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GM Rogers & A Monks

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RESEARCH ARTICLE

Restoring lost ecological function: ecological surrogates facilitate maintenance of coastal turf communities

GM Rogers^a and A Monks^b

^aScience and Policy, Department of Conservation, Dunedin, New Zealand; ^bLandcare Research—Manaaki Whenua, Dunedin, New Zealand

ABSTRACT

Lost or extinct ecosystem function presents challenges for managers of natural ecosystems for conservation. One solution is to use ecological surrogates to replace these processes but the settings under which this often controversial approach succeeds are unclear. We tested whether mammalian grazing could be used as a surrogate for grazing by an extinct avian herbivore guild in two threatened coastal turf communities that are structured by an exposure and salt gradient, and vulnerable to non-native encroachment and invasion. Prostrate species had higher cover and species density relative to erect taxa when grazed, with the effect greater for native than non-native taxa. Prostrate species, dominated by native taxa, were most abundant closest to the ocean, with a secondary peak in abundance 25–35 m inland. A positive nutrient feedback mechanism consistent with a grazing lawn was not observed suggesting a primary role for the salinity gradient, augmented by opportunistic grazing of taller species, in structuring these communities. Synthesis and application: mammalian grazers can replace the likely functional role of extinct avian herbivores in turf communities under certain environmental settings.

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Community dynamics; extinct avian guild; invasive species; mammalian grazing; *Myosotis brevis*; salinity; threatened plants

Introduction

Local extinctions, declining species densities and the disruption of ecological processes, particularly by fragmentation, contribute to an overall loss of ecological function within anthropogenically disturbed ecosystems (McIntyre & Hobbs 1999; Vaughn 2010; Boyer & Jetz 2014). These changes affect communities at different scales depending on the function impacted. At fine scales, the extinction or decline of one partner of a specialised mutualism (e.g. pollination [Montgomery et al. 2003; Sekercioglu 2006], defensive ant mutualisms [Beattie 1985]) may have little impact beyond the direct effects on the other mutualist partner. Alternatively, the loss of an ‘ecosystem engineer’ such as the mega-herbivores of the African savannah (Owen-Smith 1987) or the burrow-nesting seabirds on New Zealand offshore islands (Wardle et al. 2009; Fukami et al. 2006) may have consequences for the structure and future trajectory of the broader ecosystem. These larger changes depend on the interaction between the functional characteristics of the species

CONTACT Geoffrey M Rogers ✉ grogers@doc.govt.nz

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within the community and the ecological component or process that has been lost. For example, mega-herbivore decline in moist savannah results in taller, more densely woody vegetation than the open savannah promoted by their movements and browsing (Sankaran et al. 2008; Midgley et al. 2010).

Lost ecosystem functionality presents challenges for conservation managers intervening to promote large-scale restoration and maintenance of natural ecosystems and their native biota. Species-level ecological function can be augmented through reintroducing locally extinct species (e.g. Donlan et al. 2006) or boosting the numbers of declining species through active management (Montgomery et al. 2003). Landscape-level expansion of vegetation corridors in fragmented landscapes may help restore gene flow of both plants and animals between isolated fragments (Bennett 1998). Finally, where natural ecosystem components cannot be restored, managers can use ecological surrogacy where lost ecosystem functionality is substituted with surrogacy to replace lost functions with analogues (Caro 2007; Cushman et al. 2010; Lee et al. 2010; Trotter III & Evans 2010). These functional replacements could involve ongoing supplementary interventions such as added fertiliser to replace lost nutrient cycling processes in mine site restoration (Bell 2001) or one-off self-sustaining interventions that might achieve the same goal, such as introducing non-native extant ratites as surrogates for extinct avian mega-herbivores in New Zealand coastal forests (Tanentzap et al. 2013).

The benefits of ecological surrogacy for the conservation and management of ecosystems are uncertain. At best, the ecological surrogate may provide functional equivalence for key ecological processes, and few negative effects on ecosystem goals. However, most ecological alternatives are viewed as imperfect or poor alternatives to the species or processes they replace (Piper et al. 2009). The importance of evolution history in determining the outcomes of novel interactions (Tanentzap et al. 2014) suggests that communities might not respond equivalently to biotic surrogates. Furthermore, introducing novel biological elements into an ecosystem is often socially undesirable, especially if their release is irreversible. Here we present a case study to test whether ecological surrogates can be used to restore a near extinct ecological process, thereby enabling the persistence of a nationally threatened rare plant community.

Coastal turf communities (hereafter turfs) occur on New Zealand's most wind- and salt spray-exposed coastal topography (Johnson 1993; Meurk et al. 1994a, 1994b; Rogers & Wisser 2010). A nationally recognised historically rare ecosystem (Williams et al. 2007), turfs support many threatened and uncommon plants, many of prostrate form that appear vulnerable to smothering by taller native and non-native species (Rogers & Wisser 2010). Prehistorically, high densities of coastal birds would have secondarily influenced the extent of turf by limiting encroachment of tall erect herbs, grasses and coastal woody species, especially on the inland ecotone where the influence of salinity and exposure is lessened (Lee et al. 2010). New Zealand's diverse range of turf swards were proposed as a distinct avian-mediated vegetation type by Lee et al. (2010), with moa, geese and swans part of a guild of large-bodied avian herbivores (Tennyson & Martinson 2006; Wood et al. 2008). With habitat clearance, post-colonisation hunting by humans and introduction of mammalian pests, these coastal bird communities are now extinct (Worthy & Holdaway 2002; Tennyson & Martinson 2006). Widespread conversion of these habitats to pasture has introduced a number of invasive taller non-native species able to invade turf communities, especially inland where marine exposure is reduced

(Brownstein et al. 2014), along with associated livestock grazing. These turfs have analogues in many other habitats and locations worldwide (e.g. kettleholes [Tanentzap et al. 2014], vernal pools [Marty 2005] and salt marshes [Cargill & Jefferies 1984]), where a strong underlying abiotic gradient is augmented by grazing by avian and mammalian herbivore guilds that maintain short-statured herbaceous vegetation.

We manipulated mammalian herbivory (primarily cattle; *Bos taurus*) in two New Zealand coastal turf communities. With no extant bird community with which to compare, we indirectly tested for the ecological equivalence of mammalian and avian grazing by comparing the relative effect of grazing on prostrate and erect species between guilds from different origins. Because birds were the only vertebrate herbivores in pre-human New Zealand, the native flora exhibits more bird-adapted traits compared with the non-native flora with its shared evolutionary history with mammals (Bond et al. 2004; Lee et al. 2010; Tanentzap et al. 2013). If bird and cattle grazing are ecologically equivalent in turfs, we would expect similar responses to livestock grazing from the native and non-native flora, demonstrating that the effect of cattle transcends the differences in evolutionary history of the two floras. Specifically, we expected the abundance and diversity of native and non-native prostrate species to increase in the same way under grazing by livestock, and for erect species to decline. Finally, by measuring soil and foliar nutrients, and biomass density, we also sought to determine if livestock grazing of turfs has the same functional equivalence as in grazed systems elsewhere by fostering increased nutrient cycling rates, manifest as greater plant productivity and palatability, which in turn often promote greater grazer activity (McNaughton 1984, 1993).

Materials and methods

Data collection

Vegetation sampling

Turf vegetation, with and without ungulate herbivory, was monitored at two New Zealand sites using different sampling techniques.

Taranaki. Turf vegetation was monitored semi-annually over 9 years at Stent Road on the central Taranaki coast (173°46'39"E; 39°13'11"S) (Figure 1). This coastal terrace of consolidated andesitic lahar debris terminated in a c. 3 m high (amsl) cliff abutting a rocky surge zone. From the cliff edge, prostrate native turf of herbs and grasses grades inland into communities dominated by non-native grasses and herbs. In September 1999, 34, 0.5 × 0.5 m plots were subjectively placed in predominantly prostrate native turf within a 15 m wide coastal strip defined by the inland limits of turf along a 100 m long section of coast. Cover of individual plant species, along with aggregate classes for mosses and lichens, was estimated using a cover-abundance scale modified from Mueller-Dombois & Ellenberg (1974): 1 represents <1% cover; 2 is 1%–5%; 3 is 6%–10%; 4 is 11%–25%; 5 is 26%–50%; 6 is >51%. Plant species cover was measured annually in September from 1999 to 2006 and again in 2008. Dairy cattle accessed the site throughout the monitoring period, continuing a multi-decade-long established land use. However, in December 2002, a single, large (50 × 15 m), fenced enclosure to exclude cattle was erected over a section of the coastal zone containing 23 plots, leaving 11 plots exposed



Figure 1. Coastal turf on a lahar terrace landform at Stent Road, Taranaki. The photograph was taken in January 2009, 4 months after the last vegetation monitoring phase in September 2008. The ungrazed vegetation inside the enclosure is dominated by non-native pasture plants.

to ongoing herbivory outside the fence. The plots were sufficiently small compared with the fenced area that we treated plots with the grazing treatment as independent from one another. Species composition of the plots is provided in Table S1.

The Threatened, Nationally Vulnerable (de Lange et al. 2012) prostrate, spring-annual herb *Myosotis brevis* de Lange et Barkla occurs in turf at Taranaki. Its diminutive size and short-stature would render it vulnerable to smothering if turfs were invaded by taller-statured, native and non-native plants. We examined population trends in relation to ungulate herbivory by counting individual *Myosotis* rosettes in each plot throughout the monitoring period.

Southland. Turf vegetation was monitored at Black Point (168°56'57"E; 46°39'40"S) on the Foveaux Strait coast, eastern Southland (Figure 2). This granite terrace, approximately 15 m high (amsl), abutted a rocky surge zone. A seaward vegetation of prostrate native turf transitioned inland to tall grassland of native and non-native species. To examine vegetation trends on a gradient inland from the coast, eight, 6 × 6 m plots were located according to a stratified random design. Four plots were located along a 50 m stretch of coastline within 0–20 m of the sea ('Southland coast', Table 1). Four additional plots were located within a similar band 20–35 m from the sea ('Southland inland', Table 1). Each group of four plots consisted of two control and two enclosure plots. Enclosures consisted of fences to exclude large herbivores such as cattle but permitted herbivory by small mammals such as lagomorphs. Data were gathered from three randomly placed, parallel, 4.5 m long transects in each plot on six occasions in the months of January and December starting from January 2001 until January 2004 and again in December 2008. At 50 cm intervals along the transects, percentage cover of individual species was estimated in 10 × 10 cm quadrats. Litter and humus were recorded as litter, and rock and bare soil were recorded as bare ground at both Taranaki and Southland. For the first year of monitoring, sheep (*Ovis aries*) grazed the site followed thereafter by cattle. The site had a multi-



Figure 2. Coastal turf on a granite terrace landform at Black Point, Southland. The photograph was taken in November 2010, 2 years after the last phase of vegetation monitoring in December 2008. The ungrazed vegetation inside the enclosure is dominated by non-native and native grasses, although native grasses are an important component of coastal turf outside the enclosure.

decade-long history of grazing by farm stock. Species composition of the plots is provided in Table S2.

Distance to coastal platform edge

To disentangle the primary marine gradient from the effects of grazing, we measured the distance from the centroid of each plot, perpendicular out to the edge of the coastal terrace landform bordering the surge zone. This distance was used as a proxy for the salt and exposure gradients at the sites. Measurements were made on five occasions (1999, 2002, 2004, 2006 and 2008) at Taranaki (163 mm/year average retreat, 1.46 m over 9 years) and linear interpolation between measurements used to obtain individual plot distances for each vegetation sampling occasion as erosional retreat occurred. For the Southland site, the distance measurements were made in January 2001 and applied across all vegetation samplings because no landform retreat was evident when the measurements were repeated at the last sampling.

Biomass and nutrient concentrations

To test for differences in foliar tissue density, biomass, and nutrient concentrations of grazed and ungrazed vegetation, we analysed vegetation samples adjacent to a subset of the vegetation monitoring plots at Taranaki and Southland, in November 2009. For ungrazed plots, the enclosures were large enough to permit sampling from within the enclosures without interfering with the vegetation monitoring. We harvested all foliage (including stolons) from 310 × 230 mm plots. Sample size is given in Table 1 and the vegetation composition in online Appendix 1. The foliage samples were dried at 30 °C, weighed and the foliar tissue density and biomass concentrations calculated (see below), while nutrients, fibre and lignin were analysed following the methods of Blakemore et al. (1987), Mole & Waterman (1994), Rowland & Roberts (1994) and Prasad & Spiers (1978). For foliar tissue density and biomass concentrations, we estimated mean canopy height of the vegetation, computed the sampled volume, and calculated dry foliar tissue density in mg/mL.

Table 1. Mean (\pm SD) and *P* values of Student's *t*-test comparisons of foliar biomass and chemistry, and soil chemistry variables, between prostrate coastal turf and taller invasive vegetation outside and within fenced exclosures, respectively, at Taranaki and Southland.

	Taranaki (0–15 m)*			Southland coast (0–20 m)*			Southland inland (20–35 m)*		
	Grazed 10	Ungrazed 10	<i>P</i>	Grazed 5	Ungrazed 5	<i>P</i>	Grazed 5	Ungrazed 10	<i>P</i>
Number of samples									
Foliage									
Foliar tissue density (mg/mL)	88.41 \pm 28.8	10.91 \pm 5.65	<0.001	33.49 \pm 5.14	12.59 \pm 2.5	<0.001	27.94 \pm 2.24	10.48 \pm 2.3	<0.001
Foliar tissue biomass (t/ha)	8.84 \pm 2.88	8.34 \pm 2.65	0.69	3.35 \pm 0.05	8.48 \pm 2.81	0.004	2.79 \pm 0.02	21.31 \pm 3.86	0.02
N (%)	1.14 \pm 0.31	2.4 \pm 0.66	<0.001	1.18 \pm 0.14	1.42 \pm 0.61	0.44	1.12 \pm 0.07	0.96 \pm 0.26	0.08
P (%)	0.18 \pm 0.05	0.25 \pm 0.1	0.1	0.25 \pm 0.05	0.24 \pm 0.03	0.59	0.18 \pm 0.03	0.13 \pm 0.03	0.03
K (%)	0.4 \pm 0.1	1.53 \pm 0.56	<0.001	0.63 \pm 0.09	0.73 \pm 0.08	0.11	0.76 \pm 0.08	0.71 \pm 0.16	0.41
Ca (%)	0.3 \pm 0.09	0.67 \pm 0.4	0.02	0.23 \pm 0.01	0.63 \pm 0.05	<0.001	0.53 \pm 0.05	0.19 \pm 0.05	<0.001
Mg (%)	0.29 \pm 0.11	0.55 \pm 0.2	0.003	0.26 \pm 0.01	0.53 \pm 0.06	0.001	0.52 \pm 0.08	0.23 \pm 0.05	<0.001
Fibre (%)	41.63 \pm 1.54	33.2 \pm 4.8	<0.001	32.9 \pm 3.2	40.53 \pm 2.88	0.004	40.58 \pm 1.63	38.19 \pm 2.72	0.1
Lignin (%)	11.16 \pm 1.98	6.97 \pm 1.59	<0.001	6.32 \pm 0.98	27.2 \pm 7.93	0.004	24.7 \pm 8.1	8.45 \pm 1.42	<0.001
Soil									
pH	5.8 \pm 0.54	6.2 \pm 0.4	0.08	5.47 \pm 0.25	5.86 \pm 0.11	0.02	5.72 \pm 0.19	5.86 \pm 0.21	0.24
EC (millmho/cm)	0.2 \pm 0.1	0.4 \pm 0.1	0.04	0.34 \pm 0.06	0.34 \pm 0.02	0.91	0.38 \pm 0.15	0.35 \pm 0.09	0.6571
C (%)	6.5 \pm 3.36	8.1 \pm 2.8	0.26	17.52 \pm 4.36	13.0 \pm 3.42	0.05	6.71 \pm 2.85	5.77 \pm 1.36	0.52
N (%)	0.5 \pm 0.29	0.7 \pm 0.2	0.21	1.06 \pm 0.2	0.93 \pm 0.22	0.32	0.51 \pm 0.19	0.44 \pm 0.1	0.5
Olsen P (mg/kg)	48.3 \pm 56.7	51.7 \pm 50.4	0.89	87.27 \pm 46.48	135.32 \pm 53.36	0.17	16.16 \pm 5.88	14.89 \pm 3.27	0.67
Total P (mg/kg)	1901.0 \pm 603.39	1769.0 \pm 559.9	0.62	1970.48 \pm 370.13	2405.16 \pm 476.32	0.15	1168.44 \pm 367.21	1051.69 \pm 242.43	0.54

*Distances from the coast defined by each sample site are given in brackets. Significant differences are shown in bold.

and foliar tissue biomass in t/ha. To compare the soil chemistry of grazed and ungrazed plots, soil samples were collected beneath the harvested foliage by removing the top 50 mm of soil of the 310 × 230 mm plot. Samples were sieved, air-dried at 30 °C and chemically analysed after the methods of Blakemore et al. (1987).

Data analysis

Taranaki vegetation trends

The cover score data were converted to cover estimates by taking the midpoint of the cover range for each cover class on the log scale and then back-converting. Species were classified according to origin (non-native or native) and potential growth form (erect or prostrate) (see supporting information in Tables S1–2). Cover estimates were summed by origin and growth form to give plot-level estimates. We fitted linear mixed models to the log-transformed cover data assuming Gaussian errors. Our model included distance from the platform edge ('distance'), plant origin by growth form group ('functional group') and years since livestock were excluded ('grazing') as fixed effects. We expected a non-linear relationship between the number of years since livestock were excluded and vegetation changes, with the greatest changes soon after exclusion before plateauing over time as competitive species dominate. To test this we modelled livestock exclusion as a 2nd degree polynomial. At Taranaki, we expected that the coastal salinity gradient would inhibit erect species closer to the platform edge but that grazing effects would be similar over the comparatively short 13 m gradient that was sampled. Hence we log-transformed distance from platform edge to test for this effect. The model also included separate random intercepts for year and plot to account for similarity between plots with years and repeated measures of plots over time.

We modelled species density per plot by origin and growth form using a generalised mixed model assuming Poisson distributed errors. Model terms were as for the cover model.

We fitted a generalised mixed model to the plot-level *Myosotis* count data assuming Poisson errors with a log link. Our model included distance from the platform edge and the number of years in which livestock were excluded as fixed effects. Both variables were log-transformed. We included separate random intercepts for year and plot. Overdispersion was modelled using an observation-level random effect (Browne et al. 2005).

The variance explained by the models was calculated using the methods of Nakagawa & Schielzeth (2013). Group mean effects were calculated from the model to represent the effects for each origin by growth form combination. To assess significance of model terms we sampled from the posterior distribution of each group mean effect and calculated the 95% highest probability density intervals (HPDI). The HPDI estimates values between which the parameter estimate has a 95% probability of occurring. Parameters with 95% HPDI excluding zero were deemed significant. All analyses were carried out in R (R Core Team 2012). Predicted relationships are shown averaged over other terms in the model using package 'effects' (Fox 2003). In the Results, parameter estimates from the models are expressed as a mean, ±95% confidence limits.

Southland vegetation trends

Species were classified according to origin (non-native or native) and growth form (erect or prostrate). Cover estimates were summed to give plot-level estimates of total cover by

origin and growth form for each year. We fitted linear mixed models to the cover data. Cover estimates were discrete (i.e. to the nearest percentage) and best modelled assuming Poisson distributed errors. Our model included distance from the platform edge, plant origin by growth form group ('functional group') and years since livestock were excluded ('grazing') as fixed effects. The number of years since livestock were excluded was modelled as a 2nd degree polynomial as for Taranaki. At Southland, we sampled a larger gradient than at Taranaki and we expected that the distance from platform edge effects would be more complex. We hypothesised that salinity would affect the vegetation patterns as for Taranaki, but additionally that grazing pressures (including lagomorphs) would be higher inland with proximity to pasture, potentially inhibiting erect species at this end of the gradient too. To test for these complex patterns we modelled distance from platform edge as a 3rd degree polynomial. The model also included separate random intercepts for year, plot, transect nested within plot, and subplot nested within transect. Over-dispersion was modelled using an observation-level random effect (Browne et al. 2005).

We modelled species density per plot by origin and growth form using a generalised mixed model assuming Poisson distributed errors. The fixed effects were as for the cover model, except that years since livestock were excluded was log-transformed and distance to platform edge was modelled as a 2nd degree polynomial. As before, HPD intervals were used to assess significance. In the Results, parameter estimates from the models are expressed as a mean, $\pm 95\%$ confidence limits.

Foliar biomass and nutrient concentrations

The foliar tissue density, biomass and nutrient variables and the soil chemistry variables of grazed and ungrazed turf were compared using Student's t-tests.

Results

Grazing effects by growth form and plant origin

Taranaki

The relative effect of grazing on prostrate and erect species showed some similarities, but were not identical for native and non-native species as expected if cattle were perfect surrogates for avian herbivores. Non-native species cover increased when livestock were excluded (Figure 3A; $P < 0.05$; see Table S3 for parameter estimates); however, the increase was much larger for erect than prostrate species (difference from erect non-natives: grazing -13.65 [-20.72 – -7.19]; grazing squared -2.43 [-8.52 – 5.04]; Figure 3A–B). Native erect species in contrast to non-native erect species initially increased following grazer removal before reaching a plateau after about 3 years ($P < 0.05$; Figure 3A). In contrast, the cover of native prostrate species declined sharply from $75.9\% \pm 2.3\%$ to an average abundance of $1.7\% \pm 1.0\%$ ($P < 0.05$; Figure 3A). The average amount of bare ground (soil or litter) declined from $14.68\% \pm 1.60\%$ to $0\% \pm 0\%$ after 5 years of grazing removal ($P < 0.05$) but the overall change was small compared with the magnitude of the changes observed in the vegetation. Non-native erect species were slightly less common closer to the platform edge (Figure 3B; $P < 0.05$), whereas the cover of bare ground was slightly higher near the platform edge ($P < 0.05$; Figure 3B). Neither the abundance of native erect ($P > 0.05$) nor prostrate species of either origin showed a significant

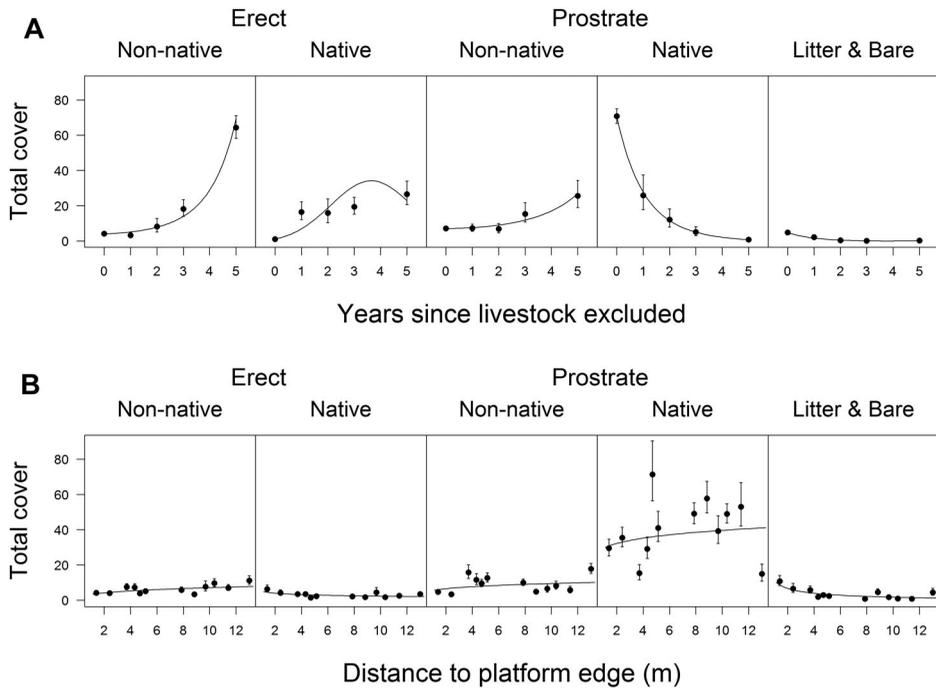


Figure 3. Effects of livestock exclusion (**A**) and distance to platform edge (**B**) by growth form and bare ground (erect/prostrate/litter and bare ground) and origin (non-native/native) on total cover within plots at Stent Road, Taranaki. The lines give the fitted relationships averaged over all other terms in the model. Points show back-transformed means (\pm SEM) of the fitted model plus the residual error for each data point. Livestock exclusion means are summarised for each year. Distance to platform edge are summarised for bins of approximately equal sample size using the midpoint of the bin range as the x-coordinate. The full model explained 55.6% of the variation in the data. The fixed effects alone explained 51.4% of the variance.

relationship with distance from platform edge (non-native prostrate $P > 0.05$; native prostrate $P > 0.05$).

As with total cover, the effect of years since livestock were excluded on species density depended on species origin and functional group with prostrate species showing declines in species density (Figure 4A). Removal of grazing increased the mean number of erect species for both non-natives and natives (both $P < 0.05$; see Table S4 for parameter estimates). By contrast, species density of prostrate species declined, with the modest declines in non-native species ($P < 0.05$) being dwarfed by the large decline (from 4.7 ± 0.1 to 0.5 ± 0.2 species per plot after 5 years of grazing exclusion) in native species ($P < 0.05$). Non-native erect species density was unrelated to distance from platform edge ($P > 0.05$; Figure 4B). However, there were slightly more native erect species per plot nearer to the coast ($P < 0.05$; Figure 4B). Both native and non-native prostrate species density increased with increasing distance from the coast (both $P < 0.05$; Figure 4B).

Myosotis brevis was undergoing rapid declines at this site prior to the installation of the non-grazing treatment (Figure 5A). However, following an additional 3 years without grazing, *M. brevis* frequency declined to zero (Figure 5A–B; grazing $-4.15 [-5.68 - 2.70]$), whereas in grazed plots *M. brevis* frequency appeared to stabilise. *Myosotis*

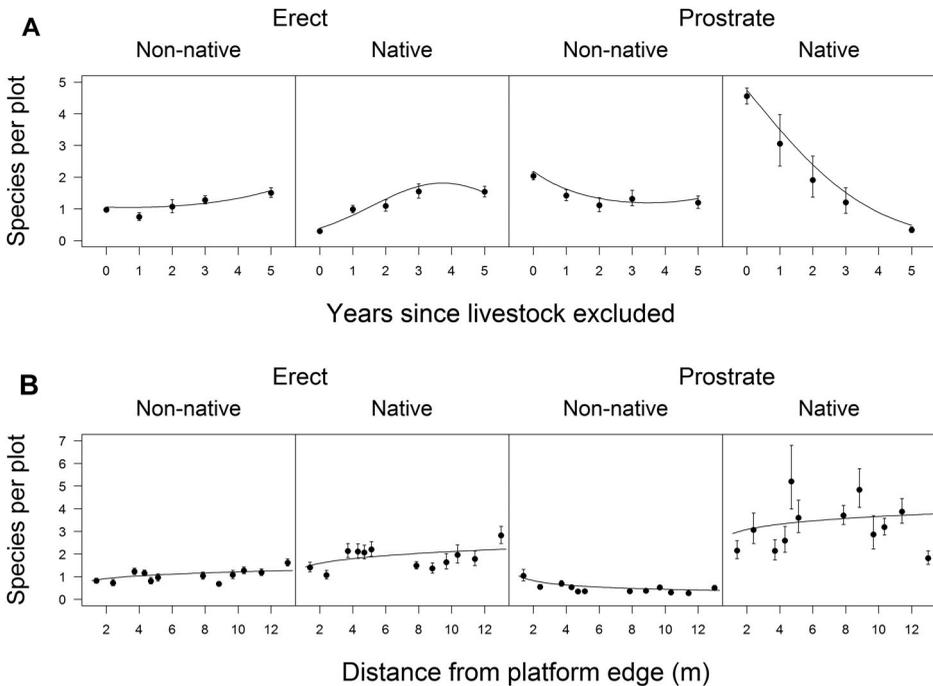


Figure 4. Effects of livestock exclusion (**A**) and distance to platform edge (**B**) by growth form and bare ground (erect/prostrate/litter and bare ground) and origin (non-native/native) on the number of species per plot at Stent Road, Taranaki. The lines give the fitted relationships averaged over all other terms in the model. Points show back-transformed means (\pm SEM) of the fitted model plus the residual error for each data point. Livestock exclusion means are summarised for each year. Distance to platform edge are summarised for bins of approximately equal sample size using the midpoint of the bin range as the x -coordinate. The full model explained 61.2% of the variation in the data. The fixed effects alone explained 61.1% of the variance.

brevis was also significantly more common in plots that were further from the sea platform edge (Figure 5C; distance 0.503 [0.187–0.834]).

Southland

As with Taranaki, there were differences between native and non-native species in the response of the growth forms to cattle grazing, with relatively bigger disparities for native species (Figure 6A). Erect non-native and native species were more abundant in ungrazed plots after 5 years of herbivore exclusion (both $P < 0.05$; see Table S5 for parameter estimates). By contrast, prostrate species remained constant or declined following grazing removal. Non-native prostrate species remained steady at very low abundance ($P > 0.05$). However, native prostrate species, the most abundant functional group, were predicted by the model to decline in percent cover from 47.1 ± 0.09 to 3.9 ± 0.18 after 5 years in the absence of grazing ($P < 0.05$). Bare ground or litter initially declined after grazing removal but then had increased past initial levels by the final sampling period (Figure 6A; $P < 0.05$). Both non-native and native erect species showed a peak in cover at 22–30 m from the ocean (Figure 6B; both $P < 0.05$). Non-native prostrate species, while at low abundance, also showed a similar peak in abundance as for the erect

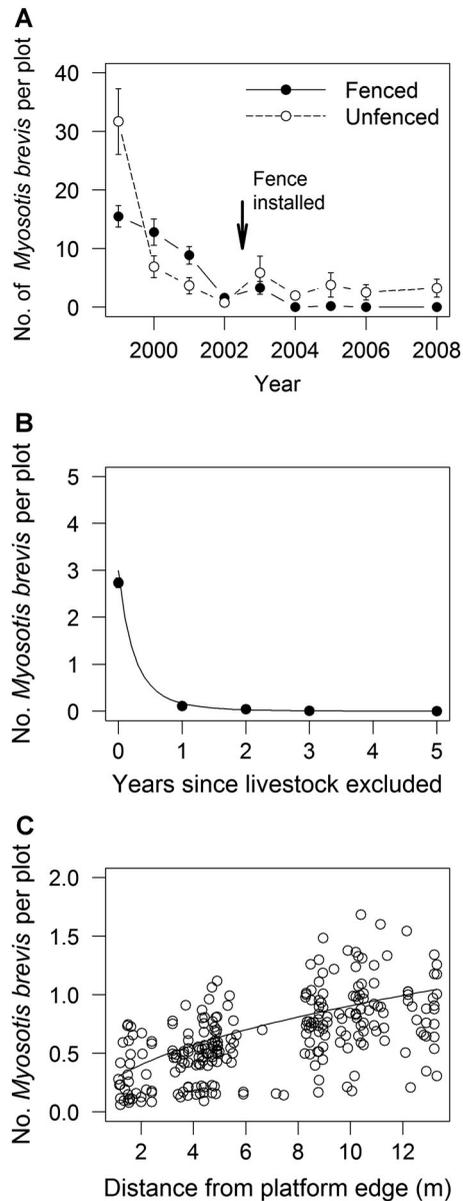


Figure 5. Frequency of *Myosotis brevis* at Stent Road, Taranaki. **A**, Mean observed frequency (\pm SEM) plotted against sample year for unfenced and fenced plots. Note that fenced plots were fenced between the 2002 and 2003 sampling events as indicated by the arrow; **B**, modelled effects of years since herbivory was excluded on the frequency of *M. brevis* per plot averaged over the other terms in the model. Points show the mean \pm SEM of the observations averaged over the other model terms; **C**, modelled effects of distance from the platform edge on the frequency of *M. brevis* per plot averaged over the other terms in the model. Points show the observations, averaged over the other model terms. The variance explained by the 'years since herbivory was excluded' and 'distance from platform edge' variables combined was 73.5%. The total variance explained by the model (fixed and random effects) was 93%.

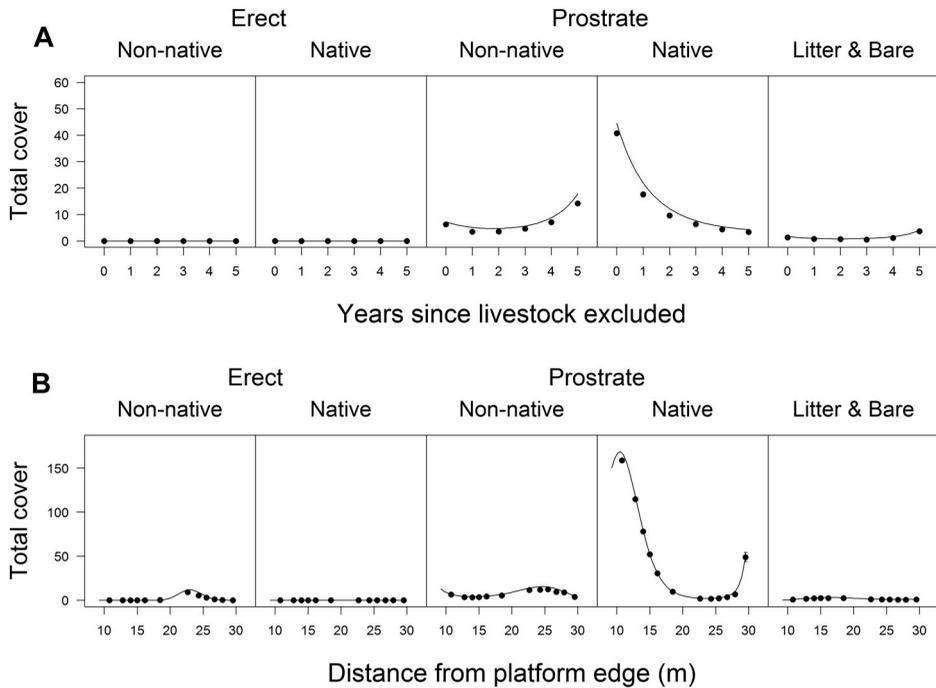


Figure 6. Effects of livestock exclusion (**A**) and distance to platform edge (**B**) by growth form and bare ground (erect/prostrate/litter and bare ground) and origin (non-native/native) on total cover within plots at Black Point, Southland. The lines give the fitted relationships averaged over all other terms in the model. Points show back-transformed means (\pm SEM) of the fitted model plus the residual error for each data point. Livestock exclusion means are summarised for each year. Distance to platform edge are summarised for bins of approximately equal sample size using the midpoint of the bin range as the x -coordinate. The full model explained 96.9% of the variation in the data. The fixed effects alone explained 68.3% of the variance.

species (Figure 6B; $P < 0.05$). Native prostrate species showed the opposite pattern to the other groups, with very high abundance close to the ocean, moderately high abundance at the furthest distance, and low elsewhere (Figure 6B; $P < 0.05$). Bare ground was more common in more seaward than inland plots with peak bare ground at around 15 m from the sea (Figure 6B; $P < 0.05$).

Erect non-native species density increased slightly with the cessation of grazing (Figure 7A; $P < 0.05$); however, native erect species showed no change (Figure 7A; $P > 0.05$; see Table S6 for parameter estimates). Both non-native and native prostrate species density declined in the absence of grazers (Figure 7A; both $P < 0.05$). While this decline produced only small changes in species density for non-native prostrate species, native prostrate species density was estimated to decline from an average of 3.3 ± 0.2 to 2.3 ± 0.2 species per plot in the 5 years following grazing exclusion. Both erect and prostrate non-native species were generally rare at the site; however, there was a significant peak in their abundance from 20–27 m from the ocean (both $P < 0.05$). The species density of both erect and prostrate native species increased with distance from the coast (Figure 7B; both $P < 0.05$).

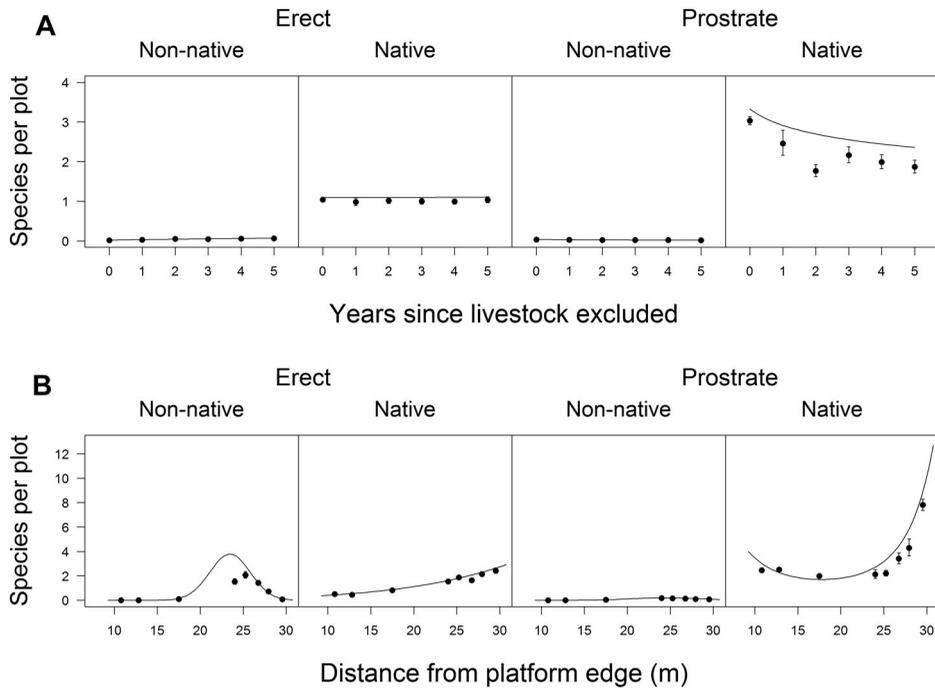


Figure 7. Effects of livestock exclusion (**A**) and distance to platform edge (**B**) by growth form and bare ground (erect/prostrate/litter and bare ground) and origin (non-native/native) on the number of species per plot at Black Point, Southland. The lines give the fitted relationships averaged over all other terms in the model. Points show back-transformed means (\pm SEM) of the fitted model plus the residual error for each data point. Livestock exclusion means are summarised for bins of approximately equal sample size using the midpoint of the bin range as the x-coordinate. The full model explained 97% of the variation in the data. The fixed effects alone explained 95.3% of the variance.

Biomass and nutrient concentrations in response to grazing

Grazing did not uniformly increase vegetation nutrient levels in grazed plots, nor create differences in soil nutrient status, indicative of a grazing-induced positive feedback mechanism. At Taranaki, most of the foliar nutrients were at significantly greater concentrations in the ungrazed turf than in the grazed turf, with fibre and lignin showing the opposite pattern (Table 1). At Southland, there were no consistent differences in the foliar nutrients between grazed and ungrazed turf in either of the two sampled zones; in the coast zone, concentrations of Ca, Mg, fibre and lignin were greater in the ungrazed turf, while in the inland zone, concentrations of P, Ca, Mg and lignin were greater in the grazed turf. The foliar tissue density of grazed turf was significantly greater than that found in ungrazed turf, at both the coast and inland zones (Table 1). However, although there was no significant difference in foliar tissue biomass of Taranaki grazed and ungrazed turf, at Southland the grazed turf had significantly less total biomass than the ungrazed turf. Few soil chemistry parameters showed significant differences between grazed and ungrazed turf at both sites (Table 1). Soil pH was marginally higher in ungrazed than grazed plots at the Southland coast (Table 1).

Discussion

Ecological equivalence of bird and mammal herbivore guilds

Our test for whether non-native cattle grazing was functionally equivalent to the largely extinct avian grazing guild in maintaining native turf community structure and composition required that the relative effects of grazing on non-native prostrate and erect growth forms were similar to that of grazing on native species. This outcome was only partially supported by the data. For both native and non-native species, prostrate taxa performed better relative to erect taxa when grazed. However, while erect species uniformly declined with mammalian grazing, only native prostrate species increased when grazed. Non-native prostrate species either declined or remained constant. Species density exhibited a more uniform response to grazing, with increases in prostrate relative to erect species at both sites with grazing, regardless of origin, although the largest increases were observed for native species. One interpretation of these results is that cattle grazing promotes native turf over erect vegetation communities more aggressively than the historic avifauna and that native turf species are able to escape the fate of non-native species because cattle are evolutionarily naive with respect to the native taxa. We think this unlikely for two reasons. First, while birds and cattle have similar tugging and tearing actions in soft vegetation (Lee et al. 2010), the differences in footprint pressure (Duncan & Holdaway 1989) and the qualitative nature of their nutrient inputs (Tanentzap et al. 2013) probably foster invasions. The greater footprint pressure exerted by cattle (Duncan & Holdaway 1989) potentially causes greater shearing of the ground surface, more damage to ground cover plants and increases in bare ground (Bilotta et al. 2007) relative to the extinct avifauna. The increase in plant fragmentation associated with higher shear pressure can benefit vegetative reproducing species such as the vast majority of the non-natives in this system because rhizome and stolon fragments are able to autonomously resprout rather than be lost to the live-biomass fraction (Mack & Thompson 1982). Nutrient inputs also vary between birds and cattle; bird faeces are comparatively higher in NO_3^- relative to NH_4^+ , and release N to the soil faster due to lower C:N ratios (Tanentzap et al. 2013). Avian faeces can enhance native regeneration in New Zealand's bird-adapted floras, which is likely negatively impacted by the extinction of the avian mega-herbivores (Tanentzap et al. 2013). Second, all erect species, regardless of origin, were reduced to equally low abundances in the presence of herbivores suggesting no large differences in palatability to cattle based on origin. There is no a priori rationale to expect that equal palatability regardless of origin should not apply to prostrate species also. Another interpretation for these results is that in the absence of erect competitors, native prostrate species are more effective competitors than the non-native prostrate species due to the interaction with the underlying environmental gradient. In our study (coastal), and many others in which turfs are found (e.g. lacustrine margins [Korsten et al. 2013] and ephemeral wetlands [Tanentzap et al. 2014]), there is a strong underlying abiotic gradient that selects species adapted to the local environmental conditions. While the prostrate growth form is one specific adaptation to salt exposure (Johnson 1993; Vononkova et al. 2008), the non-native species were pasture species and forbs and they lack the more specialised halophytic adaptations found in many of the native species (e.g. succulent leaves).

In our study, the marine and grazing gradients appear inversely related to each other resulting in bimodally distributed turf vegetation with distance from coast. Bare ground was highest at the cliff edge where the marine impact was most extreme, with the cover of primarily native prostrate species being highest within the first 13 m from the coastal platform at both sites, with low abundance of erect forms. We suggest that cattle and lagomorphs reduced their grazing close to the seaward cliff relative to inland as the short-statured vegetation driven by salt deposition cannot be efficiently harvested relative to the taller biomass available inland (e.g. Belovsky 1997). At intermediate distances (20–27 m at Southland), exposure and salt are declining but grazing is still reduced, allowing an increase in erect species, particularly high producing non-natives whose maximum biomass is stunted by marine exposure. Further inland again, grazing intensity is sufficiently high to compensate for a further decline in exposure and salt in the selection of turf ahead of erect plants (e.g. 27–32+ m at Southland). Finally, at even greater distances than sampled in our study, we expect grazing in the relative absence of exposure and salt to be insufficient to select turf ahead of an agriculturally influenced non-native herbfield.

Positive nutrient feedbacks and grazing lawns

We found little evidence of the nutrient-driven positive feedback mechanism (Wilson & Agnew 1992; Brownstein et al. 2014) necessary for the prostrate turf system to constitute a grazing lawn (*sensu* McNaughton 1984; Archibald 2008; Stock et al. 2010; Roberts et al. 2011). Only Taranaki showed a significant difference in N between prostrate and erect vegetation types, and this was higher in the erect vegetation, with other indicators (e.g. low lignin) also pointing to higher palatability. Grazing is expected to reduce the shoot to root ratio, leading in the short term to the roots supplying nutrients to less tissue, higher foliage nutrient concentrations and higher net primary productivity (McNaughton 1979; Lee & Johnson 1984; Houle & Simard 1996). At Southland, the patterns were mixed in direction and magnitude probably reflecting in part the differences between primarily native communities ('inland') and those with a larger non-native component ('coast'), especially in the ungrazed plots. We conclude that the erect vegetation is actually more attractive for herbivores, and that the turf vegetation persists due to its tolerance for the salinity gradient, secondarily augmented by herbivore control of taller species.

A model of turf dynamics and management

Our results suggest that turf represents an unstable successional community state (Figure 8). Large storm surges, depositing excess salt, can reset the affected turf community to bare ground (G.M. Rogers, pers. obs.). Mild salt deposition in the absence of grazing leads initially to a tall-statured herbfield, with likely succession to coastal shrubland (Rogers & Wiser 2010) and forest where seed sources are available. The turf state is arrested only when grazed in the presence of mild marine influences. Our results therefore raise a dilemma when setting conservation goals, between active (grazing) management promoting early successional vegetation, concomitant with high species density, and passive management, whereby the unfolding of 'natural' ecosystem processes usually fosters successional change to taller communities, with a loss of a colonising flora (after

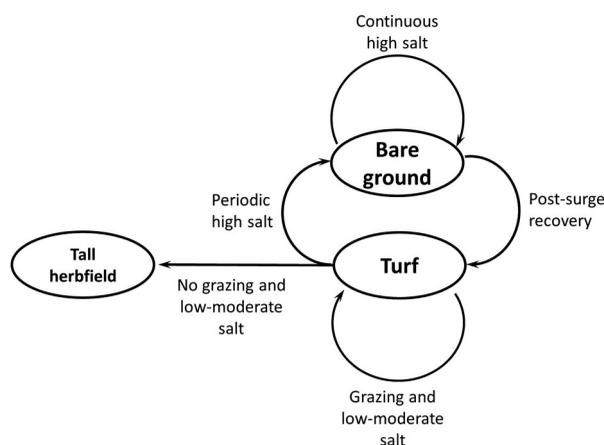


Figure 8. Vegetation dynamics under marine salt and grazing gradients in turf communities. Oval boxes indicate vegetation states. Arrows indicate transitions.

Meurk & Foggo 1988). That dilemma is exacerbated in New Zealand because of the almost universal penetration of turfs by erect non-native plants that were only contained by grazing and strong marine exposure. However, the loss of landscape-level opportunities for turf survival due to agricultural and urban expansion, and the extinction of the large avian herbivore guild, means that the natural dynamics that maintained this community in the landscape have been disrupted. This threatens both the community state and the populations of early successional species contained therein, such as the rare prostrate herb *M. brevis* at Taranaki.

Our pragmatic recommendation for the conservation management of turf communities is for herbivory to be manipulated in tune with fluctuations in the marine stress gradient, with mammalian grazing avoided after storm surges to allow the community to recover. Mammalian herbivory appears sufficiently equivalent to historic avian herbivory to fulfil this function under the relatively dry conditions studied here in which the turfs are resilient to hoof damage. Turfs with damp or wet soils should be grazed by sheep rather than cattle to prevent soil pugging (e.g. Champion et al. 2001, but see Marty 2005), or alternatively rely on marine exposure as the sole process driver. Unfortunately, our data do not extend to understanding the potential of herbivory to reverse a previous dominance of non-native plants in favour of native turf plants. Nonetheless, if the management goal is focused on maximising turf survivorship, mammalian herbivory can be viewed as a beneficial mechanism within particular environmental and management settings.

Supplementary data

Table S1. Estimated cover of plant species at Taranaki.

Table S2. Estimated cover of plant species at Southland.

Table S3. Parameter estimates for the analysis of plant cover at Taranaki.

Table S4. Parameter estimates for the analysis of species density at Taranaki.

Table S5. Parameter estimates for the analysis of plant cover at Southland.

Table S6. Parameter estimates for the analysis of species density at Southland.

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Disclosure statement

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