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 the 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).

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*, *Melicytus 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.