 47.1	177.5 ± 70.9	140.9 ± 42.2	8.266	0.003
P. alpinus	209.6 ± 69.2	258.3 ± 65.4	532.5 ± 98.6	206.6 ± 58.7	2.971	0.343
C. tayloriae	123.1 ± 97.4	291.2 ± 92.1	575.0 ± 139.0	187.2 ± 82.6	1.567	1.000
G. littoralis	67.0 ± 34.3	125.4 ± 32.4	52.5 ± 48.8	103.5 ± 29.1	0.391	1.000
M. divaricata	< 0.1 ± 22.7	68.2 ± 21.5	185.0 ± 32.3	10.4 ± 19.2	22.962	< 0.001
All 26 species	2105.9 ± 319.0	1586.8 ± 301.2	3412.5 ± 454.0	2418.0 ± 270.0	4.928	0.049

Bonferroni corrections for multiple comparisons have been applied and decades when sika deer probably became dominant over red deer are listed.

the western Kaweka area in 1998, whereas Nugent and Fraser (1993) estimated that deer had an average population density throughout New Zealand forests of ca. 4 deer km^{-2} in 1988 following two decades of intense commercial hunting. Even though sika deer are ca. half the size of red deer, this difference in biomass still represents considerably more potential browsing pressure. The ability of sika deer to occupy small home ranges may also contribute to their potential to more intensively browse forests (Endo and Doi 1996). There is also evidence from studies of sika deer in Japan relating body size to dietary preferences. Sika deer from northern study sites in Japan tend to be larger and to graze graminoids more than the smaller sika deer from southern study areas, which tend to browse on herbs (Asada and Ochiai 1996; Jayasekara and Takatsuki 2000). Deer in the south of Japan also occur in habitats with a relatively stable food supply, whereas in the north there is considerable seasonal variation in the quality of food. This places dietary stress on animals during winter (Takatsuki and Ikeda 1993; Asada and Ochiai 1999) when unpalatable plants are increasingly browsed (Takahashi and Kaji 2001).

Second, exclosure plot studies in the Kaimanawa sika deer range have shown that once deer browse was removed by fencing plots or shooting deer, mountain beech seedling growth and establishment increased after only one year (Husheer and Robertson 2005; Husheer et al. 2005). Moreover, exclosure plots established during the 1980s at Kaimanawa sites with sika deer now show that mountain beech seedling and sapling abundance increased to between 2 and 25 times higher inside fenced plots compared to paired unfenced plots (Husheer 2003). In contrast, in regions with only red deer, there was little difference (< 50%) in the density of mountain beech seedlings and saplings between fenced and unfenced plots (Hurunui, Wardle et al. 2001; Murchison Mountains, Burrows et al. 1999; Rangataua, Husheer 2003).

Finally, two small-leaved shrubs (*C. tayloriae* and *M. divaricata*), that are considered to be browse-resistant (Wardle 1984; Nugent et al. 1997; Coomes et al. 2003) were more common as seedlings in the Kaimanawa compared to other regions. This result is consistent with sika deer shifting competitive advantage away from more palatable mountain beech seedlings towards species that would be less successful in the absence of intense herbivory (Husheer et al. 2003).

Our null hypothesis that areas where sika deer had colonised most recently would show fewer signs of intense browsing by sika deer, in comparison to areas colonised first, was not supported by our results. There were only minor differences in abundance and basal area of overstorey species among Kaimanawa areas, and there was no significant difference in mountain beech seedling abundance. Instead, intensive browsing of mountain beech seedlings appears to occur during the early stage of sika colonisation, quickly reducing mountain beech seedling abundance, particularly at low basal area sites. These low basal area sites may be preferentially selected by deer due to higher productivity. Studies on the Isle of Rum in Scotland (Virtanen et al. 2002) and in a Swedish Boreal forest (Ball et al. 2000) have shown that productive sites are more attractive to deer. Alternatively, some studies (e.g. Moen and Oksanen 1998; Olofsson 2001) have shown that at unproductive sites, herbivores are food limited and therefore have greatest impacts (Oksanen 1990). Absolute impacts of deer may be greatest at highly productive sites, and relative impacts may be greatest at sites of lower productivity (John and Turkington 1997; Ball et al. 2000; Virtanen 2000; Takada et al. 2002). Differences in the occurrence of herbivore-resistant, small-leaved shrub species between areas with different histories of sika deer colonisation would not be detected if these plants quickly respond to competitive release. Husheer et al. (2003) showed that small-leaved species have increased in abundance as small trees within the last two decades throughout Kaimanawa Forest Park, while palatable, large-leaved species declined in abundance.

The increased occurrence of small-leaved divaricating plants under the presence of intense herbivory by sika deer has implications for recent studies concluding that divaricating plants, some of which are threatened or are in decline, are adapted to browsing by moa (Atkinson and Greenwood 1989) or to photoinhibition (Howell et al. 2002), but are poorly adapted to ungulate herbivory. Bond et al. (2004) concluded that most divaricating plants are susceptible to browsing damage from introduced ungulates but not from extant ratites. They also suggested that there is a group of small-leaved shrubs with stems >3 mm diameter that are resistant to mammalian browsing. This is consistent with the results of this study and those of Wardle et al. (2002) who found that small-leaved plants, often with stems >3 mm diameter, did not generally benefit from ungulate exclusion in many New Zealand regions. Most experimental studies have failed to show a benefit from the divaricating form for protection from cold, wind or low humidity (Kelly and Ogle 1990; McGlone and Clarkson 1993; Darrow et al. 2001), and so defence from herbivory may be the best explanation for this adaptation. Furthermore, climatic explanations do not show why many divaricating plant species are common across a range of habitats including the interior of forests that are sheltered from frost, wind and excessive light. We conclude that at least some divaricating plant species are resistant to intensive ungulate browsing, lowering their vulnerability to extinction.

The probable ability of sika deer to browse more intensively than red deer, and their difficulty to control due to heightened alertness and preference for dense forest habitats (Kiddie 1962), has important biological conservation implications where red and sika deer are sympatric. Sika deer have been introduced into the Czech Republic, Denmark, Germany, Great Britain, Ireland and the United States of America (Feldhamer and Marcus 1994; Goodman et al. 1996). If they are able to suppress regeneration of forests there, then sika deer may pose a serious problem for forest and conservation managers (Kelly 2002). In continental Europe, Great Britain and Ireland red deer are regarded as having the ability to adversely affect woodland regeneration (Gong et al. 1991; Scott et al. 2000). Sika deer may eliminate species that red deer are known to periodically browse such as European beech (*Fagus sylvatica* L.; Ammer 1996), sitka spruce (*Picea sitchensis* Carr.; Duncan et al. 2001), Scots pine (*Pinus sylvestris* L.; Scott et al. 2000) and Norway spruce (*Picea abie* Karst.; Gill 1992). Regeneration of these species in forests recently colonised by sika deer needs to be monitored, particularly at productive sites where the magnitude of impact may be greatest. In Scotland, sika appear to be able to competitively displace red deer, and reach higher densities (Chadwick et al. 1996) over an increasingly large area (Rose 1994). Moreover, by preferring forest or shrub habitats (Marques et al. 2001) sika may suppress forest regeneration in Europe where red deer do not (Goodman et al. 1996). If sika deer have higher levels of impacts on forest regeneration than red deer, then the same may be true for widespread sika–red hybrids (Abernethy 1994). This may pose additional management problems where red and sika deer are sympatric in Britain, Czech Republic, Denmark, Germany, Ireland, New Zealand and the United States of America.

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