



Fencing in nature? Predator exclusion restores habitat for native fauna and leads biodiversity to spill over into the wider landscape



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ABSTRACT

Large areas of habitat are being fenced globally to restore and relocate species that can no longer survive in their surrounding landscapes, such as because of introduced predators. Despite their promise, the contributions of fenced and intensively-managed reserves towards achieving wider biodiversity goals are contentious. There has been little empirical evidence that fenced reserves can restore communities or ecological function over larger landscapes in ways that justify their large economic and sometimes social costs. Here we tested whether the exclusion of introduced predators restored mammal-sensitive habitat after 8 years within a mainland fenced reserve in southern New Zealand. We also asked whether the abundance of bird-dispersed fruiting trees and frugivorous birds was elevated immediately outside the reserve as compared with the broader landscape. We found that only saplings of fleshy-fruited tree species sensitive to browsing and seed predation by introduced mammals increased over time within the reserve. These mammal-sensitive trees were also more abundant in the surrounding unfenced landscape when close to the reserve, i.e. within 500 m. Our results suggested that mammal-sensitive trees were benefitting from increased fruit dispersal that was spilling over the fenced boundary as mammal-sensitive frugivores responded to predator control. Using point count surveys at 278 unique sites throughout the broader region, we found that the native frugivore community that evolved in the absence of mammalian predators was a third more abundant within the reserve and immediately outside the fenced boundary than at sites 20 km away in the surrounding landscape. Non-endemic frugivores did not show the same spatial pattern. Our work provides among the first evidence that an intensively-managed wildlife reserve can measurably restore populations of threatened flora and fauna and disperse conservation benefits into wider landscapes.

1. Introduction

Fenced and intensively-managed nature reserves are gaining traction as a strategy to separate the world's most vulnerable biota from threats in their surrounding environments. The aim of fenced reserves is often to maintain ecological processes and species that could not otherwise survive in the surrounding landscape because of pressures such as predation or poaching (Hayward and Kerley, 2009; Hayward and Somers, 2012). Fenced reserves have also been used as sites in which to restore biological communities, such as through species translocation (e.g. Ewen et al., 2011). In many cases, species persistence is aided by extensive control of non-indigenous species, especially predators, which have been introduced in many regions to the detriment of local endemics (Doherty et al., 2016). By using intensive predator control, fenced reserves may subsequently function similarly to offshore islands that are used for species conservation (Jones et al.,

2016). Fenced reserves are now found on all inhabited continents, notably protecting thousands of hectares in Australia and New Zealand over the last two decades, though their exact numbers worldwide remain unknown (Hayward and Somers, 2012).

The contributions of fenced reserves towards achieving biodiversity goals are contentious despite their promise. Some have gone so far as to equate reserves that exclude non-indigenous predators with 'expensive zoos', because they maintain a collection of wildlife without any chance that these species could persist outside the fenced area (Pickard, 2007; Scofield et al., 2011). One of the challenges in assessing the success of fenced reserves is that complete eradication of pressures on threatened species, such as from non-indigenous predators, has been nearly impossible to achieve on larger land masses. By contrast, conservationists have been very successful at eradicating non-indigenous mammal pests and restoring viable populations of native fauna and flora on offshore islands (Bellingham et al., 2010; Glen et al., 2013a; Jones et al., 2016).

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Fenced reserves may also play an important role in conserving biodiversity outside of protected areas. Many organisms are highly mobile, such as volant animals and wind-dispersed plants, and so cannot be entirely confined within fences. Populations may therefore extend beyond reserve boundaries and bring their associated ecological functions and benefits, such as seed dispersal, into the broader landscape (e.g. Dirzo et al., 2014). However, little evidence exists as to whether terrestrial reserves benefit ecosystem processes in their surrounding landscapes, i.e. positive spill-over effects. In the most definitive study of this question to date, Brudvig et al. (2009) found that the species richness of animal-dispersed plants increased in plantation forests surrounded by actively restored savannas. The greater species richness was attributed to birds moving between patches of savanna by flying along their connecting corridors (Levey et al., 2005). This finding suggests that habitat patches that are more distant from each other should receive fewer dispersed seeds because seed retention and connectivity will decline with greater travel distance, especially in human-modified landscapes. Studies of deforestation and agricultural land-use conversion have supported these predictions by showing increased distance from primary habitat reduces the spill-over of biodiversity and ecosystem services into the broader landscape (Ricketts et al., 2001; Lucey and Hill, 2012; Gilroy et al., 2014, 2015).

In New Zealand, fenced reserves have been proposed to be an important part of government strategy to eradicate major non-indigenous predators: rats (*Rattus* spp.), possums (*Trichosurus vulpecula*), and stoats (*Mustela* spp.) at a national scale by 2050 and protect the country's unique biodiversity (Russell et al., 2015). Fenced reserves are desirable because they are seen as a way to concentrate conservation action into manageable sites where populations of threatened species can be protected and subsequently dispersed into the surrounding landscape, i.e. producing a 'halo' effect (Innes et al., 2012; Glen et al., 2013b). Here we tested whether the exclusion of mammals introduced to New Zealand, such as rats and possums, succeeded in achieving these outcomes. Introduced mammals kill native fauna and lead to the loss of pollination and seed dispersal services that native plants rely upon (Kelly et al., 2005, 2010; Anderson et al., 2011; Wotton and Kelly, 2011). Additionally, introduced mammals can displace native plants by preying upon seeds and seedlings (Allen et al., 1994; Campbell and Atkinson, 2002; Wilson et al., 2003; Tanentzap et al., 2009; Grant-Hoffman et al., 2010), inhibiting seed production (Clout, 2006), and dispersing highly-competitive exotic weeds (Williams et al., 2000).

Our specific aim was to test whether fencing and predator removal restored mammal-sensitive native habitat, and promoted the abundance of bird-dispersed fruiting trees and native birds immediately outside a reserve boundary. The approach we used was to monitor vegetation plots immediately before and 8 years after the construction of a predator-proof fence surrounding 307 ha of forest within a larger contiguous block in South Island, New Zealand. We used extensive data on the feeding preferences of introduced mammals to test the prediction that their exclusion has increased the regeneration of saplings (10–200 cm tall) by reducing mortality and seed predation. We focused on saplings because any increases in recruitment would have had insufficient time to grow into the canopy given the relatively slow growth rate of New Zealand trees in shaded understoreys (Coomes et al., 2009). We expected recruitment would be strongest for species with both the most palatable foliage and dispersed by fleshy fruit, as these taxa would have been suppressed by both browsers and seed predators. We also compared sapling counts to surrounding forests where mammals were present. We expected more regeneration of fleshy-fruiting trees with palatable foliage nearer the reserve than further away because native frugivores that evolved in the absence of mammals should benefit strongly from predator removal (Innes et al., 2010), and spill over the boundary fence and be more abundant immediately around the reserve. Testing this prediction involved surveying bird communities in 278 unique forest patches in a 20 km radius of the reserve and comparing their spatial distributions to patterns of tree regeneration.

2. Materials and methods

2.1. Study site and predator removal

Our study area traversed approximately 55,000 ha of forest fragments and mixed agricultural land located outside of Dunedin, South Island (45°52'S, 170°30'E). Within this study area, Orokonui Ecosanctuary (45°46'S, 176°36'E) was established in 2006 from a contiguous forest block with the largest elevation range so as to capture the full range of woody vegetation in the surrounding landscape. Representation of the surrounding landscape was confirmed by detailed habitat mapping (Lloyd et al., 2015), as well as forest plot data (see Sections 2.2 and 3.2 below). The site was also selected to be readily accessible to management and eventual visitors and not because it represented the best quality habitat in the study area.

In July 2007, the Orokonui reserve was enclosed by a 2 m tall, 8.7 km predator-proof fence. Shortly thereafter, programmes began to eradicate all introduced mammals: goat (*Capra aegagrus hircus*), possum, cat (*Felis catus*), European hare (*Lepus europaeus*), hedgehog (*Erinaceus europaeus*), stoat (*Mustela erminea*), weasel (*M. nivalis*), and rat (*Rattus rattus*). Approximately 64 km of trapping lines are regularly monitored to detect re-invasions by pest mammals and contingency responses result in pest mammals being maintained at effectively zero densities. Mice (*Mus musculus*) remain present in small pockets but are actively controlled. Vegetation at the site is secondary forest dominated by kanuka (*Kunzea robusta*) and broadleaved trees (*Fuchsia excorticata*, *Griselinia littoralis*, *Meliclytus ramiflorus*) with a few large emergent Podocarpaceae. Many rare and endemic bird and reptile species have been actively reintroduced within the site after establishment of the reserve, including kākā (*Nestor meridionalis*), Haast tokoeka (*Apteryx australis australis*), and tuatara (*Sphenodon punctatus*). There are no extant mammals native to the site and the only native predators aside from tuatara are the harrier (*Circus approximans*), New Zealand falcon (*Falco novaeseelandiae*), and the morepork (*Ninox novaeseelandiae*).

2.2. Permanent forest plots

We surveyed vegetation in 47 permanently marked 10 m × 10 m plots that were established across Orokonui and dominated by native forest. The plots were first measured between 2005 and 2007 and resurveyed between 2013 and 2014. Within each plot, we estimated basal area (BA) from diameter at breast height (1.35 m height) of all woody plants > 2 m tall and counted by species all woody plants 10 to 200 cm tall. Species were classified as either sensitive or insensitive to introduced mammals based on whether they were both preferred relative to other forage by ungulate browsers, such as goats, and/or possums, and produced fleshy fruits that could be preyed upon by rodents (Table A1). Preferences were based on diet studies and leaf functional traits from Peltzer et al. (2014) with some modifications (Table A1). All measurements were also taken from 2011 to 2014 in 14 control plots located in the larger contiguous forest outside of Orokonui and in 17 control plots in forest up to 20 km away (Fig. 1). Species in the sapling layer that occurred in fewer than three plots or less than six times across all plots in each measurement period were removed from the temporal analysis. We applied the same criterion in the spatial analysis but conditioned on whether minimum occurrences were satisfied both inside and outside the reserve.

We tested whether fencing enclosed an otherwise average habitat by comparing stand composition inside and outside of Orokonui with a permutational multivariate analysis of variance (PERMANOVA). The summed BA of trees > 2 m tall for each species in each plot was used to calculate a Bray-Curtis dissimilarity matrix, which was the dependent variable in the PERMANOVA. Treatment × measurement period was a fixed factor. *p* values were generated from 999 permutations of the raw data.

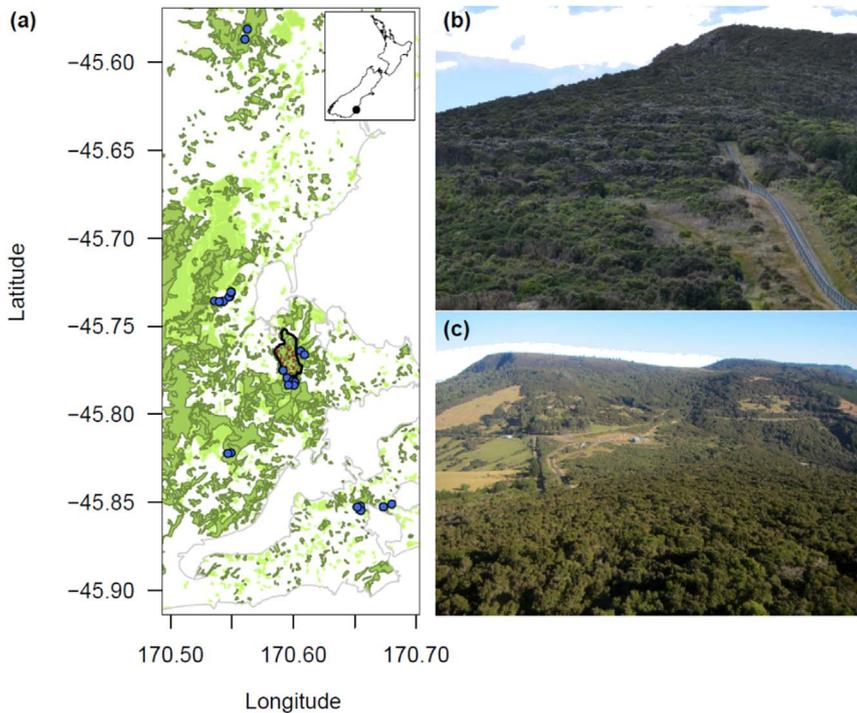


Fig. 1. Study site in South Island, New Zealand. (a) Location of forest plots inside (brown) and outside (blue) Orokouui Ecosanctuary. Polygons denote exotic/harvested (light green) and native (dark green) forest. Black outline is fence-line enclosing Orokouui, grey outline is coastline. Inset shows position of study region relative to New Zealand. (b) Eastern boundary of Orokouui facing northwards and showing predator exclusion fence dividing reserve (left-hand side) from adjacent unprotected area (right-hand side). (c) Eastern boundary of Orokouui facing southwards, with predator exclusion fence visible in the distance (i.e. middle of photograph). Forest in the immediate foreground is outside the reserve, showing that there is abundant native habitat around Orokouui. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3. Bird counts

We surveyed bird communities in and around Orokouui between 2014 and 2015. In total, 417 point counts were collected at 278 unique sites, with 71 of the sites sampled more than once and some up to 7 times. At 23 sites, between 2 and 4 repeat surveys were also carried out on the same date to help estimate detectability in our statistical models. Surveys utilised similar forest types to Orokouui within a 20 km radius of the reserve (Table A2), a distance over which native birds have been found to disperse (Brunton et al., 2008). The surveyed forest patches ranged from 0.4 to 1556.7 ha in size and none of the counts were conducted along obvious habitat edges as our aim was to target forest bird species. All birds heard or seen within 100 m were counted by one or more observers during a 5 min period. Birds were counted during the spring breeding season when male song was most intense and restricted to mornings to help standardise changes in the intensity of bird song as the day progressed. Each count also recorded weather and background noise, which could influence the detectability of birds, as well as the density of understorey vegetation.

We focused our analysis on all the frugivores that could account for fruit dispersal of native plants in our study region (Kelly et al., 2006): bellbird (*Anthornis melanura*), blackbird (*Turdus merula*), brown creeper (*Mohoua novaeseelandiae*), chaffinch (*Fringilla coelebs*), eastern rosella (*Platycercus eximius*), fantail (*Rhipidura fuliginosa*), house sparrow (*Passer domesticus*), kākā, kererū (*Hemiphaga novaeseelandiae*), redpoll (*Carduelis flammea*), silvereye (*Zosterops lateralis*), song thrush (*Turdus philomelos*), starling (*Sturnus vulgaris*), tomtit (*Petroica macrocephala*), and tui (*Prothemadera novaeseelandiae*). We expected that the endemic species (bellbird, brown creeper, fantail, kākā, kererū, tomtit, tui) would be most sensitive to introduced mammals because they did not coevolve and so would respond positively to predator control (i.e. higher numbers near and around the reserve). By contrast, we separately modelled the response of non-endemic frugivores to predator control because they coevolved with mammals. For each of the two groups, we summed total counts for each observation in each site.

2.4. Modelling sapling responses

We first tested whether sapling counts of mammal-sensitive species increased over time within Orokouui, as expected where the pest-free reserve reduced tree mortality and seed predation. If plants were responding primarily to mammal exclusion, we also expected that sapling counts of species insensitive to mammals would be unchanged over time. We tested these predictions by allowing each species i in plot j to respond differently at measurement period k given the plot's stand development class l . In a national-scale analysis, we have shown that sapling regeneration is slower in plots that experience strong competition for light despite reductions in herbivore densities (Wright et al., 2012). We therefore classified plots after Coomes and Allen (2007) into development stages of either thinning (increasing mean dbh and decreasing stem density between measurement periods, $n = 34$) or disturbed (all other changes; $n = 13$). Sapling densities were then modelled with mean λ_{ijkl} from a Poisson-lognormal distribution with error $\varepsilon_{ijkl}^{(1)}$ to account for overdispersion:

$$\log(\lambda_{ijkl}) = \alpha^{(1)}_i + \alpha^{(2)}_{k[i]} \text{time}_{ijk} + \alpha^{(3)}_{l[i]} \text{class}_{jkl} + \alpha^{(4)}_{kl[i]} \text{time}_{ijk} \text{class}_{jkl} + \alpha^{(5)}_{iS_{ijk}} + \alpha^{(6)}_{iB_{jk}} + \nu_j^{(1)} + \varepsilon_{ijkl}^{(1)}, \quad (1)$$

where $\alpha_i^{(1)}$ was the expected density pre-mammal exclusion of species i in disturbed plots, $\alpha_{k[i]}^{(2)}$ was the change in density for species i post-mammal exclusion, $\alpha_{l[i]}^{(3)}$ was the change in density for species i in thinning plots, $\alpha_{kl[i]}^{(4)}$ was the change in density for species i post-mammal exclusion only in thinning plots, S_{ijk} was the total BA of species i in plot j at measurement period k and allowed sapling densities to increase with local seed sources by a magnitude of $\alpha_i^{(5)}$, B_{jk} was the BA of all species in plot j at measurement period k and for which larger values are associated with greater canopy cover that limits understorey regeneration, and $\nu_j^{(1)}$ accounted for spatial autocorrelation among plots. For each species i , we sampled a vector α with length of six elements from a multivariate normal distribution with a distinct mean across species for each element and estimated covariance matrix Σ . We derived $\nu_j^{(1)}$ by randomly sampling an error term for each plot j from a zero-mean multivariate normal distribution with covariance matrix equal to the product of an estimated standard deviation (SD) and a Gaussian spatial correlation structure described by $e^{-(\theta D)^2}$, where θ was

the estimated strength of the spatial correlation across all plots and \mathbf{D} was a matrix of pairwise distances among plots (after Dormann et al., 2007). This error term also allowed us to account for differences among plots due to vegetation communities, elevation, and other factors that could explain variation in sapling counts but that were not of primary interest to our study hypotheses (i.e. ‘nuisance’ variables). We re-fitted the model to mammal-insensitive saplings.

We also tested whether plots outside of Orokonui had increasingly fewer saplings of fruiting trees in 2013–2014 as they were located at a greater distance d_j from the nearest point inside the reserve. We again accounted for variation in regeneration among development stages, but measured with the Gini coefficient g_j as we lacked data on change in size structure through time in non-Orokonui plots. g_j summarises the inequality in the standing diameter distribution of a given plot, with values of 0 when all individuals are equal and values approaching 1 when inequality is maximized (Weiner and Solbrig, 1984). In our study, g_j successfully distinguished between thinning and disturbed plots. Plots that were disturbed by 2013–2014 had greater size disparity (i.e. larger g_j) than plots that had undergone thinning, because recruitment following disturbance elevated densities only in smaller size classes while thinning resulted in more even-sized stands (Wilcoxon rank test comparing g_j between 47 Orokonui plots classed as either disturbed or thinned: $W = 315$, $p = 0.025$). We also allowed sapling densities to vary among plots that were located in different contiguous forest blocks, which may have had different management histories. The effect of forest block $v_{\text{block}[j]}^{(3)}$ was estimated from a zero-mean normal distribution with estimated SD. The mean number of saplings γ_{ij} was then modelled from a Poisson log-normal distribution as:

$$\log(\gamma_{ij}) = \alpha^{(7)}_i + \alpha^{(8)}_i d_j + \alpha^{(9)}_i b_j + \alpha^{(10)}_i s_{ij} + \alpha^{(11)}_i g_j + v^{(2)}_j + v^{(3)}_{i,\text{block}[j]} + \varepsilon^{(2)}_{ij}, \quad (2)$$

which is analogous to our model in Eq. (1) and again accounted for overdispersion and spatial correlations in the data with $\varepsilon_{ij}^{(2)}$ and $v_j^{(2)}$, respectively. As in our previous analysis, we re-fitted the model to species that were insensitive to mammals (i.e. non-fleshy-fruiting trees), expecting that they would not benefit from being closer to Orokonui.

2.5. Modelling frugivore responses

We tested whether the two frugivore groups were more abundant closer to Orokonui, as expected if there was a positive spill-over of biodiversity into the surrounding landscape following predator control. Our approach accounted for the fact that animals are often imperfectly detected from their local populations (Kéry, 2010).

We specifically considered that counts c_{ijkm} of each species i in point j at time k by observer m could be modelled from a Binomial distribution where the abundance φ_{ij} of each species in the local habitat patch associated with point j was detected with a probability p_{ijkm} . As φ_{ij} was unknown, we could estimate it from a Poisson distribution with mean λ_{ij} that we related to d_j and the area of the forest fragment associated with the point count a_j . Mean abundance in each sampling point was allowed to vary among 6 broad vegetation types $\alpha_{\text{hab}[j]}^{(1)}$ (listed in Table A2), with the density of understorey vegetation $\omega_{\text{und}[j]}$ (scored as either sparse, moderately dense, or dense), and with the spatial distances to other point counts $v_j^{(4)}$ and forest block in which each point count was located $v_{i,\text{block}[j]}^{(5)}$, both as in Eq. (1). The inclusion of $v_{i,\text{block}[j]}^{(5)}$ allowed us to account for non-random effects governing abundance, such as the unmeasured presence of mammals in some forest patches but not others. All of a_j , $\alpha_{\text{hab}[j]}^{(1)}$, $\omega_{\text{und}[j]}$, $v_j^{(4)}$, and $v_{i,\text{block}[j]}^{(5)}$ effectively functioned as nuisance variables. In other words, they were not directly relevant to our hypotheses but needed to be considered in our analyses as they likely explained some variation in abundance and could thereby conceal the effect of interest d_j .

As for p_{ijkm} , we estimated a different value depending on the presence of cloud cover $\text{cld}_{[jk]}$, weather on the sampling day (i.e. maximum

temperature t_{jk} , rainfall r_{jk} , maximum wind speed w_{jk}), and Julian day of year y_{jk} , which was transformed to a circular scale so that day 1 was as close to day 365 as it was to day 2. Populations may be less detectable as J_{jk} increases and site affinity during breeding ceases, and we allowed this effect to vary among habitats. Finally, we also let error in p_{ijkm} vary with sampling hour $\omega_{\text{hr}[jk]}$, observer experience $\omega_{\text{obs}[m]}$ (categorically scored as either low, medium, or high), and background noise levels in the environment $\omega_{\text{noi}[jk]}$ (low, medium, or high). All ω 's were randomly sampled from zero-mean normal distributions. Our final model took the form:

$$\begin{aligned} c_{ijkm} &\sim B(\varphi_{ij}, p_{ijkm}), \\ \varphi_{ij} &\sim \text{Pois}(\lambda_{ij}), \\ \log(\lambda_{ij}) &= \alpha^{(1)}_{i,\text{hab}[j]} + \beta^{(1)}_i d_j + \beta^{(2)}_i a_j + \omega_{i,\text{und}[j]} + v^{(4)}_{ij} + v^{(5)}_{i,\text{block}[j]}, \end{aligned} \quad (3)$$

$$\begin{aligned} \text{logit}(p_{ijkm}) &= \beta^{(3)}_{i,\text{cld}[jk]} + \beta^{(4)}_i t_{jk} + \beta^{(5)}_i r_{jk} + \beta^{(6)}_i w_{jk} + \alpha^{(2)}_{i,\text{hab}[j]} y_{jk} \\ &\quad + \omega_{i,\text{hr}[jk]} + \omega_{i,\text{obs}[m]} + \omega_{i,\text{noi}[jk]}, \end{aligned} \quad (4)$$

where α 's were estimated as in Eq. (1) from a multivariate normal distribution with a distinct mean for each element and estimated covariance matrix.

2.6. Model estimation

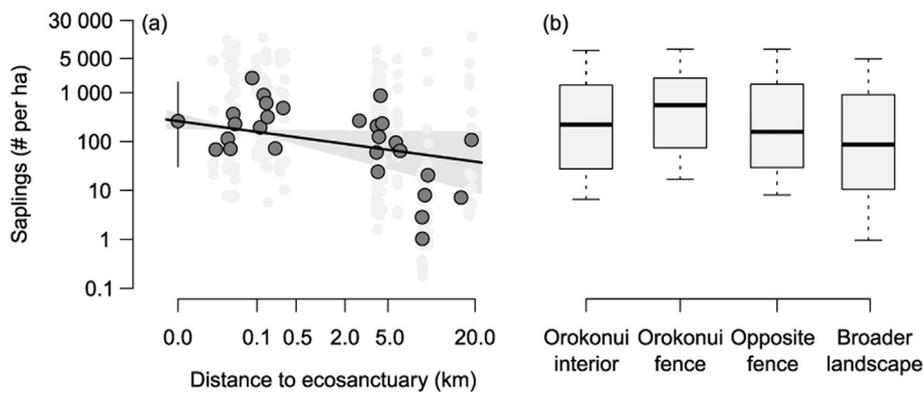
We fitted the models described by Eqs. (1)–(3) using Markov chain Monte Carlo (MCMC) sampling by calling Stan v.2.9 from R v.3.2; JAGS 3.4 was used for the bird count models as Stan cannot impute integer distributions. Four MCMC chains of at least 2000 iterations were simulated with a burn-in period of at least 1000 runs. Details of prior distributions and model convergence are given in Appendix S1.

To test our hypotheses, we estimated 95% credible intervals (CIs) for each parameter by drawing a subset of at least 800 simulations. We then calculated the mean change in stem counts over time for each of the two stand types, with positive 95% CIs that excluded zero indicating an increase after fencing of Orokonui. Similarly, 95% CIs that were negative and excluded zero for the effect of distance to Orokonui on either sapling counts or bird densities suggested that there was positive spill-over of biodiversity closer to the fenced reserve.

3. Results

3.1. Increased regeneration over time of mammal-sensitive trees only

We found that only saplings sensitive to introduced mammals increased over time within Orokonui. The temporal increases were restricted to disturbed plots, wherein densities for an average mammal-sensitive species increased by a mean of 100 (95% CI: 14 to 556) saplings ha^{-1} from a plot-level mean of 137 (95% CI: 37 to 659) saplings ha^{-1} between 2005 and 2007. Counts of mammal-sensitive saplings did not change in plots that underwent competitive thinning (95% CI: -115 to 55 saplings ha^{-1}). Densities of mammal-insensitive saplings also did not change over time in either stand class (95% CI for temporal change: -43 to 44 and -38 to 11 saplings ha^{-1} for disturbed and thinning, respectively), consistent with our predictions. As expected, both mammal-sensitive and -insensitive species were more abundant in plots with larger conspecific basal area, presumably reflecting greater local seed sources (95% CI for effect on log-scale: 0.63 to 2.14 and 1.17 to 2.53 , respectively). Only mammal-sensitive saplings were less abundant where total basal area was higher (95% CI: -0.77 to -0.20), as expected where palatable species are fast-growing and thus inhibited by competition for light (95% CI for mammal-insensitive: -0.39 to 0.17). All model parameter estimates are reported in Table A3.



noting inter-quartile range. Whiskers are 2.5% and 97.5% quantiles.

Fig. 2. Fleshy-fruited saplings are rarer further from Orokonui Ecosanctuary. (a) Sapling densities for each of 9 fleshy-fruited species where present across 78 plots ($n = 702$ total species \times plot occurrences). For clarity, plots within the reserve (i.e. distance = 0 km) are aggregated as a single point denoted by a median \pm inter-quartile range ($n = 47$ plots \times 9 species = 423 occurrences). Remaining dark points are median densities across all species in each plot located outside the reserve with species-level observations in each plot denoted in grey ($n = 31$ plots \times 9 species = 279 occurrences). Solid line is mean effect of distance to the reserve with polygon denoting 95% CI. (b) Sapling densities for each of 9 fleshy-fruited species summarised within the interior and edge (i.e. along the fence-line) of Orokonui, outside Orokonui but immediately opposite the fence-line, and within the broader landscape. Solid lines are medians with boxes denoting inter-quartile range.

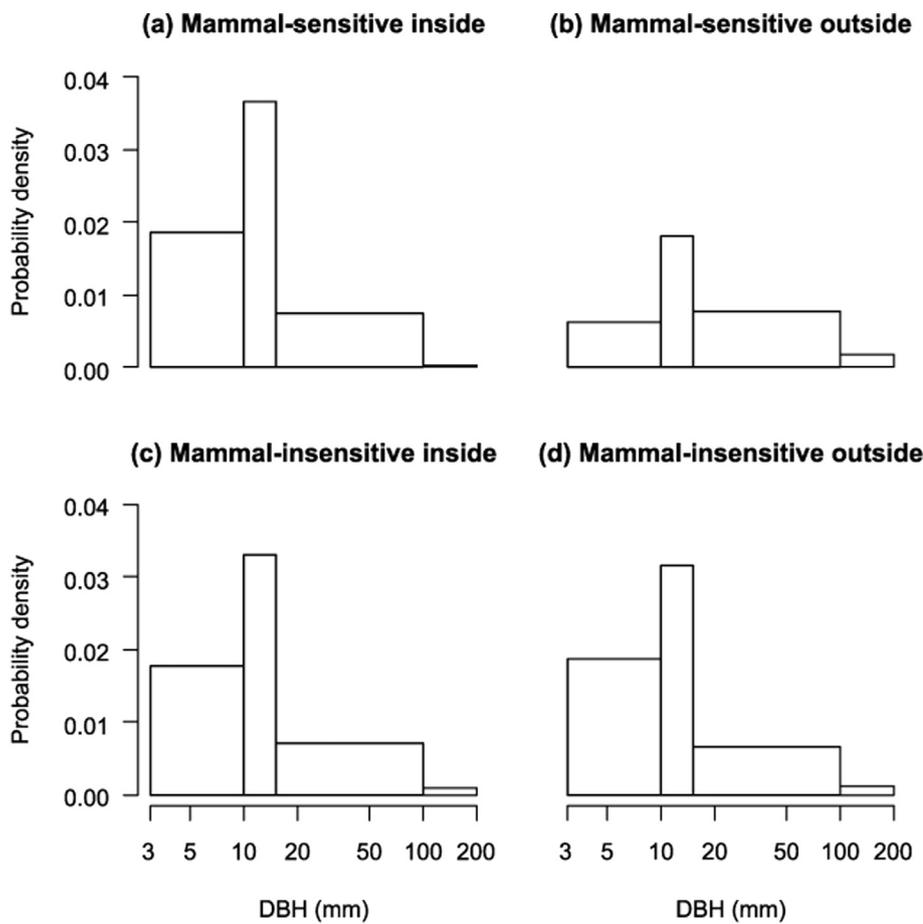


Fig. 3. Forest size structure (a, c) inside and (b, d) outside Orokonui Ecosanctuary at the second measurement period for all trees classed as either sensitive or insensitive to introduced mammals. Smaller sized trees (3 to 10 mm DBH) are reduced well beneath that expected from the inverse J-shaped distribution found in undisturbed stands (Peltzer et al., 2014), with mammal-sensitive species noticeably reduced outside of Orokonui.

3.2. Regeneration decreases with distance from reserve

Only saplings sensitive to introduced mammals benefited from being closer to the fenced reserve. Densities of mammal-sensitive saplings declined with increasing distance from Orokonui (95% CI for effect on log-scale: -1.16 to -0.03 ; Fig. 2a), but mammal-insensitive species showed no response to distance (95% CI: -0.61 to 0.55). The reductions were evident immediately outside of the reserve, as seen by comparing plots within 100 m of each other straddling the fence-line (Fig. 2b). The average density for a mammal-sensitive species was lower by a mean of 219 (95% CI: 117 to 326) saplings ha^{-1} across six external plots within 50 m of the reserve fence as compared with four neighbouring plots within Orokonui, where densities averaged 555 (95% CI: 15 to 11,586) saplings ha^{-1} (i.e. compare opposite fence

versus Orokonui fence in Fig. 2b). Nonetheless, densities predicted for a mammal-sensitive species in a new location between 50 and 500 m outside of the reserve averaged 148 (95% CI: 34 to 589) saplings ha^{-1} and were at least twice as large, for example, than at a distance of 5000 m from Orokonui by a mean of 68 (95% CI: 3 to 374) saplings ha^{-1} . Generally, we found that the average number of mammal-sensitive species was greater than mammal-insensitive species within Orokonui and the immediate vicinity (within 500 m) by a mean of 187 (95% CI: 159 to 218) and 248 (197 to 298) saplings ha^{-1} , respectively. Over greater distances in the surrounding landscape, mammal-sensitive species became as abundant as mammal-insensitive species with a mean difference between groups of 15 (95% CI: -1 to 33) saplings ha^{-1} , and mean densities for the latter group of 15 (95% CI: 1 to 8564) saplings ha^{-1} .

Stand structure also predictably influenced sapling densities. Both mammal-sensitive and mammal-insensitive species benefited from a greater conspecific BA (95% CI for effect on log-scale: 0.31 to 1.42 and 0.90 to 1.83, respectively). Total plot-level BA also reduced sapling densities, as expected if it reflected competition for light, but only for mammal-sensitive species (95% CI: -0.91 to -0.40), consistent with our temporal analysis (95% CI for mammal-insensitive species: -0.42 to 0.02). We found further evidence that competition for light was important as sapling densities were consistently greater in plots with a larger size inequality, as measured by the Gini coefficient, and which indicated more disturbed stands (95% CI: 0.16 to 0.78 and 0.02 to 0.53, for mammal-sensitive and -insensitive species, respectively). All other parameter estimates are reported in Table A4.

We have little evidence that the distance effect arose simply because the reserve originally protected a unique forest as compared with the surrounding landscape. Forest structure was indistinguishable, on average, inside the reserve between both measurement periods and versus the control plots, suggesting that seed sources were comparable over space and time (PERMANOVA $p = 0.123$; Fig. A1). Regeneration outside the reserve was also unlikely to have increased to the same extent as within Orokonui, because forest stand structure in the broader landscape exhibited a clear signature of pest mammals (Fig. 3).

3.3. Mammal-sensitive bird counts greater nearer the reserve

We found that endemic frugivores were more abundant closer to Orokonui, suggesting that populations spilled over from the fenced reserve into the surrounding landscape. Endemic frugivores were, on average, 33% more abundant within Orokonui, occurring at a mean of 6.5 (95% CI: 5.4 to 7.6) individuals per count versus 4.9 (95% CI: 4.6 to 5.2) individuals per count at 10 km away in the broader landscape (Fig. 4; 95% CI for effect of distance on log abundance: -0.23 to -0.03). By contrast, non-endemic frugivores were not associated with distance to the reserve (95% CI for effect: -0.07 to 0.16), as expected if they were more adapted to introduced predators or outcompeted by endemic birds within the reserve. The size of the forest fragment also promoted patch-level abundances of endemic frugivores (95% CI: 0.01 to 0.20), while non-endemics that are more associated with human-modified landscapes were less abundant in larger patches (-0.30 to -0.06).

Our models fitted the observed counts very well (Bayesian R^2 : 0.67 and 0.71 for endemic and non-endemics, respectively) and suggested that detection varied with local weather conditions. Mean detection probabilities ranged from 0.23 to -0.67 and 0.11 to 0.85 for endemic and non-endemic frugivores, respectively, and were lower on rainy days for endemics (95% CI for effect on logit detection: -0.26 to -0.02)

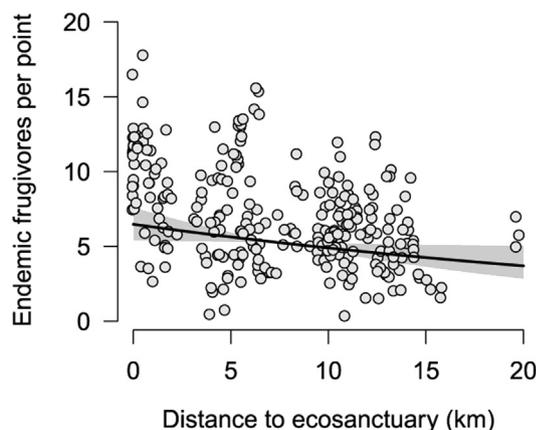


Fig. 4. Endemic frugivore populations are smaller further from Orokonui Ecosanctuary. Solid line is mean effect of distance to the reserve at mean levels of all other variables with polygon denoting 95% CI. $n = 278$ point counts.

and warmer and windier days for non-endemics (95% CIs: -0.26 to -0.02 and -0.41 to -0.10 , respectively). All other parameter estimates are reported in Table A5.

4. Discussion

Here we have found among the first evidence that a fenced pest-free reserve can promote external populations of flora and fauna, challenging claims that they have limited value in broader landscape-level conservation (Scofield et al., 2011). Our results also suggest that the exclusion of introduced mammals from even a relatively modest-sized area can benefit biodiversity in the surrounding landscape by leading to positive spill-over of key ecosystem functions such as seed dispersal and pollination. Evidence for spill-over effects from terrestrial reserves has been very limited and, to our knowledge, exclusively shown to reduce rates of land clearance (Andam et al., 2008; Ament and Cumming, 2016). Positive spill-over would also support theoretical claims that fenced reserves can concentrate conservation action into manageable sites from which benefits radiate into the surrounding landscape like the glow of a halo (Russell et al., 2015). While stronger evidence for the value of fenced reserves would come from an experimental design that enabled the difference made by management to be compared with trends in the absence of intervention, so as to account for variation between the reserve and control plots in initial conditions and management history, our analyses suggest that other such factors only partially contributed to our reported patterns.

4.1. Role of a fenced reserve in mainland restoration

We found that exclusion of introduced browsers and seed predators benefited forest regeneration. Introduced browsers not only prevent forest regeneration (Wardle et al., 2001; Wright et al., 2012; Peltzer et al., 2014), but in some cases, they can also kill mature seed sources (Nugent et al., 2001) and inhibit seed production (Cowan and Waddington, 1990). Therefore, browsers can shift successional pathways towards mammal-avoided species over very short periods, i.e. decades (Coomes et al., 2003). Reversing or redirecting successional changes can take much longer because mammal-preferred species need to accumulate seed sources and may require different abiotic conditions for establishment (Tanentzap et al., 2012). Here we found that the impacts of introduced browsers on mammal-sensitive tree communities could begin to be reversed after < 10 years. The short time-scale contrasts with other studies of recovery where browsers were likely at much higher densities for longer periods of time prior to management (Tanentzap et al., 2009, 2011; Wright et al., 2012), emphasising the general non-linearity between animal densities and recovery rates (Tanentzap et al., 2012).

Our finding that mammal-sensitive saplings with fleshy fruit were more abundant immediately outside (i.e. within 500 m) of Orokonui than in the broader landscape, but less so than within the reserve itself, is unsurprising if volant frugivores were spilling over the reserve fence and depositing seeds into the surrounding landscape. While the main limitation of our study is the lack of vegetation data in control plots from before Orokonui was established, we expect that saplings would have originally occurred at similar densities across the entire landscape. There is little evidence to suggest otherwise, whereby stands protected by fencing had initially higher sapling densities because they were less disturbed, grazed or pest-invaded than those in the surrounding landscape. First, 14 of the 31 control plots were located immediately on the other side of the fence-line and within the same contiguous forest block that was eventually divided by either the reserve fence or adjacent road. Second, overstorey composition within Orokonui was indistinguishable from the surrounding landscape (Fig. A1; Lloyd et al., 2015), suggesting that seed sources were comparable, and our models did account for variation in management history (e.g. grazing pressures) associated with forest blocks that could have influenced sapling

densities. Third, stand structure outside of Orokonui exhibited a clear signature of mammalian herbivory (Beschta and Ripple, 2009; Tanentzap et al., 2011; Peltzer et al., 2014). Numbers of smaller mammal-preferred trees were notably limited (Fig. 3), suggesting that regeneration has not increased over time to a similar extent as inside Orokonui. Finally, sapling densities could have not been elevated closer to the reserve fence by disproportionately more pest control. Coordinated efforts to cull possums only exist at distances > 500 m to the west of Orokonui (OSPRI, 2015), which is sufficiently far so as to exclude the home ranges of animals close to the reserve (Efford et al., 2000).

Consistent with the idea that fleshy-fruited trees were being more readily dispersed outside of the reserve, we found that endemic frugivore community was most abundant nearest to Orokonui. Predation by introduced mammals is the primary factor limiting numbers of endemic birds across New Zealand (reviewed in Innes et al., 2010). Fewer endemic birds can subsequently limit pollination, seed production, and native plant density (Anderson et al., 2011), and here we have shown that the latter effects may be reversible on mainland sites through predator removal. While the lack of temporal data prevents us from excluding the possibility that endemic birds were always more abundant within the large continuous forest block enclosed by the nature reserve (Barnagaud et al., 2014), overstorey composition did not differ from the surrounding landscape prior to fencing (Fig. A1). We also found that populations of non-endemic frugivores were not larger closer to the reserve, again, as might be expected if spatial variation in bird abundances was driven by the establishment of the reserve and not pre-existing patterns. Some non-endemic frugivores receive little benefit from the control of introduced mammals and instead remain abundant as mammals predators increase (Diamond and Veitch, 1981; Innes et al., 2004; Graham and Veitch, 2002; Elliott et al., 2010; Starling-Windhof et al., 2011). They may have also evolved to partition food resources better with omnivorous mammals, which are thought to out-compete endemic birds (MacLeod et al., 2015). Plots that jointly monitor plant and animal responses across the landscape would further strengthen our conclusions.

4.2. Fenced reserves: new tools for old problems?

The tremendous global success of island restoration projects has been difficult to replicate within unfenced mainland areas (Burns et al., 2012; Russell et al., 2015; Byrom et al., 2016), but our work provides among the first evidence that similar achievements may be possible by using fenced reserves to disperse benefits into the surrounding landscape. This finding is in fact expected from meta-population theory. Bolstering populations of a species in a given patch by controlling predators should create sources of emigrants to augment populations in neighbouring regions subject to less intensive predator management (Glen et al., 2013b). For example, localised poisoning of introduced red fox (*Vulpes vulpes*) in Western Australia allowed endangered rock-wallabies (*Petrogale lateralis lateralis*) to forage outside of areas where foxes were controlled (Kinnear et al., 2010). An important determinant of broader landscape-level success will however be the level of management in the intervening areas. Reserves cannot act as islands in an otherwise inhospitable landscape. Habitat must be available and provide connectivity among source populations within the intervening matrix if fenced reserves are to deliver wider benefits.

Although we have shown that fenced reserves can help achieve restoration outcomes, they pose several challenges that remain to be overcome. For example, fences are unlikely to benefit all species, especially those that migrate with seasonal resources (Woodroffe et al., 2014). Fences may similarly be less effective at restoring populations and functions outside of the fence where species under protection are unable to penetrate the fence-line, e.g. flightless birds. Fenced reserves are also costly to operate and can siphon limited conservation resources from government investment that protect species over considerably

larger areas. For example, Scofield et al. (2011) estimated that the annual cost of maintaining one 3400 ha fenced reserve in North Island, New Zealand equated to the entire budget of the endangered species programme for a 3.8 million ha area. Efforts to fund reserves without large government investment can also effectively privatise public land in ways that risk excluding local communities (Langholz and Lassoie, 2001). Nonetheless, as the global biodiversity crisis deepens, our work suggests that fenced reserves can help deliver conservation benefits into wider landscapes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.08.001>.

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