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Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control

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Summary

1. Ungulates have reached such high densities in some natural ecosystems that culling is frequently used to reduce their impacts on vegetation. However, much is still unknown about the outcomes of landscape-level control, in part because monitoring vegetation recovery requires decades.

2. We report long-term vegetation changes in permanent plots located in forest, shrubland and grassland communities across a mountain range in southern New Zealand. We test whether *c.* 92% reduction in the population of invasive non-indigenous red deer *Cervus elaphus* since 1964 has led to the recovery of deer-preferred species.

3. Tree seedlings, saplings and the number of seedlings per adult tree increased over time. There was lower recruitment, however, of highly palatable forest species compared with less palatable species, and the recruitment of saplings was lower in browsed forest plots compared with deer exclosures.

4. The total number of occurrences and absolute number of palatable species per plot increased over time in shrublands and grasslands respectively. The height of both shrublands and palatable grassland snow tussocks *Chionochloa* spp. increased, although the occurrences of most individual species remained unchanged over time.

5. Vegetation recovery at our site in response to long-term and significant herbivore reductions may be limited by several factors, including the slow growth rates of New Zealand species, density-dependent diet switching by deer, altered successional trajectories and below-ground processes.

6. *Synthesis and applications.* Our results suggest that after nearly four decades, even low densities of introduced herbivores may restrict ecosystem recovery, and therefore, restoring herbivore-disturbed ecosystems by solely manipulating herbivore population numbers may require a long-term perspective. Management strategies can accelerate recovery by protecting existing palatable plants within deer-exclosures, and planting or seeding palatable species within these refugia. However, in addition to increasing seed sources, restoration may only become apparent following large-scale disturbance events and canopy turnover.

Key-words: browsing, culling, forests, grasslands, grazing, herbivory, introduced species, restoration, shrublands

Introduction

Ecosystem recovery is a type of ecological restoration in which the expectation is that the system will regain desirable attributes through ‘natural’ processes (Meffe, Carroll & Pimm 1997). For example, once disturbances imposed by invasive

non-indigenous organisms on native species are reduced by control measures, it may be possible for an ecosystem to recover to a pre-disturbance state (Paine, Tegner & Johnson 1998). However, where disturbance impacts exceed the capacity of species to recover, ecosystems can change permanently, even when disturbances are reduced (Hobbs & Norton 1996). Barriers to vegetation community restoration in many instances result from reduced dispersal and seedbank recruitment of

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pre-disturbance species, competition, and biogeochemical and physical changes associated with disturbances (Suding, Gross & Houseman 2004). Feedbacks between species and ecosystem properties may further prevent recovery to the pre-disturbance state, and in some situations, positive feedbacks themselves may initiate trophic cascades that permanently shift ecosystems to alternate states (Bazely & Jefferies 1997; Wolf, Cooper & Hobbs 2007).

Grazing and browsing by large mammalian herbivores is one form of disturbance that can have a major impact on ecosystems. For example, high densities of deer in North America, Europe, Japan and New Zealand have been responsible for altering the structure and composition of forests (Gill 1992; Coomes *et al.* 2003; Côté *et al.* 2004) and open-hill habitats (Rose & Platt 1987; Takahashi & Kaji 2001; Albon *et al.* 2007; Wolf *et al.* 2007). These changes can reduce the recruitment of deer-preferred species and lead to modifications in nutrient cycling and successional trajectories that may be difficult to reverse (Côté *et al.* 2004). As such, deer are a conservation problem in many countries where they have been introduced, and also in their native ranges, when populations are allowed to increase. However, the long-term responses of ecosystems to deer population control are not well described, mainly because there are few places where deer control has been imposed for a length of time that is meaningful in terms of the generation times of long-lived plant species. Although restoration of plant communities is possible following release from high levels of deer browsing, the time scale for monitoring recovery often requires decades rather than years (Anderson & Katz 1993; Rose, Suisted & Frampton 2004; Webster, Jenkins & Rock 2005; Long, Pendergast & Carson 2007). Studies of long-term (> 30 years) patterns of vegetation change rarely consider the influence of mammalian herbivory, and those that do are in the context of increasing herbivore populations (Rooney & Dress 1997; Schütz *et al.* 2003; Rooney *et al.* 2004) or focus on the recovery dynamics of individual species (Anderson & Katz 1993; Lee *et al.* 2000; Webster *et al.* 2005) or habitat types, e.g. forests (Stewart, Wardle & Burrows 1987; de la Cretaz & Kelty 2002) or grasslands (Rose & Platt 1987; Rose *et al.* 2004). Hence, much is still unknown about the outcomes of different restored communities within multi-habitat landscapes.

In New Zealand, several species of deer introduced for recreational hunting have become abundant in natural habitats. By the 1960s, red deer *Cervus elaphus scoticus* ranged over most of the country (King 2005), measurably impacting forest composition and structure by reducing populations of the most palatable species (Nugent *et al.* 2001b; Wardle *et al.* 2001; Husheer, Coomes & Robertson 2003; Husheer 2007). Similar impacts have been observed in grasslands, where the recovery times for native plants following reductions in deer densities may be in the order of decades (Rose & Platt 1987; Lee *et al.* 2000; Rose *et al.* 2004). Introduced red deer colonized our study site, the Murchison Mountains, Fiordland National Park, New Zealand, in the 1930s and reached relatively high densities (c. 11 deer km⁻²) in the late 1950s (Parkes, Tustin & Stanley 1978), measurably impacting vegetation (Wilmschurst 2003). Browsing by deer reduced the abundance of palatable species

in forests and subalpine shrub (Wardle, Hayward & Herbert 1971) and in grasslands, overgrazing reduced the stature and density of palatable tussocks (Mills, Lee & Lavers 1989). In their native range, red deer similarly alter vegetation composition, structure and dynamics when present at densities > 10 deer km⁻² (Côté *et al.* 2004). However, the impacts are likely to be greater in New Zealand because of the slow growth rate of native plants (Bee, Kunstler & Coomes 2007) and lack of specific adaptations of plants to mammalian herbivores (Bond, Lee & Craine 2004).

The objectives of our study were to test whether control of introduced red deer since 1962 has led to: (i) vegetation changes across a 518 km² landscape in New Zealand over a period of 39 years, and (ii) the recovery of earlier depleted deer-preferred species. Our study site is a unique example of long-term deer control, because the mountains have been prioritized for deer culling by successive governments to protect the habitat of the only remaining wild population of takahe *Porphyrio hochstetteri*, an endangered flightless rail (Mills & Mark 1977). We predicted that deer-palatable species would be initially uncommon, but that regeneration of these species would occur by the end of our study period, given that culls reduced deer to the levels at which regeneration of palatable species is thought to be possible (< 2 deer km⁻²; Husheer 2007) by 1986 (Nugent & Sweetapple 1989).

Materials and methods

STUDY SITE

The Murchison Mountains occupy an area of 518 km² within Fiordland National Park (45°14'S, 167°33'E; Fig. S1, Supporting information). The major soil types are Upland and Hill country podzolized yellow brown earths and podzols [New Zealand Department of Scientific and Industrial Research 1968]. There is a steep rainfall gradient from c. 2000 mm per annum in the east of the mountain range to c. 4000 mm in the west. Beech *Nothofagus* spp. forests and mixed beech–conifer forests comprise the majority of vegetation up to c. 1000 m a.s.l., and the forest ground layer is characterized in places by a dense cover of ferns, consisting of either *Blechnum discolor* or *Polystichum vestitum* (Wardle *et al.* 1971). Subalpine shrub vegetation forms a distinctive transition zone between the forest and grassland communities, with snow tussock grasslands *Chionochloa* spp. dominant above the shrub zone (above c. 1000 m a.s.l.; Wardle *et al.* 1971). Limited red deer control in the Murchison Mountains began in 1948, but population reductions were considered minimal until systematic culling began in 1962 (Parkes *et al.* 1978). Introduced wapiti *Cervus elaphus nelsoni*, possums *Trichosurus vulpecula* and chamois *Rupicapra rupicapra* are also controlled in the region, and have always occurred in very low numbers relative to red deer (King 2005).

ESTIMATES OF DEER POPULATION SIZE FROM A POPULATION RECONSTRUCTION MODEL

The minimum population size of red deer in the Murchison Mountains from 1964 to 2008 was estimated from known annual harvest rates of animals during state-managed culling. Accurate data on hunting effort and the number of deer killed annually are not available prior to 1964. Harvest rates were related to an estimated popula-

tion age-structure derived from 216 deer jawbones collected between 1998 and 2001 and that were aged from layers in the dental cementum (Fraser & Sweetapple 1993). A negative exponential curve was fitted to the age structure and used to predict the proportion of the total annual kill within or older than each age class. Population reconstruction (Downing 1980) was then applied to the harvest data using the minimum-number-alive technique (McCullough *et al.* 1990; see Appendix S1, Supporting Information).

MONITORING VEGETATION CHANGES IN FORESTS, SHRUBLANDS AND GRASSLANDS

Changes in forest vegetation were surveyed in 32 permanently marked 20 × 20 m plots that were located across the Murchison Mountains (Fig. S1, Supporting Information). Five of these plots were established in 1969, and the remaining 27 plots in 1976, at 270-m intervals along eight transects randomly located from valley floor to ridge crest. All plots were measured in 1976 and 1998. Twenty-nine plots were measured in 2008, with the remaining three measured between 2002 and 2006 and grouped with the 2008 measurements. Within each plot, we followed standard methods adopted in permanent forest plots (Hurst & Allen 2007). All tree seedlings (15–135 cm height) were identified by species and counted in systematically located circular understorey subplots ($n = 24$ per plot; 49 cm radius). Saplings (< 20 mm diameter at breast height, DBH, > 135 cm height) and trees (> 20 mm DBH; > 135 cm height) were counted within plots by species and recorded as either dead or alive.

Five exclosure plots (2.5-m tall fences) encompassing areas of 200–400 m² were established in the forest at unknown dates between 1960 and 1975. Locations were not random, but rather positioned on fertile soils where changes were expected to occur. Within each exclosure, the largest plot possible within the fenced boundaries was established in 1998. The exclosures were compared with either one or two control plots of identical size and positioned on opposite ends of the exclosure at a distance of up to 15 m. All of the exclosure and control plots were re-measured in 2004, and measurements were identical to methods used in the other forest plots.

Subalpine shrub vegetation across the Murchison Mountains was sampled in 22 permanently marked 2 × 5 m plots. Plots were located at 100-m intervals along seven randomly located transect lines established in 1975, and all plots were re-measured in 2000 (Fig. S1, Supporting Information). Plots were measured with a modified point-height intercept method (Scott 1965). At each of 50 points within a plot, a 5-cm diameter pole, 2 m in height, was positioned vertically into the plot so as not to disturb the vegetation by sideways displacement. Where an individual plant contacted the side of the pole within 180° of the north-west corner of the plot, the species and the height above the ground to the nearest 5 cm were noted. Ground cover below the pole was recorded as rock, soil, litter, moss or vegetation.

Alpine grassland vegetation was monitored in 19 permanently marked 20 × 20 m plots that were positioned at 76.2 m altitudinal intervals along six randomly located transects across the Murchison Mountains (Fig. S1, Supporting Information). Transects were established in 1969, and all plots were re-measured in 1976 and 2008. Similar to the forest plots, we followed standard methods applied to permanent grassland plots nationwide (Wiser & Rose 1997). We determined the frequency of occurrence of individual species in each plot by recording the presence of species in 50 circular quadrats. Circular quadrats were 15 cm in diameter and spaced at 40-cm intervals along a transect running through the centre of each plot. In 1976 and 2008, the maximum-extended leaf length and diameter of the dominant snow tussock *Chionochloa* spp. species nearest the centre of eight

randomly located points in each plot was recorded, and this was repeated for the nearest conspecific. The distance from each point to the nearest snow tussock, and distance from that snow tussock to its nearest neighbour were also recorded to estimate tussock density per plot (see Appendix S1, Supporting Information for details).

STATISTICAL ANALYSES

Changes in individual species: Trends in seedling and sapling densities were analysed in R version 2.7 (R Development Core Team 2008) after grouping forest species into the following deer diet choice preference classes: highly preferred, preferred or less preferred (Table S1, Supporting Information). Classifications were based on reviews of ungulate diet preferences across New Zealand (Nugent *et al.* 2001b; Forsyth *et al.* 2002). Linear-mixed effects models were fitted to the data (*lmer* in the *lme4* package) with plots entered as a random factor and a Poisson error structure was used since the data represented counts. As a result of the non-random location of exclosures, we compared permanent forest plots separately from exclosure plots and their corresponding controls. Transects were not included as a random effect in any of our models as they did not explain additional variance to that accounted for by plot effects. The palatability of species to deer, measurement period (as a blocking factor), and the effects of exclosure treatment (where appropriate) were entered as fixed factors along with interactions among these factors. The significances of model parameters were estimated by comparisons to a probability distribution obtained by 10 000 Markov Chain Monte Carlo simulations (*mcmc* function in *lme4* package). This approach is more applicable for testing mixed effects models than conventional ANOVA *F*-tests, particularly for small sample sizes (Baayen, Davidson & Bates 2008), and we report significance tests as P_{MCMC} . No *F*-statistics or degrees of freedom are calculated for mixed models.

We also compared the ratio of numbers of seedlings to mature trees among permanent forest plots over all measurement periods for 25 species to further determine the extent to which regeneration was occurring across our site. Species were pooled in these analyses according to palatability. The ratio of seedlings to trees was square-root transformed to normalize the data, and linear models were used to predict the effects of palatability and measurement period. We also compared exclosures with their corresponding controls between 1998 and 2004 to determine the effect of exclosure treatment, and only 11 species were common to both sets of plots. *F*-statistics are reported for these models as no random effects were considered.

We followed similar statistical procedures to determine changes in shrubland and grassland composition and structure. We tested for changes among measurement periods in the number of palatable and unpalatable species per plot and the total number of occurrences of these species using linear-mixed effects models, with plots as a random factor. Additional palatability classifications of 38 palatable and 56 unpalatable shrubland and grassland species derived from observed browse damage in the Murchison Mountains (Mills & Mark 1977; Bee *et al.* 2009; S. Lake & R. Ewans, unpublished data) enabled us to group species that occurred in our plots as either palatable or unpalatable (Tables S2–S3, Supporting Information). We also used mixed effects models to determine whether changes within individual shrubland height tiers within each plot significantly differed over time, using height as a random factor nested within plots. Changes in grassland structure were determined from comparing snow tussock height and diameter per cover point, and density per plot, between 1976 and 2008 with mixed effects models, with plots as a random factor. A Poisson error structure was applied for count data (number of species and occurrences), and tussock data were square-root transformed.

Changes in overall community composition: forest, shrubland and grassland communities were each analysed separately following the same methods. To determine whether plots changed in composition over time we used analysis of variance with Bray-Curtis distance matrices (*adonis* function in *vegan* package, R version 2.7; see Appendix S1, Supporting Information for details). Where plots differed significantly over time, we examined temporal trends for all species of known palatability to deer with a separate linear-mixed effects model for each species, entering plots as a random factor and measurement period as a fixed blocking factor. A Poisson error structure was applied for the forest plots as the data represented seedling or sapling counts. Lastly, we used non-metric multidimensional scaling ordination with Bray-Curtis distance measures to relate the degree of compositional changes in plots that differed over time to environmental factors (see Appendix S1, Supporting Information for details). Compositional change was calculated as the distance in the ordination space between observations of the same plot at two different measurement periods. Plots with larger distances between measurement periods were less similar than plots that were closer together in the ordination. No environmental variables were correlated with compositional changes (Table S4, Supporting Information).

Results

DEER POPULATION DENSITY

Deer population density has declined significantly over time in the Murchison Mountains from the greatest density recorded of 8.7 deer km⁻² in 1964 to a low of 0.58 deer km⁻² in 1988 (Mann-Kendall trend test: $\tau = -0.612$, $P < 0.001$; Fig. 1). This period does not include the period of estimated peak densities (c. 11 deer km⁻²) in the late 1950s (Parkes *et al.* 1978). Between 1988 and 2000, deer densities rose to between 0.6–1.1 deer km⁻², representing increases of up to 83% ($\tau = -0.891$, $P < 0.001$) and reflecting fewer deer being culled over time ($\tau = -0.316$, $P = 0.002$; Fig. 1). Increased numbers of deer killed from 2000 onwards has since reduced densities to the levels that were observed during the late 1980s to early

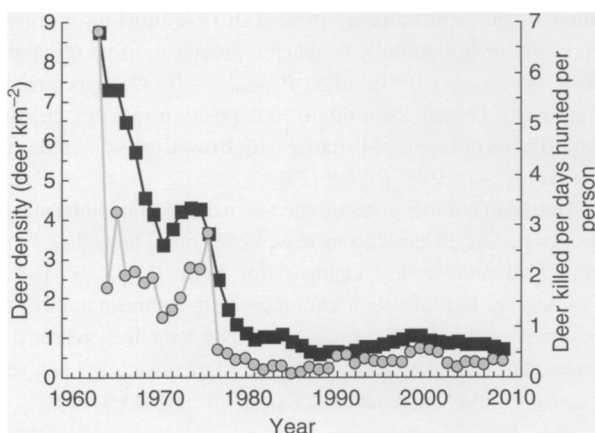


Fig. 1. Estimated annual red deer density in the Murchison Mountains (square symbols) and annual number of deer killed per days of ground hunting per person (circle symbols; New Zealand Department of Conservation, unpublished data), 1964–2008.

1990s, i.e. < 0.8 deer km⁻² (Fig. 1). Overall, the c. 92% reduction in the minimum number of deer alive in each year between 1964 and 2008 is mirrored by similar reductions in the actual number of deer culled annually (94%) and the number of deer killed per days of ground hunting per person (93%). Densities differed from the mean among habitats since animals are not evenly distributed among forests, shrublands and grasslands (Nugent & Sweetapple 1989).

PERMANENT FOREST PLOTS

The regeneration of deer-preferred species was limited both in absolute numbers and relative to the abundances of adult trees. Less preferred seedlings and saplings were most common whilst highly preferred species were least common (for both seedlings and saplings, $P_{\text{MCMC}} < 0.001$; Fig. 2a,b). Similarly, the ratio of seedlings to adult trees also differed with palatability: highly preferred species were the only palatability class with a mean ratio of < 1 seedling per adult ($F_{2,66} = 4.34$, $P = 0.017$; Fig. 2c).

We predicted that the regeneration of deer-palatable species would occur following reductions in deer densities, and densities of both seedlings and saplings significantly increased between 1976 and 2008 ($P_{\text{MCMC}} = 0.048$ and $P_{\text{MCMC}} < 0.001$ respectively; Fig. 2a,b). The mean number of seedlings per adult tree across species also increased from 0.7 in 1976 to 2.1 in 2008, with the greatest relative increases occurring for highly preferred species ($F_{2,66} = 4.27$, $P = 0.018$; Fig. 2c). A decline over time in the number of adult trees per plot contributed to the increased ratios, reflecting self-thinning processes since total basal area per plot increased, but cannot entirely explain the magnitude of increases in the ratio of seedlings to adults (Table S5, Supporting Information). In particular, the relative abundance of adults of highly preferred species declined the least among palatability classes (Table S5, Supporting information), suggesting that increased ratios of highly preferred species were largely a result of greater seedling densities. Although highly preferred seedlings and saplings, and the ratio of highly preferred seedlings to adult trees, increased with time, absolute values exceeded neither densities nor ratios of the other palatability classes (for all, P_{MCMC} or $P > 0.200$).

Sapling, but not seedling, community composition changed significantly over time ($F_{2,95} = 0.43$, $P = 0.012$ and $F_{2,95} = 0.36$, $P = 0.616$ respectively). Between 1976 and 2008, 17 species were significantly more abundant, and two significantly less abundant, with a greater percentage of highly preferred and preferred species increasing in abundance compared with less preferred species (Table S1, Supporting Information).

DEER EXCLOSURE PLOTS IN FORESTS

Exclosure and control plots were not entirely representative of the forest as a whole, and this was probably because of their position on fertile sites. In 1998 and 2004, preferred seedlings and saplings were most abundant across exclosures and controls, and less preferred species were least abundant (seed-

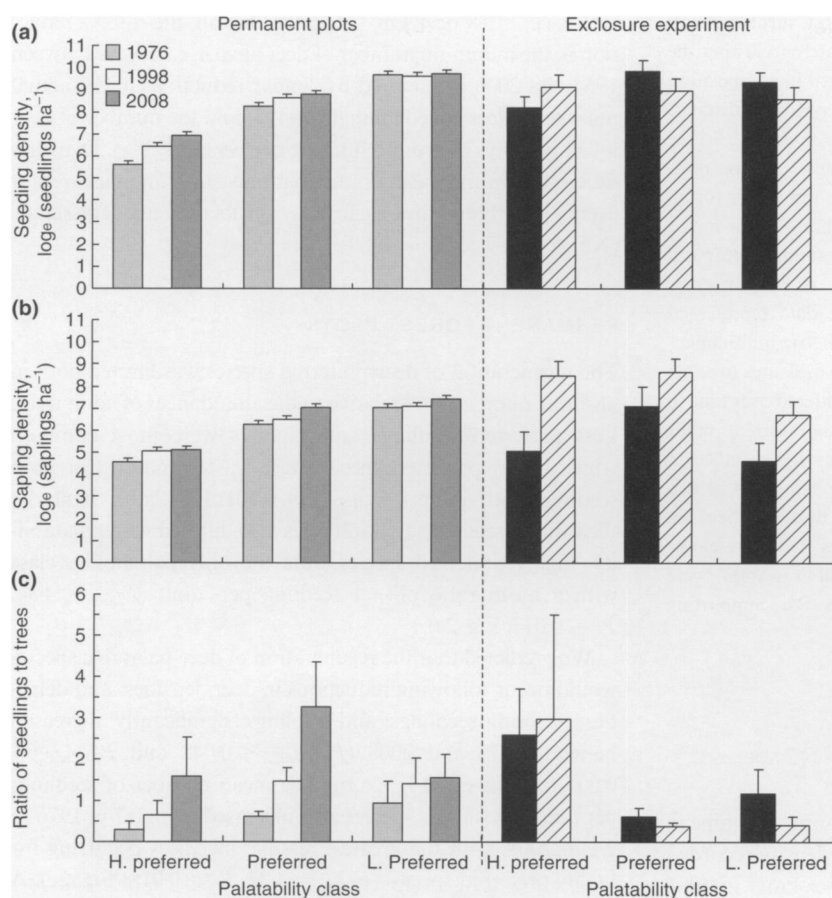


Fig. 2. (a) Mean seedling and (b) mean sapling densities, and (c) mean ratio of seedlings to adult trees, for permanent forest plots ($n = 32$) in 1976 (light grey bars), 1998 (open bars), and 2004 (dark grey bars), and exclosures (hatched bars, $n = 5$) and their corresponding control plots (black bars, $n = 8$) in 2004. Bars are standard error of the mean. Means are classified into three deer palatability classes: highly preferred, preferred and less preferred (Forsyth *et al.* 2002). Only 2004 values are plotted for exclosures and exclosure-control plots since densities did not vary between 1998 and 2004 (see text).

lings, $P_{\text{MCMC}} = 0.031$; saplings, $P_{\text{MCMC}} < 0.001$; Fig. 2a,b), whereas the converse was true for the permanent forest plots. The ratio of seedlings to adult trees did not differ among palatability classes ($F_{2,32} = 2.10$, $P = 0.140$), and the larger ratio of seedlings to adult trees for highly preferred species reflected the high ratio of seedlings to adults of *Myrsine australis* compared with all other species in the group (10.8 vs. 0.9 respectively; Fig. 2c). No interaction terms were significant (for all, $P > 0.650$).

We predicted that the regeneration of deer-palatable species would increase in response to deer exclusion, and sapling densities for all palatability classes were significantly greater within exclosure plots than in controls by 1998 (23–38 years after fences were erected). This difference persisted in 2004 ($P_{\text{MCMC}} = 0.006$; Fig. 2b). The greater densities within exclosures suggested that deer were still limiting recruitment outside the exclosures, and the difference between exclosures and controls was greatest for highly preferred species (interaction between palatability and exclosure treatment: seedlings, $P_{\text{MCMC}} = 0.310$; saplings, $P_{\text{MCMC}} < 0.001$). Conversely, seedling densities occurred at similar densities within exclosures and browsed control plots in 1998 and 2004 ($P_{\text{MCMC}} = 0.520$; Fig. 2a), and the ratio of seedlings to adult trees did not differ between exclosure and control plots and did not change over time ($F_{1,32} = 0.498$, $P = 0.486$ and $F_{1,32} = 0.338$, $P = 0.565$ respectively). Neither the densities of saplings nor seedlings changed over time ($P_{\text{MCMC}} > 0.400$).

SHRUBLANDS

The number of palatable species per height tier but not plot increased over time, partially consistent with our prediction of greater palatable species regeneration in response to deer culling ($P_{\text{MCMC}} = 0.002$ and $P_{\text{MCMC}} = 0.124$ respectively; Fig. 3a,b). Unpalatable species were also more abundant within height tiers over time but did not change within individual plots, suggesting that the crowns of both palatable and unpalatable shrubs already present in 1976 must have grown vertically or horizontally to reach a greater number of height tiers ($P_{\text{MCMC}} = 0.002$ and $P_{\text{MCMC}} = 0.499$ respectively; Fig. 3a,b). Overall community composition did not change within plots (analysis of variance with Bray-Curtis dissimilarity matrix, $F_{1,42} = 0.38$, $P = 0.120$).

The mean number of occurrences of palatable and unpalatable species per height tier also increased over time, suggesting both horizontal and vertical changes (for both $P_{\text{MCMC}} < 0.001$; Fig. 3c). The lack of a significant increase in the mean number of occurrences of palatable species at the plot-level likely reflected a lower statistical power for plot-level comparisons (palatables, $P_{\text{MCMC}} = 0.085$; unpalatables, $P_{\text{MCMC}} < 0.001$; Fig. 3d).

GRASSLANDS

We predicted greater regeneration of palatable species in response to deer culling, and the number of palatable species

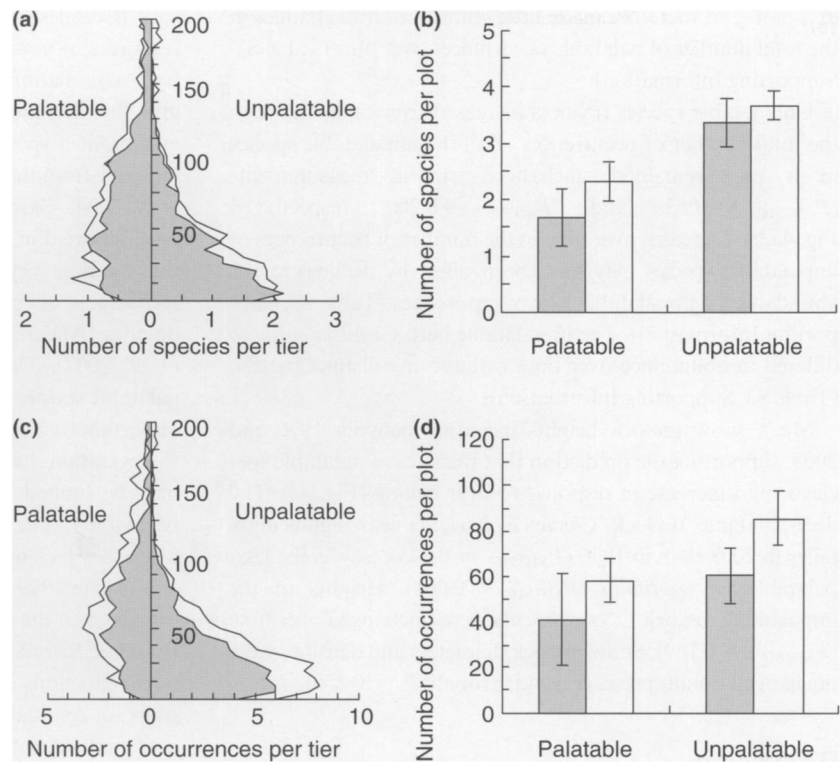


Fig. 3. Subalpine shrub species composition and structure in 1975 (grey bars) and 2000 (open bars). (a) Mean number of palatable and unpalatable species per 5 cm height tier and (b) per plot. (c) Mean number of occurrences of all palatable and unpalatable species within 5 cm height tiers, and (d) per plot. Bars are standard errors of the mean, and are not plotted in (a) and (c) for clarity.

per plot increased over time ($P_{\text{MCMC}} = 0.045$; Fig. 4a), leading to changes in overall grassland community composition ($F_{2,54} = 2.19$, $P < 0.001$). Five species that were present in 2008 and absent in 1969 were uncommon, never occurring more than twice per plot and contributing little to the total

number of occurrences of all palatable species within a plot, which did not change over time ($P_{\text{MCMC}} = 0.245$; Fig. 4b). Similarly, increased abundance of the palatable herb *Dolichoglottis scorzonoides* between 1969 and 2008 represented < 5% of the total number of occurrences of palatable species

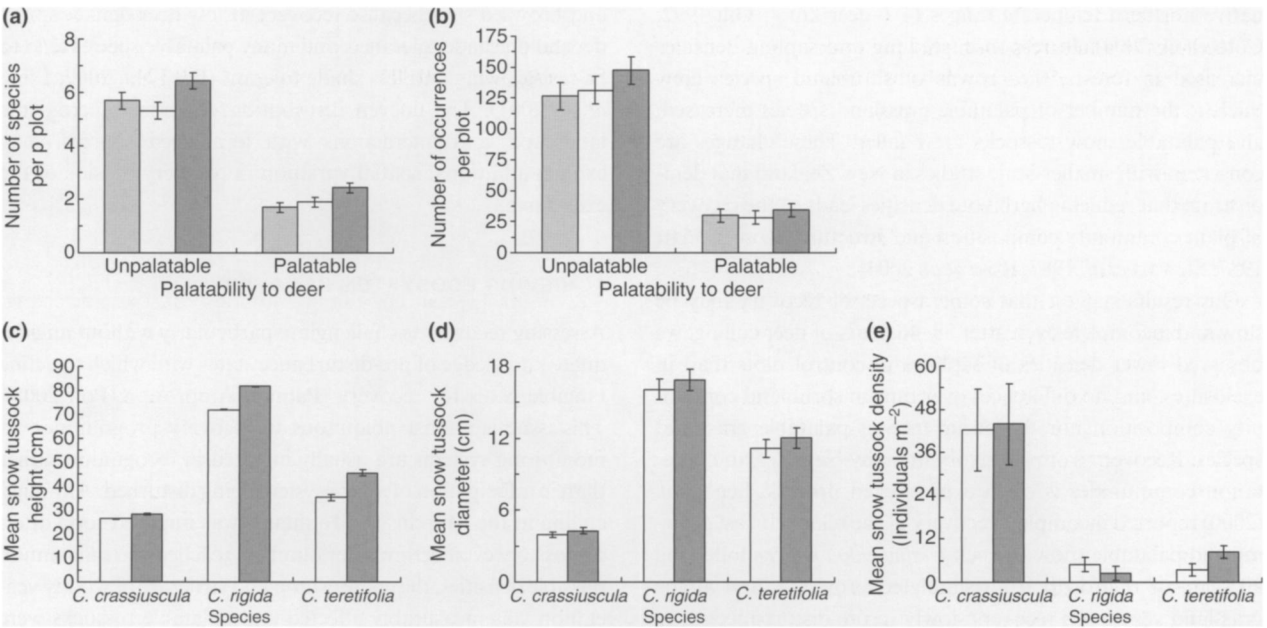


Fig. 4. Composition and structure of 19 grassland plots in the Murchison Mountains in 1969 (light grey bars), 1976 (white bars) and 2008 (dark grey bars). (a) Number of species per plot and (b) number of occurrences per plot of species that can be classified as either unpalatable or palatable to deer. (c) Height, (d) diameter and (e) density of the dominant snow tussock species *Chionochloa* spp. per plot. Bars are standard errors of the mean.

in a plot, and therefore made little contribution to changes in the total number of palatable occurrences over time (Table S3, Supporting Information).

Unpalatable species richness increased over time, although the total number of occurrences of all the unpalatable species in a plot remained unchanged among measurements ($P_{\text{MCMC}} = 0.083$ and $P_{\text{MCMC}} = 0.200$ respectively; Fig. 4a,b). Increases over time in the number of occurrences of unpalatable species may have been offset by declines in the abundance of unpalatable *Carex* spp. sedges (Table S3, Supporting Information). The unpalatable herb *Celmisia coriacea* differed in abundance over time without any distinct pattern (Table S3, Supporting Information).

Mean snow tussock heights increased between 1976 and 2008, supporting the prediction that the sizes of palatable species would increase in response to deer culling (Fig. 4c). The deer-palatable tussock *Chionochloa rigida* was significantly taller in 2008 than in 1976 ($P_{\text{MCMC}} = 0.033$), as was the less-palatable *C. teretifolia* ($P_{\text{MCMC}} < 0.001$). Heights of the unpalatable tussock *C. crassiuscula* were unchanged over time ($P_{\text{MCMC}} = 0.169$). Snow tussock diameters and densities were unchanged for all species (Fig. 4d,e; for all, $P > 0.250$).

Discussion

LIMITED VEGETATION CHANGE DESPITE DEER CONTROL

Red deer densities in the Murchison Mountains were reduced below the threshold predicted for palatable tree regeneration at another site in New Zealand (< 2 deer km^{-2} ; Husheer 2007), and were considerably less than the densities predicted to allow regeneration of browse-intolerant plants in their native northern temperate ranges (4–6 deer km^{-2} ; Gill 1992; Côté *et al.* 2004). In response, seedling and sapling densities increased in forests, the crowns of shrubland species grew thicker, the number of palatable grassland species increased, and palatable snow tussocks grew taller. These changes are consistent with smaller-scale studies in New Zealand that demonstrate that reducing herbivore densities leads to the recovery of plant community composition and structure (Rose & Platt 1987; Stewart *et al.* 1987; Rose *et al.* 2004).

Our results suggest that some aspects of recovery may be slow and incomplete even after 38–46 years of deer culling: we observed lower densities of saplings in control plots than in exclosures, and no differences over time in shrubland community composition nor the occurrence of palatable grassland species. Recovery from herbivory in many New Zealand vegetation communities is often a protracted process: Lee *et al.* (2000) reported incomplete recovery of the relatively fast growing and palatable snow tussock *Chionochloa pallens* following 20 years of re-growth from simulated browsing, and alpine grassland vegetation recovers slowly to pre-disturbance states (Lloyd *et al.* 2003). The slow growth rates of New Zealand species relative to elsewhere in the world may contribute to the slow re-growth of plants following browse damage (Bee *et al.* 2007). This response may occur as a result of nutrient-poor

soils (Coomes *et al.* 2005), a disproportionate allocation of resources in younger more palatable leaves to maximize carbon assimilation (Gaxiola-Alcántar 2006), which inhibits growth when these leaves are preferentially removed, and the evolution of species under disturbance regimes that differ in intensity from those imposed by mammalian herbivory (Bond *et al.* 2004). Slow recovery from high deer densities has also been reported in northeastern North American forests, where the lag time between reductions in deer densities and the recruitment of certain palatable species may be in the order of decades (Anderson & Katz 1993; Webster *et al.* 2005; Long *et al.* 2007). Deer reduce local seed sources from which palatable species recruit (Côté *et al.* 2004), and this may be an important bottleneck in restoring disturbed ecosystems.

Vegetation recovery in response to herbivore reductions may be limited by several factors related to deer foraging behaviours. Deer frequently consume less-palatable species when they lack more nutritious food sources (Latham, Staines & Gorman 1999; Bee *et al.* 2009), even consuming litterfall as forage when the availability of live vegetation is low (Nugent, Fraser & Sweetapple 2001a; Takahashi & Kaji 2001). Therefore, reductions in deer density may not reduce browse pressures on residual palatable plants, but rather, the remaining deer may narrow their diet towards more desirable species when competitors are removed (Nugent *et al.* 2001a; Coomes *et al.* 2003). This may explain why abundances and heights of some unpalatable species increased following reductions in herbivore densities. Less-palatable plants that established during high deer densities may also inhibit the regeneration of other more palatable species through asymmetric competition for light or nutrients, resulting in altered successional trajectories (de la Cretaz & Kelty 2002; Husheer *et al.* 2006). This may account for differences in palatable species between exclosures and browsed sites because recovery at low deer densities may depend on shade tolerance, and many palatable species tend to be fast-growing and less shade tolerant (Bee *et al.* 2007; Long *et al.* 2007). The uneven distribution of animals across the landscape, and interactions with local seed sources, may explain additional spatial variation in recovery outside of the exclosures.

ACHIEVING ECOSYSTEM RECOVERY

Assessing recovery is challenging, particularly without an adequate knowledge of pre-disturbance states with which to define tangible goals for recovery (Palmer, Ambrose & Poff 2003). This issue is almost ubiquitous to recovery programmes, as monitoring systems are usually initiated in recognition rather than in anticipation of an ecosystem being disturbed. Although culling in the Murchison Mountains was imposed soon after, or possibly even before, deer numbers reached their maximum possible densities, the composition and structure of woody vegetation was measurably affected and palatable tussocks were reduced in height or entirely removed within 20–30 years of deer invasion (Holloway 1950; Wardle *et al.* 1971; Mills *et al.* 1989; Mark 1989). Pollen analyses have revealed significant declines in deer-palatable grasses, sedges, trees and under-

storey herbs during the period of peak deer densities (Wilms-hurst 2003).

Species-specific management approaches to controlling invasive non-native species are often unsuccessful in allowing ecosystems to recover to their pre-disturbance states (Zavaleta, Hobbs & Mooney 2001). At our site, the reduction of red deer populations is yet to result in landscape-level increases in the abundances of most palatable species, although some deer-palatable species have increased in abundance and stature. Deer affect ecosystem properties such as nutrient cycles in addition to directly influencing plant community composition and structure, and as such, the removal of large numbers of animals may not precipitate a return to a pre-deer disturbed state (Wardle *et al.* 2001; Côté *et al.* 2004). Altered successional trajectories occur particularly where herbivores interact with other disturbances (Royo & Carson 2006). As a result, management approaches that focus solely on herbivore removal rather than addressing the ecosystem-level effects of herbivory are unlikely to result in successful ecosystem restoration within a multi-disturbance environment.

Restoration of ecological processes and functioning may be a more achievable goal than restoring a given compositional state (Palmer *et al.* 2003). Small-scale active management strategies that restore either pre-disturbance ecological processes and/or biota may be a viable alternative for accelerating recovery via 'natural' processes (Atkinson 2001; Benayas, Bullock & Newton 2008). Such strategies have been successfully applied to restore other systems in which herbivore removal has not facilitated vegetation recovery (Handa & Jefferies 2000). Fencing established palatable plants, planting or seeding palatable species within deer exclosures, and in some regions, re-introducing ecological engineers or predators that restore ecological processes may also accelerate recovery (e.g. Wolf *et al.* 2007). However, our results suggest that vegetation recovery in response to extensive herbivore reductions occurs on the time scale of decades, and given the difficulty in uniformly eliminating deer even with high culling effort, land-managers should accept that rapid and complete ecosystem recovery is unlikely. Managers may instead need to develop long-term strategies to maximize desired gains at lowest possible cost, e.g. it may be more economically sustainable to maintain herbivores at low densities that cause only slightly more damage than if these species were removed. An alternative strategy where seed sources persist may be to delay major investment in herbivore control until natural or induced disturbances create large-scale opportunities for regeneration of palatable plants.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Location of plots in the Murchison Mts., New Zealand.

Table S1. Mean number of saplings per forest plot

Table S2. Palatability of shrubland species

Table S3. Mean percentage occurrences per grassland plot

Table S4. Correlations between environmental factors and compositional changes

Table S5. Changes in adult trees

Appendix S1. Supporting methods (extended methods description).

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