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Impacts of culling and exclusion of browsers on vegetation recovery across New Zealand forests

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ABSTRACT

Introduced browsing animals negatively impact New Zealand's indigenous ecosystems. Eradicating introduced browsers is currently unfeasible at large scales, but culling since the 1960s has successfully reduced populations to a fraction of their earlier sizes. Here we ask whether culling of ungulates has allowed populations of woody plant species to recover across New Zealand forests. Using 73 pairs of permanent fenced exclosure and unfenced control plots, we found rapid increases in sapling densities within exclosures located in disturbed forests, particularly if a seedling bank was already present. Recovery was slower in thinning stands and hampered by dense fern cover. We inferred ungulate diet preference from species recovery rates inside exclosures to test whether culling increased abundance of preferred species across a national network of 574 unfenced permanent forest plots. Across this network, saplings were observed irrespective of their preference to ungulates in the 1970s, but preferred species were rarer within disturbed sites in the 1990s after long-term culling and despite nationwide increases in sapling densities. This indicates that preferred species are relatively heavily affected by browsing after culling, presumably because remaining animals will increase consumption of preferred species as competition is reduced. Our results clearly suggest that culling will not return preferred plants to the landscape immediately, even given suitable conditions for regeneration. Complete removal of ungulates rather than simply reducing their densities may be required for recovery in heavily browsed temperate forests, but since this is only feasible at small spatial scales, management efforts must target sites of high conservation value.

1. Introduction

Browsing ungulates strongly influence the dynamics of temperate forests, often to the detriment of habitat conservation and timber production. They are particularly problematic where they are non-native and their population density is high (Putman and Moore, 1998; Takatsuki, 2009). Culling has been used to reduce ungulate populations (Côté et al., 2004; Milner et al., 2006), but assessing the effectiveness of control programmes in terms of vegetation "recovery" is challenging; responses of plant populations to browsing are spatially variable and it is difficult to manipulate ungulate densities across large spatial scales (Hester et al., 2000). Further, long-term (i.e. decades) data are required to detect changes in population sizes of most woody plants because of their relatively slow responses to reductions in ungulate browsing (Tanentzap et al., 2011a, 2009). As resources for conservation management are often limited, an understanding of the regeneration requirements of woody species is required to prioritize sites where ungulate culling is most likely to result in vegetation recovery.

We use data collected over 33 years from fenced exclosures and adjacent, unfenced areas at 73 sites located throughout New Zealand forests to predict population recovery of woody plants within the reach of browsing ungulates (i.e. <2 m above ground level). Seven species of deer (all Cervidae), as well as goats (*Capra hircus*), were introduced into New Zealand in the 19th and 20th centuries (Nugent and Fraser, 2005). These introduced browsers, particularly deer, spread rapidly, depleting preferred forage from forest understories and providing opportunities for unpalatable species to dominate communities (Allen et al., 1984; Husheer et al., 2003; Veblen and Stewart, 1982). Concern that introduced browsers prevent regeneration of indigenous forests has led to a number of government sponsored culling programmes since the 1930s, with the

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number of deer culled nationally reaching a peak in the 1960s and 1970s (Travers, 1964; Davidson and Fraser, 1991; Jane, 1994; Nugent and Choquenot, 2004). By the 1990s, deer densities were reduced by 90% across South Island forests (Challies, 1991), due to both culling and depletion of food supplies (Forsyth and Caley, 2006; Forsyth et al., 2011). There were similar reductions in densities of goats across much of their range (Parkes, 2001, 1993). During the 1970s and 1980s many exclosures were established to ascertain the ongoing impacts of ungulates and to discover whether forests were recovering in areas in which ungulates were being culled (Allen et al., 1984; Bellingham and Allan, 2003; Husheer et al., 2005; Jane and Pracy, 1974; Smale et al., 1995). We compare plots in these exclosures with unfenced control plots in which browsing pressure is probably much reduced from levels in the 1960s, in order to test the effectiveness of culling programmes in allowing population recovery at a broad spatial scale.

Local environmental variation influences plant regeneration and may obscure the effectiveness of culling. Fast-growing species that are preferred by ungulates should respond positively to herbivore removal (Bee et al., 2007), but since these species are often light-demanding (Krueger et al., 2009), disturbances that increase canopy gaps may be required before recovery is possible (e.g. Coomes and Allen, 2007; Coomes et al., 2003; Runkle, 1982). For example, growth rates of Canadian *Abies balsamea* seedlings increased as deer density declined in forests that had been subjected to clear-cutting but were unchanged within intact, shaded stands (Tremblay et al., 2007). Recent analyses in New Zealand forests indicate that some highly ungulate-preferred species increase in abundance and re-enter the canopy of disturbed stands within 30 years after browsers are excluded (Mason et al., 2010). We expect to find similar responses within the understorey with recovery of fast-growing, ungulate-preferred species occurring primarily in disturbed stands.

We also expect to find recovery of less preferred species because as ungulates deplete stands of highly-preferred fast-growing species, they are forced to consume less-preferred, slow-growing species, leading eventually to reductions in herbivore density as the total food resource is reduced (Caughley, 1970; Nugent et al., 2001; Tremblay et al., 2005). Consequently, we predict recovery of both preferred and less preferred saplings within exclosures, but because they are slower growing, the latter group may take many years to reach the canopy layer.

The pattern of recovery following culling should also differ from that following complete herbivore removal. Exclusion of ungulates leads to the recovery of fast-growing, highly palatable species (Mason et al., 2010; Tanentzap et al., 2009, 2011a), but these species may not recover following culling because even when the plants are rare, they are preferentially targeted by ungulates (Nugent et al., 2001). Ungulates subsisting on less-preferred species will switch diets to more highly preferred species as soon as they become available, suppressing population recovery. Thus, while both preferred and less-preferred species should recover following complete exclusion of herbivores, we predict culling should result in recovery of less-preferred, slow-growing species but not preferred fast-growing species.

Availability of seeds and establishment sites can also influence how woody species respond to reductions in herbivory (Liang and Seagle, 2002; Wilson et al., 2006). Sites with abundant mature trees are anticipated to recover relatively quickly because plentiful seed will be available. A dense layer of seedlings on the forest floor is likely to be equally effective. However, unpalatable species may also form a dense ground layer at some sites, competitively inhibiting seedling regeneration. For example, monospecific stands of hay-scented fern (*Dennstaedtia punctilobula*) establish under intense browsing in the understorey of eastern US forests and cast a deep shade that suppresses growth of seedlings of trees that leaf-out in late spring while species with earlier foliar development are unaffected (de la Cretaz and Kelty, 2002). In New Zealand forests dense fern layers are widespread (Coomes et al., 2003; Gaxiola et al., 2008), and we predict that recovery will decline with increasing fern dominance.

We test how herbivore diet selection and local environmental variation affect woody vegetation recovery following ungulate removal by addressing the following questions: (a) is disturbance required for recovery? (b) Is this recovery positively related to the growth rate of species? And (c) do seed and establishment limitation constrain recovery? We first quantify ungulate diet preference using data from a series of ungulate exclosure and control plots, measuring preference by comparing the extent to which woody species have increased within exclosure relative to control plots. We then use this measure of diet preference to explain changes in the density of woody plants over time in a separate network of 574 permanent forest plots, aiming to determine whether culling in recent decades has returned ungulate-preferred species to the national landscape.

2. Methods

2.1. Data recorded on permanent control and exclosure plots

We used data from 73 sites, each consisting of a pair of exclosure and unfenced ("control") plots which had been measured at least twice, with an average interval of 16 years between censuses (see Fig. S1 in Supplementary material). Plots were 20 m × 20 m in size and sampled using standard methods (Hurst and Allen, 2007). All stems >1.35 m tall and with diameter at breast height (dbh) >30 mm were tagged, had their dbh measured and were identified to species. Saplings of each species were counted, saplings being defined as woody stems >1.35 m tall and <30 mm dbh. The presence or absence of small seedlings (stems <15 cm tall) was recorded on twenty-four 0.75 m^2 subplots within each plot. Large seedlings (stems >15 cm and <1.35 m tall) were counted within the subplots but were too sparse to be considered further in our analysis. These sites also provided some of the tree data analysed by Mason et al. (2010), but we concentrate on the temporal responses of sapling densities because they allow us to investigate the responses of both fast and slow-growing species to browser exclusion; slower growing stems may not have grown large enough during the study period to be counted by Mason et al. (2010).

The sites had often been selected to monitor the effectiveness of ungulate control operations in areas where ungulate impacts were of concern to conservation managers. Although we have no information on the initial density of ungulates or changes over time at individual sites, it is likely that ungulates were sufficiently abundant at these sites to impact forest regeneration (Forsyth et al., 2002). From 1950 to 1970 ungulate populations were substantially reduced within most of the regions in which our study sites were located, reaching minimums during the 1980s and 1990s, and increasing in recent years (Forsyth et al., 2011).

2.2. Data recorded on national forest plot network

We used data from 574 permanently marked plots which comprise part of the National Vegetation Survey Databank of New Zealand (Wiser et al., 2001), registered in the Global Index of Vegetation Plot Databases (Dengler et al., 2011). Plots were 20 m × 20 m and measured using identical methods to the control and exclosure plots (Hurst and Allen, 2007). We selected plots that have been measured at least twice and, for those in which multiple censuses have been carried out, we chose the oldest and the most recent censuses. The selected plots are nested within 24 survey areas, with each survey area containing from 4 to 94 plots, and with the survey areas spread throughout New Zealand indigenous forests (Fig. S1). Start dates and census intervals differ both between and within survey areas with an average census interval of 16 years (earliest census 1972 and most recent 2002).

2.3. Relating recovery in exclosure and control plots to disturbance, growth, and seed and establishment limitation

Analyses were restricted to the 43 most common species in the exclosure and control plots, defined as those present at over 10% of sites or constituting at least 10% of the total number of adults or saplings found across sites (Table S1). For each species we calculated the annual rate of population change in control plots proportional to the initial population size (R_C):

$$R_C = \frac{1}{100 \times \Delta t}\left(\frac{C_2 - C_1}{\overline{C_1}}\right), \tag{1}$$

where C_1 and C_2 are the number of saplings at the initial and final censuses, Δt is the census interval and $\overline{C_1}$ is the mean count across all control plots in which the species was initially present. In the majority of cases populations increased in size over time so we henceforth refer to positive changes simply as recovery. Expressing recovery as an annual rate allowed meaningful comparisons among sites that differed in census interval. Recovery in exclosures (R_X) was calculated in the same way. Additional recovery in exclosures (over and above that occurring in the control plots) was calculated for each site as $R_E = R_X – R_C$. Recovery indices were cube-root-transformed prior to statistical modelling, in order to make distributions approximately normal and prevent several populations that underwent very small or large changes in stem density from exerting undue leverage on model estimates. Transformation of the data also proved to be the most tractable approach after attempting to fit models with various non-normal error distributions.

We modelled R_E and R_C to explore the extent of recovery in unbrowsed and browsed forests, respectively. Species effects were included in the models as normally-distributed random variables. The following variables were included as fixed effects to test four predictions:

1. *Stand Development Phase (SDP)* was included to test whether recovery was fastest in disturbed forests. Using the approach developed by Coomes and Allen (2007), stands were categorised as "thinning" if the number of stems decreased, and mean tree size increased, between the two censuses. All other stands were categorised as "disturbed".
2. *Growth rates of trees of each species (G)* were included to test whether faster growing species recovered more rapidly than slower-growing species. Diameter increments were calculated in both the exclosure and national-level forest plot datasets for all small stems (30–80 mm dbh) because we expected these to represent sapling growth rates more closely than diameter increments calculated for large canopy trees. We converted diameter increments to an annual growth rate as $\Delta d/\Delta t$, where Δd is the change in diameter over the census interval Δt. Growth of small trees is approximately linear with size for New Zealand species (Coomes et al., 2011). We then fitted a mixed-effects model with annual growth rate as the response, and with site and species as normally distributed random effects, and extracted median rates predicted for each species for use in modelling R_E and R_C.
3. *Seedling abundance (SA)* was included to test whether recovery was fastest in sites where seedlings were already established (i.e. low establishment limitation). Seedling abundance was estimated as the proportion of subplots occupied by each species.
4. *Fern cover (F)* was included to test whether dense fern layers impeded regeneration. F was estimated for each site as the proportion of subplots occupied by large fern species (Appendix S1 lists the species included).

Fixed effects (G, SA, and F) were standardised (i.e. centred around the mean with a standard deviation of 1) so that effect strengths could be directly compared with one another; none of the fixed effects were strongly inter-correlated (Spearman's rank correlation, $\rho < 0.11$). We included interactions between SDP and all other variables, to test whether responses differed between disturbed and thinning forests. Hence, our model for recovery in exclosures had the form:

$$R_E = \alpha_{D1} + \alpha_{D2}G + \alpha_{D3}SA + \alpha_{D4}F + \varepsilon_{D1} + \varepsilon_D, \text{in disturbed forests},$$

$$R_E = \alpha_{T1} + \alpha_{T2}G + \alpha_{T3}SA + \alpha_{T4}F + \varepsilon_{T1} + \varepsilon_T, \text{in thinning forests},$$

where α_{D1}, α_{D2}, α_{D3}, α_{D4}, α_{T1}, α_{T2}, α_{T3}, α_{T4} are coefficients associated with fixed effects, ε_{D1} and ε_{T1} are species effects drawn from normal distributions and ε_D and ε_T are residual error terms. Identical models were fitted to predict recovery in controls (R_C).

2.4. National recovery of ungulate-preferred saplings

We tested whether species highly preferred by ungulates recovered across New Zealand forests in response to culling. We used R_E as a measure of ungulate preference, consistent with other studies (Tanentzap et al., 2011a; Wardle et al., 2001). Species with $R_E > 0$ increased following ungulate exclusion relative to the controls (high inferred preference), while those with $R_E \leqslant 0$ declined when ungulates were excluded (low inferred preference). Our approach was to estimate the probability (p) of observing saplings of each species within plots in the national-level dataset when conspecific adults were present (i.e. presence or absence of saplings was recorded for each plot where adults were found). We modelled p using a mixed-effects logistic regression with a Bernoulli error structure and separately fit this model to the first and last censuses of each plot:

$$\text{logit}(p) = \beta_{D1} + \beta_{D2}R_E + \tau_{D1} + \tau_{D2}, \text{in disturbed forests},$$

$$\text{logit}(p) = \beta_{T1} + \beta_{T2}R_E + \tau_{T1} + \tau_{T2}, \text{in thinning forests},$$

where β_{D1}, β_{D2}, β_{T1}, β_{T2} are coefficients associated with fixed effects, τ_{D1} and τ_{T1} are species effects and τ_{D2} and τ_{T2} are plot effects, all drawn from normal distributions. We restricted our analysis to the 22 species that occurred in over 10% of plots or constituted at least 10% of the total number of adults or saplings found across plots in the national-level dataset.

2.5. Model estimation

Mixed-effects models were fitted to the data using the MCMCglmm package (Hadfield, 2010) in R ver. 2.12 (R Development Core Team, 2010). MCMCglmm uses Markov Chain Monte Carlo simulations to generate posterior estimates of parameter values and their credible intervals. We used uninformative priors, i.e. broad normal distributions for fixed and random effects with means of zero and variances of 1×10^8 and covariance among effects following an inverse Wishart distribution with covariance parameters set to one and degree of belief parameters set to zero. We ran models for $\geqslant$50,000 iterations in the burn-in phase, followed by $\geqslant$100,000 iterations. We used a thinning interval of 10 to generate posterior samples, from which we calculated species medians to predict differences in recovery rates among species in disturbed and thinning forests. To infer the strength of effects in our model, we calculated 95% credible intervals (CIs) from posterior distributions. We consider effects to have significantly affected recovery if 95% CIs do not overlap zero. A feature of our data was that at many sites there was slow recovery of all species, but at some there was rapid recovery in both the exclosures and controls. We sought to determine whether species had the same potential to recover rapidly, and used the upper credible limits of R_C and R_E as a measure of the fastest potential recovery rate for each species in the presence and absence of ungulates respectively.

3. Results

3.1. Species population recovery in ungulate exclosure plots

Ungulate exclusion increased sapling population densities in exclosure plots irrespective of whether forests were classed as disturbed or thinning (95% CIs for mean sapling recovery of all species combined, R_X, in disturbed and thinning forest exclosure plots: 0.7–12.1% yr^{-1} and 0.6–4.8% yr^{-1}, respectively). The majority of species recovered at <5% yr^{-1} but several recovered much more rapidly, especially in disturbed forests (eight species with mean recovery rates in disturbed forests ⩾25% yr^{-1}, Fig. 1, Table S1). Similarly, a small number of species showed a much greater potential recovery rate than the majority, with sapling densities of nine species more than doubling annually in disturbed forests (Upper 95% CIs, Fig. 1).

Although recovery rates varied among species, there was no indication that faster growing species recovered more rapidly than slower-growing species (Table 1). A large seedling bank at the time of plot establishment aided recovery in all exclosures, but in thinning stands having dense fern cover on the plot reduced recovery (Table 1).

Table 1
Factors influencing the sapling population recovery of species in ungulate exclosures and control plots established in disturbed and thinning forests. Mean parameter estimates ("Effect") and 95% credible intervals are given for each factor included in the model. Fixed factors (seedling bank, growth rate, fern cover) are standardised (i.e. centred around the mean with a standard deviation of one) so that effect strengths can be directly compared with one another. Effects marked in bold type have 95% CIs that do not overlap zero and have a statistically significant influence on recovery. Intercepts represent the mean annual recovery rate in each forest type assuming all fixed factors are at mean levels and can be back-transformed to the data scale by raising to the power three.

	Exclosures			Control plots		
	Effect	5%	95%	Effect	5%	95%
Disturbed forest						
Species (variance)	0.21	0.10	0.32	0.01	<0.01	0.03
Intercept	**0.35**	0.19	0.50	**0.20**	0.15	0.26
Seedling bank	**0.18**	0.11	0.26	**0.09**	0.05	0.14
Growth rate	−0.03	−017	0.12	−0.01	−0.06	0.04
Fern cover	0.04	−0.04	0.10	0.03	−0.02	0.07
Thinning stands						
Species (variance)	0.12	0.04	0.22	0.04	<0.01	0.08
Intercept	**0.23**	0.08	0.36	**0.15**	0.07	0.24
Seedling bank	**0.16**	0.08	0.24	−0.03	−0.08	0.02
Growth rate	−0.08	−0.21	0.05	−0.05	−0.13	0.03
Fern cover	**−0.10**	−0.19	−0.01	0.03	−0.03	0.08

3.2. Species population recovery in control plots

While reductions in browsing have allowed recovery within unfenced control plots, the pattern of recovery in control and exclosure plots nevertheless differed. Combined across all species, sapling population densities increased slowly in both disturbed and thinning forests (95% CIs for mean sapling recovery in disturbed and thinning control sites: 0.4–1.7% yr^{-1} and <0.1–1.3% yr^{-1}, respectively). Mean recovery rates were similar in control and exclosure plots based on comparison of CIs (compare preceding figures with those reported for exclosure plots, Section 3.1), suggesting that culling has been largely effective in allowing an understorey to redevelop. However recovery rates of some species in control plots were much lower than within exclosures, with only

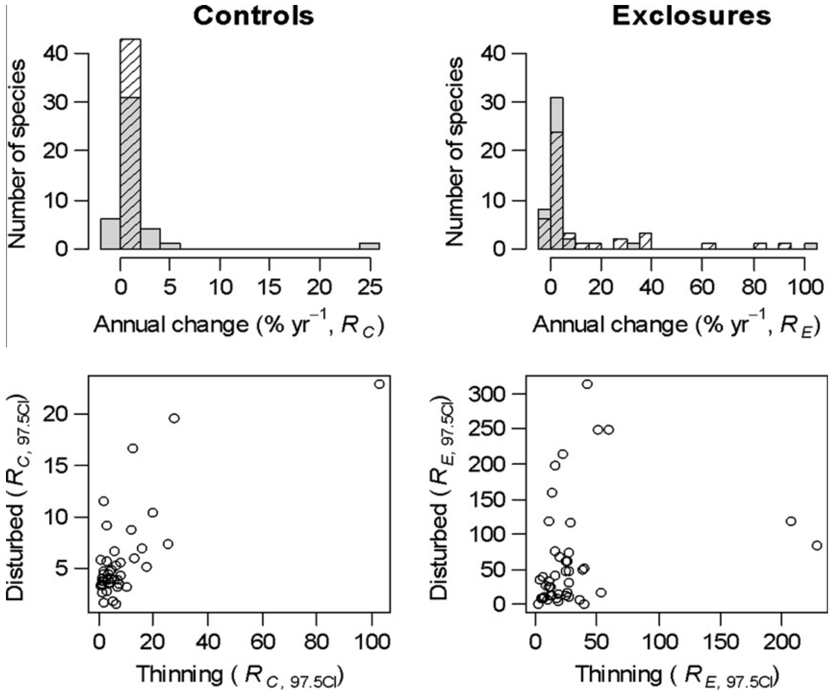

Fig. 1. Species responses to ungulate exclusion and stand disturbance. Upper panels display mean annual recovery rates of species in controls and exclosures. Grey shaded bars indicate distribution of species means in thinning sites. The overlaid hatched bars represent the distribution of species means in disturbed sites. Lower panels compare the fastest potential recovery rate of each species in thinning and disturbed sites, represented by the 95% upper credible limits of species recovery rates estimated from our data (one point for each species).

one species recovering at a mean rate >20% yr^{-1} and with smaller upper 95% CIs, indicating that ungulates still disrupt regeneration of these species (Fig. 1). Where ungulates were excluded the same species responded most rapidly in disturbed and thinning stands (Spearman rank correlation $\rho = 0.45$, $P = 0.003$, Fig. 1). This relationship was much less pronounced in the control plots where browsing was reduced ($\rho = 0.24$, $P = 0.130$; Fig. 1).

Similar to exclosures, seedling banks aided recovery, but only in disturbed forests where competition for light was less intense (Table 1). Neither species growth rates nor dense fern cover influenced recovery rates in thinning and disturbed control stands (Table 1).

3.3. Influence of ungulate diet preference on recovery at a national scale

Ungulates continue to affect understorey composition across New Zealand forests despite some recovery of sapling populations. At the first census of each plot in the national surveys (mean sampling year ± SD: 1979 ± 3.5), inferred preference class was not significantly related to the probability of finding a sapling in either disturbed or thinning plots (95% CIs, β_{D2}, β_{T2}: -0.77 to 0.10 and -0.73 to 0.78, respectively; Fig. 2). In contrast, the probability of finding a sapling at the final census of each plot (mean year ± SD: 1995 ± 4.9) declined significantly with inferred preference class in disturbed but not thinning plots (95% CIs, β_{D2}, β_{T2}: -0.73 to -0.06 and -0.67 to 0.71, respectively; Fig. 2). Although saplings were equally likely to be found at either census, sapling densities increased nationally over time (mean sapling density ± SE at first and final censuses: 1 398 ± 107 saplings ha^{-1} and 1 964 ± 192 saplings ha^{-1}, respectively; Wilcoxon signed rank test: $V = 22\ 810$, $P < 0.001$).

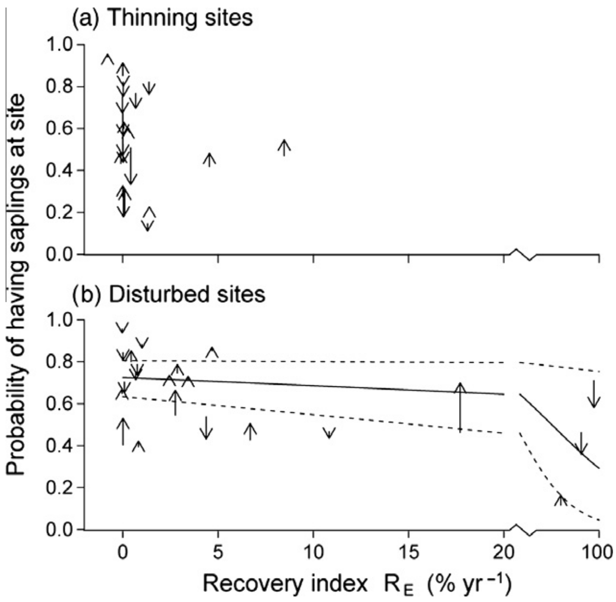

Fig. 2. Change between initial and final censuses of 574 New Zealand forest plots in probability of finding saplings in plots in which parent trees were present, compared with a measure of how rapidly that species recovers following ungulate exclusion. Preferred forage species increase most rapidly within exclosures (high R_E values). Arrows represent the change in the probability of finding saplings of a species between the two censuses. The solid curve in (b) represents the significant mean relationship (±95% CIs, dashed lines) between sapling probability and R_E in disturbed sites at the final census. There was no significant effect of R_E on sapling probability in thinning sites. $n = 22$ species.

4. Discussion

4.1. Forest recovery after culling

Suppression of the forest understorey by ungulates has been widely reported throughout forests in New Zealand (Husheer et al., 2005; Jane, 1994; Mark and Baylis, 1982; Veblen and Stewart, 1980; Wardle and Hayward, 1970), and internationally (Kuijper et al., 2010; Royo et al., 2010; Tanentzap et al., 2011a), and here we demonstrate consistent patterns for a large number of species growing in a range of different forest types. Our results show that culling has increased recovery of sapling populations across New Zealand, but species preferred by ungulates remain negatively impacted by browsing. We also found that low fern cover and large seedling banks can increase population recovery but that their effects depend on stand disturbance and the presence or absence of browsing ungulates. Mason et al. (2010) found shifts in canopy composition towards dominance of more palatable species when ungulates were excluded. These were most pronounced in disturbed stands, indicating that these sites were most negatively impacted by ungulate browsing. Recent declines in palatable species despite culling emphasize that the impacts of ungulates are not linearly related to their density (Nugent et al., 2001; Royo et al., 2010), so management may need to target sites where forest recovery is most likely to occur.

4.2. Influence of disturbance, growth rates, and establishment limitation on population recovery

Stand disturbance and its interaction with browsing moderated the effects of establishment limitation on population recovery. We found that fern cover reduced population recovery but only in thinning stands in the absence of ungulates. Inhibition of tree seedling recruitment and growth by dense layers of understorey plants, particularly ferns, has been widely reported in temperate forests (George and Bazzaz, 1999a,b; Royo and Carson, 2006), with competition for light being the suggested mechanism (Coomes et al., 2005). Outside of exclosures, trampling by ungulates may have disturbed the fern layer, allowing sufficient light to reach seedlings (e.g. Gremmen et al., 2003). Trampling has a similar role in the Scottish Highlands, reducing the cover of the dominant heathland vegetation (*Calluna* spp.) and subsequently increasing the abundance of light-demanding grasses and small herbs (Hester and Baillie, 1998). We did not observe an effect of fern cover in disturbed sites because light levels may have been sufficiently elevated, even beneath ferns, that competition for light would have been weak. Another explanation is that saplings may have established on raised surfaces in disturbed sites, such as fallen logs, where their growth was unaffected by competition for light from ground layer ferns (Bellingham and Richardson, 2006; Ogden, 1971).

Tanentzap et al. (2009) predicted that recovery following reductions in ungulate densities would be limited by propagule availability and our results support this, also indicating that the influence of seedling banks is moderated by understorey light levels. In browsed thinning sites, the lack of a positive effect of seedling banks may have occurred because browsing overwhelmed any benefit to recovery from large seedling banks. Ungulates of similar size to deer and goats have been shown to have a greater influence on sapling than seedling recruitment (Kuijper et al., 2010; Rooney et al., 2002), perhaps because saplings occur at lower density than seedlings. As a result saplings growing slowly under intense competition for light are unlikely to survive repeated ungulate browsing regardless of the size of the seedling bank from which they emerged. In their native range, ungulates can eliminate regeneration of slow-growing species at densities as low as 4 animals km^2 (Alverson et al., 1988). In disturbed sites, where sapling growth rates are higher and stems can escape ungulate browse by growing rapidly through the browse tier, the size of the seedling bank may be a stronger constraint on sapling recovery patterns.

Our finding that the fast growing species did not recover quickly from ungulate browsing was consistent with our predictions. Fast-growing woody species are preferentially selected by both ungulates and invertebrate leaf chewers (Tanentzap et al., 2011b), and therefore, may remain impacted by herbivores at all but the lowest ungulate densities. However slower growing species did not appear to have gained an advantage and were also recovering slowly, counter to our predictions. This might be because New Zealand trees grow much more slowly than species in other forest types worldwide (Bee et al., 2007), and so ungulates will need to be reduced to very low densities to allow recovery across the broader landscape (e.g. <1 animal km^2; Tanentzap et al., 2009).

4.3. Influence of ungulate diet preference on recovery

We found that ungulate preferred species were negatively affected by browsing despite overall increases in sapling densities following culling. As ungulate densities are reduced, and food competition is eased, the remaining animals will increase consumption of the most highly preferred species and reduce intake of less-preferred species (Dumont et al., 2005; Latham et al., 1999; Tremblay et al., 2005). Thus, relatively unpreferred species may recover without concomitant increases in preferred forage (Coomes et al., 2003; Nugent et al., 2001; Tanentzap et al., 2009). Our results support this prediction and are indicative of non-linear functional relationships between ungulate and plant species densities. As a result it may be difficult to reduce ungulates to densities at which preferred species will recover across the landscape. Rather, other approaches may be necessary to expedite the recovery of preferred species, such as targeting culling towards sites most affected by browsing or fencing.

Climatic changes may have altered the suitability of our study sites for recovery of some tree species, leading to changes in recovery patterns that may simply have been exacerbated by ungulate browsing preferences, although this is unlikely. Ecosystems can move between alternative stable states that can differ dramatically in both composition and function, with evidence for such regime shifts having been found in diverse ecosystems, often as a result of anthropogenic impact (e.g. Gatto and Rinaldi, 1987; Collie et al., 2004; Lockwood and Lockwood, 1993). Large disturbances are not always necessary to initiate a regime shift; when multiple drivers exist a small change in one factor may lead to a disproportionately large shift in ecosystem composition or function that occurs only when a second factor assumes certain values (a cusp catastrophe, see Hooley and Cohn, 2003). For example, variation among stands in density of the understorey herb *Laportea canadensis* (determined by historical factors) in eastern US forests was exacerbated by white-tailed deer (*Odocoileus virginianus*) browsing, resulting in alternative states with either high or low *Laportea* densities (Augustine et al., 1998). Across New Zealand, mean annual temperature has increased by 0.3 °C in the 30 years spanned by our vegetation measurements (Mullan et al., 2010), but the most sensitive of plant responses to these changes, i.e. growth at the edges of species' climatic envelopes (Harsch et al., 2009), has remained unchanged within the last 50 years. Regeneration in treeline forests is instead dependent on stand disturbance (Cullen et al., 2001), in agreement with our findings that sapling numbers increased most rapidly in disturbed stands. Pulses of *Nothofagus* recruitment over the past 300 years were also found to be unrelated to temperature trends (Cullen et al., 2001). Therefore we consider it unlikely that climate warming has appreciably altered tree recruitment patterns during the period of the study, although we cannot rule out such effects spanning the 150 years since ungulates were first introduced. Extrapolating back from 20th century temperature trends (Mullan et al., 2010) indicates that there may have been a total increase of up to 1.4 °C in 150 years, a change approaching the magnitude of the 1.5 °C to 3 °C rises that were associated with major vegetation changes in New Zealand during the Holocene (Wilmshurst et al., 2007).

4.4. Conservation implications

Even when reduced to very low population densities by hunting, ungulates continue to suppress regeneration of preferred plant species in temperate forests, indicating that total removal of browse pressure may be required to allow community recovery. A study in the Murchison Mountains, South Island, showed that most forest species were recovering slowly even though red deer (*Cervus elaphus*) populations have been reduced by 92% from their peak densities in the 1960s to less than 1 deer km^{-2} (Tanentzap et al., 2009). Preferred species may thus be unable to regenerate in the continued presence of ungulates. However, ungulate eradication is neither politically nor economically viable at the national scale and some species continue to gradually extend their range through illegal liberations (Fraser et al., 2000). There is also a lack of political will to eradicate ungulates across New Zealand because of their associated economic and recreation benefits (Nugent and Choquenot, 2004).

Forest managers may be forced to attempt eradication at small spatial scales to ensure regeneration of ungulate-preferred species, prioritising sites with the highest conservation values. Fenced sanctuaries for indigenous biota and offshore islands may be the most suitable sites. Goats have been successfully eradicated from islands as large as 361 km^2 (Lana'i, Hawaii) and from Raoul Island 29.4 km^2 in New Zealand (Campbell and Donlan, 2005). Goats have almost been eradicated from Great Barrier Island (285 km^2) and deer from an 81 km^2 island in New Zealand, which will represent the largest area to date where deer eradication has occurred. Localized management at the scale of several square kilometres can also be used to control ungulates if their home ranges are relatively discrete and animals are philopatric (McNulty et al., 1997), although this approach is likely to be less effective for less philopatric species such as red deer. In Germany, sport hunting facilitated tree regeneration across 25,000 km^2 within 3 years of implementing harvest quotas based upon trends in ungulate browsing within local game management districts (each ca. 33 km^2 in size; Hothorn and Müller, 2010). Although culling will need to be carefully targeted even in the presence of favourable regeneration conditions, e.g. large seed sources and ample understorey light levels, we show that recovery should be possible in small areas where ungulates can be eradicated.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.04.033.

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