Understanding the role of birds in sustaining indigenous turf communities in a lacustrine wetland in New Zealand

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Abstract: Since human settlement, wetland ecosystems in New Zealand have been severely modified by fire and reduced by drainage for agricultural development. Those remaining are problematic to manage, with modified water regimes, invasive weeds and grazing by livestock. Before settlement, wetland habitats supported diverse avian herbivores, the majority of which are now extinct. However, introduced birds are increasing in wetlands. We sought to understand the role of grazing birds in the maintenance of local turf communities in a lacustrine environment in Otago, New Zealand. To determine the causes of the vegetation patterns, we investigated the influence of abiotic (water table and soil nutrients) and biotic (direct via grazing and indirect via faeces deposition) effects of the birds on the vegetation. Four plant communities were distinguished, two dominated by *Leptinella* and two by *Carex* species. The occurrence of the communities was correlated with the distance from the nearest permanent water, soil phosphorus levels, and amount of faecal deposition. The results indicate that avian grazing decreased the proportion of dominant exotic plant species by biomass removal, but not through enhanced nutrient inputs via faecal deposition. Results from this site suggest that naturalised geese facilitate the maintenance of indigenous plant species in the face of exotic invasion, and have a conservation role in highly modified wetland systems, perhaps restoring a herbivore function lost with the extinction of native avian grazers. The long-term conservation management of wetlands in New Zealand may require the utilisation of both native and introduced avian grazers to facilitate the dominance of indigenous plants.

Keywords: avian herbivory; grazing; positive-feedback switch; turf; wetland restoration

Introduction

Which environmental factors, both abiotic and biotic, determine vegetation patterns and species composition of plant communities is often unclear, especially when modified vegetation is recovering after intensive disturbance. Identifying the primary environmental drivers is of practical importance for conservation management when the vegetation type is rare and conservation strategies are required for its protection. The restoration of wetland habitats in New Zealand is a major focus for biodiversity protection, the provision of ecosystem services, and maintenance of recreational hunting opportunities. Since European settlement in the 1850s, wetlands have diminished significantly in lowland and montane areas in response to the expansion of agriculture. Currently only about 10% remain (McGlone 2009), and most of these are severely modified, with significant ingress of exotic plant species.

The conservation management of wetlands is challenging because of the high level of catchment and habitat modification, and the diversity of plant communities on different types of permanently or seasonally waterlogged soils (Johnson & Gerbeaux 2004). One of the most distinctive vegetation types associated with wetlands is turfs, low-statured (< 5 cm), herb-dominated plant communities often with a diverse flora (Johnson & Rogers 2003). These nationally rare communities (Williams et al. 2007) contain a remarkably large portion (20%) of the indigenous vascular flora. Recently Lee et al. (2010) proposed that these turfs represent an evolutionary response to avian herbivory, analogous to marsupial lawns in Australia (Kirkpatrick et al. 2011; Roberts et al. 2011) and mammalian

lawns in the Serengeti (McNaughton 1984). As proposed by McNaughton (1984), the gregarious behaviour of grazers modifies the vegetation and can improve feeding efficiency (i.e. nutrient intake per bite), while grazing-resilient herbs and grasses benefit from reduced competition from tall grasses and woody species, and locally high levels of soil nutrients due to faeces deposition. However, in all these situations abiotic factors are also critical, with either periodic impoundment or fire retarding the natural succession to woodland or forest.

Managing wetland turfs is challenging because removal of grazing frequently results in dominance by exotic species, especially in nutrient-rich systems where tall sedges and grasses can establish (Johnson & Rogers 2003). Wetlands in prehuman New Zealand were extensively grazed by native avian herbivores, including ducks, geese, and rails (Worthy et al. 2007). In many wetland areas mammalian grazing is still uncommon, but deliberately-introduced bird species (e.g. mallard duck *Anas platyrhyncos,* black swan *Cygnus atratus,* and Canadian geese *Branta canadensis*) are present in large numbers and are seasonally hunted or culled (Nugent 1992). However, introduced species may be substituting functionally for the extinct or now-rare native species such as Finsch's duck (*Chenonetta finschi*) and the South Island goose (*Cnemiornis calcitrans*). Currently, plant–herbivore interactions in New Zealand wetlands are poorly understood (Win 2001), which limits conservation management and assessment of the impacts of bird control in these areas.

In this study we examined the role of three potential main drivers of vegetation pattern in structuring lakeshore plant communities at Waihola, South Island, New Zealand: (1) abiotic

factors such as water level and soil nutrient status, (2) biotic factors such as avian herbivory and faeces deposition, and (3) species-pool constraints such as the limited composition of the soil seed bank. At this site, small, discrete patches of waterside turf occur among taller sedge/grass communities. Our hypothesis is that the turf is a grazing-mediated plant assemblage (dominated by short-statured indigenous plant species) maintained directly via grazing or indirectly via enhanced soil nutrients from faeces.

Materials and methods

Study site

The study was conducted in an area of c. 3000 m^2 in the Sinclair Wetlands (46°02′ S, 170°06′ E) on the eastern side of the lower Taieri Plain, 10 km upriver from the coast and 30 km south-west from Dunedin, Otago, New Zealand. The region is characterised by an annual mean temperature of 10.6°C and average annual rainfall is 816 mm (NIWA 2011). The Sinclair Wetlands are a lacustrine ecosystem with fluctuating groundwater reflecting catchment runoff and changes in level of the Waipori Stream, which is tidal but normally with backed-up fresh water in this section of the catchment. The seasonal pattern shows low water levels in summer and extensive ponding in winter.

The wetland system supports turf vegetation, *Carex* sedgelands and grasslands dominated by *Agrostis stolonifera*[1] and *Schedonorus phoenix*. Further vegetation types in the area include aquatic communities in persistent ponds, rushlands, sparse scrubland (*Coprosma propinqua, Leptospermum scoparium*) and riparian willows (*Salix fragilis*). The study site was grazed by livestock (sheep and cattle) until 2002, but since then has been grazed only by native and naturalised waterfowl and invertebrates. There are no grazing mammals present (e.g. lagomorphs) because of natural barriers (e.g. streams and rank vegetation limiting access). Currently the area is managed by the New Zealand Department of Conservation with the aim of biodiversity protection.

Vegetation sampling

A representative area (3 ha) adjacent to the major backwater system (NZTM grid 771 021) was sampled using 110 0.25-m^2 quadrats, placed across the entire area by restricted randomisation (Greig-Smith 1983). Plant shoot presence (Greig-Smith 1983) of all vascular plant species was recorded in each quadrat. Soil cores (8 cm in diameter and 10 cm deep) were taken from each quadrat. The above-ground vegetation of these cores was removed, oven-dried at 70° for 3 days and served to estimate the biomass of each plot. The soil cores were retained for seed bank estimation.

Abiotic factors

The surface topography of the sampling area was surveyed with a Survey Laser Infrared Beam 200 m (*Leica*, Singapore) surveyor's level (accuracy: ± 2.6 mm per 30 m). To determine the water level adjacent to each quadrat, a soil core of 30 cm depth was removed and the resulting hole left to fill with water over a period of 1 h. The distance from the soil surface to the water table was recorded and subtracted from the surface topography measurements to determine the water table depth. In addition, the distance to the nearest permanent water body was determined.

Five soil samples were collected from each of the four communities identified through the vegetation sampling (see below). The soil cores were split into halves. Moisture content (oven-dried at 105°C for 24 h), pH in deionised water, electrical conductivity using a 1:5 soil: water mixture (Blakemore et al. 1987) and organic matter (oven-dried soil fired at 500°C for 2 h) were determined for one half. Total carbon, mineral nitrate, ammonium, and Olsen-available phosphorus (Olsen et al. 1954; Blakemore et al. 1987) were determined in the second half.

Herbivory

To determine the effect of grazing exclusion, three paired control and animal-exclosure plots (1 × 1 × 0.5 m) were set up in winter 2006 in each of three of the communities identified in the vegetation survey. One randomly selected quarter of 0.25 m^2 from each exclosure or control plot was harvested in summer 2007 and another in 2008. Canopy height and above-ground biomass of each vascular plant species were used to assess the impacts of avian herbivory. A subsample of the above-ground biomass was dried, ground and assayed for total N.

Faecal densities were used as an indicator of nutrient input, an indirect effect of herbivore pressure. Pellets were collected monthly from March to August 2008, in permanent quadrats of 0.25 m^2 beside each of the 110 sampled plots, and their source identified to species. Pellets were then oven-dried at 70°C for 48 h and weighed.

Seed bank

Each soil sample to be used for seed bank analysis was sliced into centimetre cubes and mixed with sterile sand (1:1 ratio). Half was mixed with 80 mg of air-dried bird faeces previously collected from the area. Samples were spread over 500 cm^3 on a bed of sterile sand in a 2-litre plastic container in a shade house. As seedlings emerged, all vascular plant species were identified and counted. Ten pots, with sand only, served as controls for external contamination.

Analyses

To identify plant communities, cluster analysis was performed on the species data, using the Jaccard measure of similarity and the flexible sorting strategy with beta = −0.25 (Clifford & Stephenson 1975). Repeated-measures analysis of variance was performed for the soil components, the environmental data, biomass and the seed bank.

We modelled the effects of grazing on total biomass and the proportion of biomass that was exotic, using linear mixed-effects models. Plot nested with plot pair was modelled as random effects, whereas herbivory treatment, community, and year of sampling were included as fixed effects.

To determine how the biomass composition of the communities changed in the absence of grazing we calculated the quantitative Jaccard dissimilarities (using the 'vegdist' function in the R package 'vegan'; R Development Core Team 2011) between plot pairs from different communities, which were collected in the same year from the same grazing treatment. We fitted a linear model of year × grazing interaction to all the dissimilarities calculated for each pair of communities. Due to the lack of independence of the dissimilarities, statistical significance of the model coefficients was assessed using a permutation test (5000 permutations). Our null model

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[1] Nomenclature follows http://nzflora.landcareresearch.co.nz (accessed 16 Decemebr 2012).

assumed random treatment and year, but maintained the paired structure of the grazed and ungrazed plots within communities. Therefore across the subplot records for each plot pair (four subplot records, one for each year and grazing treatment combination), we randomly reassigned year and treatment, but held community constant.

We excluded two paired plots from both the mixed model and the dissimilarity analyses. One paired plot was excluded because it could not be sampled in 2008. The other paired plot was excluded as an outlier: in 2008 this plot (ungrazed) was invaded by tall fescue (*Schedonorus phoenix*), a prolific grass that was not present in any of the other herbivory plots, and was never observed in the grass community in the vegetation survey.

To determine whether the species composition of the seed bank differed between communities, or was affected by addition of goose faeces, we used canonical correspondence analysis with faeces addition and community coded as dummy variables. Permutation tests were used to assess statistical significance of the variation explained by each variate (using function 'anova.cca' in the R package 'vegan'; R Development Core Team 2011).

Results

A cluster analysis of the vegetation survey data identified four main communities (Table 1). The introduced grass *Agrostis stolonifera* (creeping bent) was widespread across all communities with a frequency of >90%. Two communities (will be referred to as turf communities) were low-statured swards (c. 3 cm high) of turf and grass characterised by the presence of the asterad forb *Leptinella dioica*. The Leptinella-Potentilla community was differentiated from the Leptinella community by the presence of *Potentilla anserinoides* (92% frequency) and *Eleocharis acuta* (32%). The other two communities were taller (c. 13–18 cm high) (referred to as *Carex* communities) and characterised by the presence of the sedge *Carex sinclairii* (>70%). In the Carex-Eleocharis community *Eleocharis acuta* (72%) was dominant, whereas the Carex-Schedonorus community was distinguished by the presence of the introduced grass *Schedonorus phoenix* (tall fescue; 64%).

While the turf communities typically occurred closer to the nearest water body (on average 20 m away) than the *Carex*-dominated communities (on average 35 m; $F_{3,106}$ = 17.88, P < 0.001; Duncan's test: P < 0.05), there was no association between the community present, surface topography ($F_{3,106}$ = 1.202, P = 0.31) and water-table levels ($F_{3,106}$ = 0.0786, P = 0.97). Of the soil components, available-phosphorus levels significantly differentiated the Leptinella community from the Carex-Schedonorus community ($F_{3,16}$ = 3.7, P = 0.034, Duncan's test: : P < 0.05). The pH values ranged from 6.1 to 6.6 with community Carex-Schedonorus being significantly lower than all other communities ($F_{3,16}$ = 3.67, P < 0.035, Duncan's test: P < 0.05). No other significant correlations with soil chemistry were present.

Herbivory

Feral geese (*Anser anser*) contributed over 85% of the faecal material, with small amounts from paradise ducks (*Tadorna variegata*) and black swans (*Cygnus atratus*). The distribution of faecal biomass indicated that the birds grazed predominantly in low-statured swards (turf communities), rather than in the taller-statured sedge communities (Fig. 1). This pattern of use is mirrored in the nitrogen content of the foliage. Nitrogen (N) was significantly higher in foliage from turf communities (mean 1.89% N (SE ± 0.13) for Leptinella-Potentilla and 1.80 ± 0.23 for Leptinella) than in the Carex-Eleocharis community (1.18

Table 1. Two-way table of species' frequencies in the four communities, and community classification in the wetland ecosystem; * exotic species, ** New Zealand endemic species.

Species/Communities (# of quadrats)	Leptinella-Potentilla (38)	Leptinella (14)	Carex-Eleo. (25)	Carex Sched. (31)
*Agrostis stolonifera**	100	100	100	94
*Callitriche stagnalis**	5	0	4	0
*Carex sinclairii***	0	0	72	85
Cotula coronopifolia	8	0	0	0
*Crassula sinclairii**	0	7	4	0
*Crepis capillaris**	5	0	0	6
Eleocharis acuta	32	0	72	42
Isolepis cernua	5	0	0	0
*Leptinella dioica***	92	100	4	0
*Lilaeopsis novae-zealandiae***	21	14	0	0
*Lotus pedunculatus**	42	7	0	42
*Potentilla anserinoides***	92	0	4	18
*Rumex crispus**	5	0	0	3
*Schedonorus phoenix**	3	0	0	64
Selliera radicans	13	29	0	0
*Trifolium repens**	63	50	0	33

± 0.06) ($F_{2,6}$ = 10.23, P = 0.012). Vegetation samples were unavailable for the Carex-Schedonorus community.

The exclosures were placed in the Leptinella-Potentilla, Leptinella, and Carex-Eleocharis communities. Total biomass was higher where avian grazing had been prevented by exclosures (Fig. 2). Within exclosures, biomass was similar among the three communities, whereas in the adjacent grazed plots biomass was lowest in the Leptinella-Potentilla community plots and highest in the Carex-Eleocharis community plots (grazing × community interaction, $F_{2,6}$ =

6.34, P = 0.033). The proportion of biomass contributed by indigenous species was significantly higher in grazed than ungrazed Leptinella-Potentilla community plots, and to a lesser degree in Leptinella community plots, but not in the Carex-Eleocharis community plots (grazing main effect: $F_{1,6}$ = 6.86, P = 0.040; grazing × community interaction, $F_{2,6}$ = 7.89, P = 0.021; Fig. 3). Both in the exclosures and controls, none of the pairs of communities changed in their similarities across the two years.
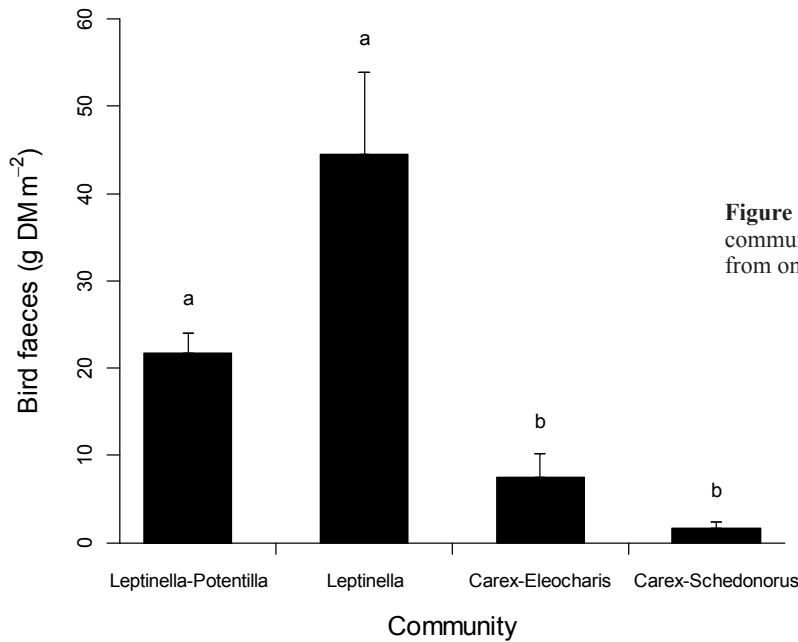

Figure 1. Mean (±SE) biomass (DM, dry matter) of bird faeces, by community. Bars with the same letters are not significantly different from one another at P < 0.05 (Tukey's post-hoc test).
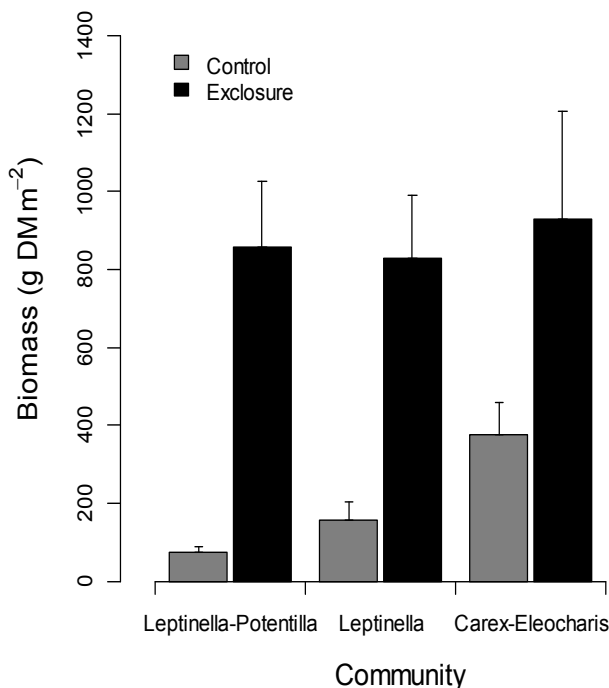

Figure 2. Mean (±SE) (over 2 years; year non-significant) vegetation biomass (DM, dry matter) in control (grey) and exclosure (black) plots, by community.
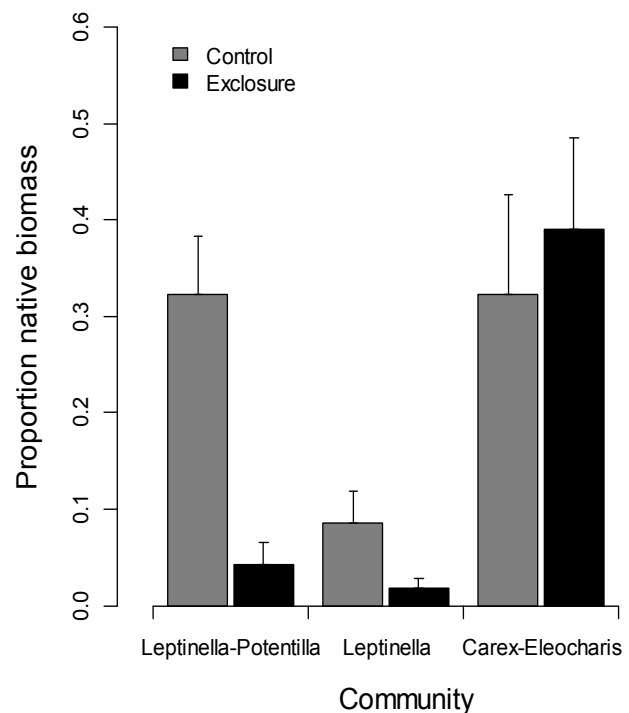
Figure 3. Mean (±SE) (over 2 years; year non-significant) proportion of the vegetation biomass (DM, dry matter) that was indigenous in control (grey) and exclosure (black) plots, by community.
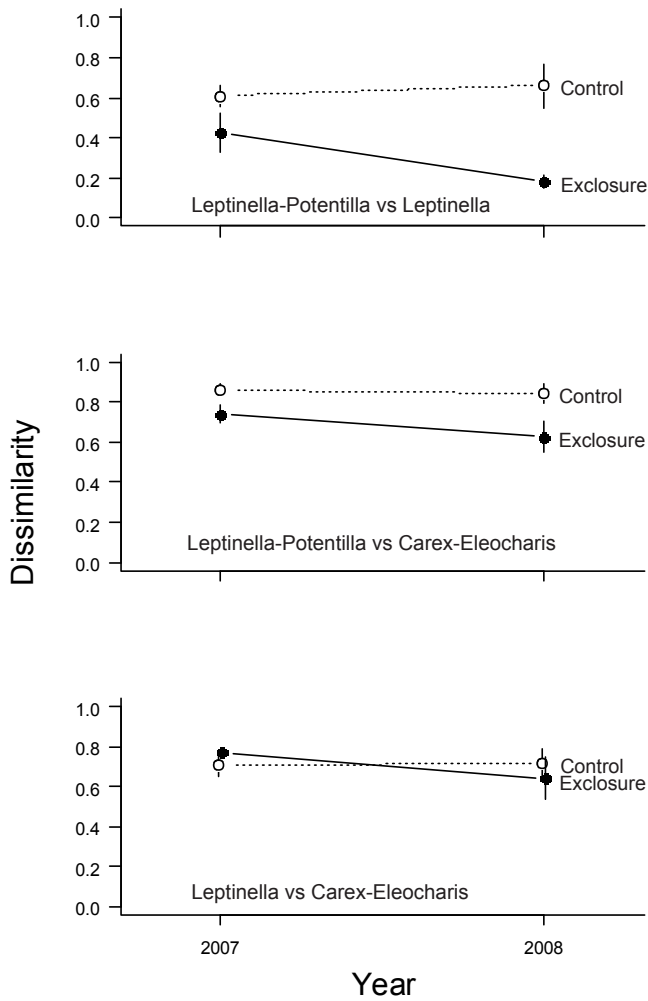
Figure 4. Mean (±SE) dissimilarity values between plot pairs of different communities, by year and treatment, for the herbivore exclosure experiment.
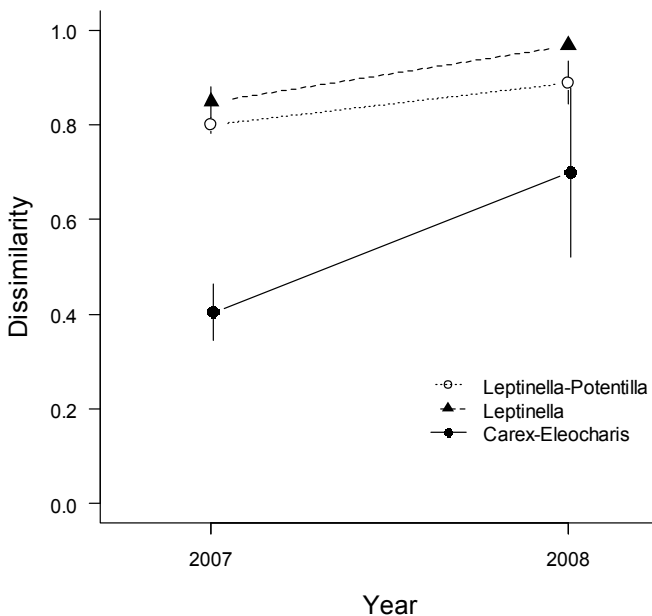
Figure 5. Mean (±SE) dissimilarity values between exclosure and control plot pairs within the same community type, by year and community, for the herbivore exclosure experiment.

There was a trend for the turf communities to become more similar in the absence of grazing (Fig. 4), but this effect was not significant (grazing main effect, $P = 0.20$; grazing × year interaction, $P = 0.17$). Comparison between grazed and ungrazed plots within communities indicated that the initial community response to cessation of grazing in the Leptinella-Potentilla ($P < 0.0001$) and Leptinella ($P = 0.0032$) communities was much greater than in the Carex-Eleocharis community (Fig. 5). Thereafter, grazed and ungrazed plots continued to diverge (year main effect, $P = 0.027$) at a similar rate across all (except the Carex-Eleocharis community) communities (year × community interaction, all $P > 0.05$).

Seed bank

Plant species germinating in the seed bank experiment are shown by community in Table 2. Exotic species dominated, particularly in the Carex communities (87% and 86%), being least in the Leptinella community (66%).

Discussion

We identified a zonation of two broad riparian communities (turf and sedge communities) at our Waihola study site. The Leptinella-Potentilla and Leptinella communities were short in stature (<15 cm) and occurred closer to the water's edge than the Carex-dominated communities. Lakeshore vegetation patterns arise in the absence of herbivory as a direct consequence of inundation cycles and the disturbance associated with wave action, both factors limiting the species that establish (Jansson et al. 2000; Riis & Hawes 2002; Hawes et al. 2003). Many of the species at our Waihola site, e.g. *Cotula coronopifolia*, *Lilaeopsis novae-zelandiae*, and *Eleocharis acuta*, are indicative of a high water table (Johnson & Rogers 2003; Johnson & Gerbeaux 2004). However, while we observed a relationship between community and distance from the nearest water body, the water table was at the same depth across all communities indicating that water is not directly driving community structure at the scale of the study. However, water table fluctuations have been observed between seasons. Neither is wave action appreciable at the study site as the small convoluted waterways attenuate the wave action generated on the main body of the lake. The Taieri River adjoining these wetlands experiences minor tidal saline intrusions during dry summer periods (Schallenberg & Krebsbach 2001). *Leptinella dioica* and *Selliera radicans* are likely indicator species for low levels of salt intrusions at our study site (Peter Johnson, Landcare Research, pers. comm., 2013).

We suggest that proximity of water primarily affects community composition via the activities of water fowl. 'Grazing lawns' (McNaughton 1984), i.e. short-statured vegetation maintained by high densities of herbivores, have been described for many Northern Hemisphere lakeshores where large quantities of waterfowl gather over the summer months to breed (e.g. Bazely & Jefferies 1989; Mulder & Ruess 1998). The vegetation in these lawns is typically clipped short by high densities of feeding herbivores, maintaining a composition that is tolerant of periodic grazing and favoured by the associated nutrient loads. We suggest that, at Waihola, birds selectively use vegetation close to the water's edge to avoid or escape from mammalian predators and hunting pressure. This behaviour leads to high densities of waterfowl, particularly of geese, foraging in small areas. The resulting vegetation pattern contains elements that are functionally analogous to the Northern

Table 2. Numbers of individuals (mean ± SE) germinating by species and community in the seed bank experiment (details in Methods). * exotic plant species

Species	Community			
	Leptinella-Potentilla	Leptinella	Carex-Eleocharis	Carex-Schedonorus
*Agrostis stolonifera**	12.45 ± 1.71	7.21 ± 2.12	11.00 ± 1.33	17.82 ± 3.18
*Callitriche stagnalis**	0.29 ± 0.11	–	0.92 ± 0.51	0.82 ± 0.64
*Cirsium vulgare**	0.18 ± 0.11	0.14 ± 0.10	0.12 ± 0.07	0.09 ± 0.05
Cotula coronopifolia	6.00 ± 1.41	14.64 ± 6.40	3.08 ± 1.17	3.97 ± 1.50
*Crepis capillaris**	0.05 ± 0.05	–	0.20 ± 0.12	0.09 ± 0.05
*Juncus articulatus**	25.84 ±4.37	31.14 ± 5.17	28.92 ± 4.29	27.33 ± 3.9
Leptinella dioica	5.47 ± 1.13	8.29 ± 3.63	2.72 ± 1.03	2.79 ± 0.83
*Lotus pedunculatus**	0.11 ± 0.11	–	–	–
Myosotis laxa subsp. *caespitosa*	0.05 ± 0.04	0.07 ± 0.07	–	0.58 ± 0.38
*Poa pratensis**	2.79 ± 0.97	1.43 ± 0.80	0.88 ± 0.28	2.12 ± 0.52
Potentilla anserinoides	0.05 ± 0.05	0.21 ± 0.21	–	0.94 ± 0.38
*Ranunculus repens**	0.45 ± 0.32	–	–	0.03 ± 0.03
*Rumex crispus**	0.08 ± 0.06	–	0.04 ± 0.04	0.09 ± 0.05
*Sagina procumbens**	0.61 ± 0.35	–	1.56 ± 0.63	1.67 ± 0.72
Senecio biserratus	0.16 ± 0.07	0.21 ± 0.15	–	0.09 ± 0.07
*Solanum dulcamara**	0.05 ± 0.04	0.07 ± 0.07	0.08 ± 0.06	–
*Stellaria media**	–	–	–	0.36 ± 0.33
Trifolium spp.*	0.24 ± 0.10	0.43 ± 0.29	0.72 ± 0.25	0.45 ± 0.15
Proportion exotic	0.76 ± 0.02	0.66 ± 0.05	0.87 ± 0.03	0.86 ± 0.02

Hemisphere grazing lawns, albeit over a smaller extent.

The maintenance mechanism for grazing lawns involves a positive-feedback switch (Wilson & Agnew 1992), whereby grazing and defecation increase the rate at which nutrients are cycled, increasing leaf nutrient status, leaf density, plant productivity and leaf palatability, and the productivity and palatability lead to higher grazer densities, completing the loop (McNaughton 1984). Indeed, herbivore activity and offtake were highest in the two Leptinella communities, closest to the water, as indicated by faecal deposition and the large differences in biomass between grazed and ungrazed plots (Fig. 2). Higher palatability is suggested by the higher leaf nitrogen found in the two Leptinella communities than in the Carex-Eleocharis community (1.85 %N vs 1.18 %N respectively); high-N leaves are typically more palatable to herbivores and are preferentially grazed (Olff & Ritchie 1998). Interestingly, the high levels of nitrogen in the foliage of the more intensively grazed communities were not mirrored in the soils. Nitrogen availability varies seasonally and with fluctuations in groundwater depth and rainfall (Smika et al. 1977; Bechtold et al. 2003). However, foliage integrates plant available nitrogen levels over the lifespan of the leaves and is thus a more reliable guide to net nutrient availability in the soil (Boto & Wellington 1983).

We expect that bird faeces are a locally important nitrogen input to the grazed communities, and contain high levels of water-soluble N (primarily NO_3^- with smaller quantities of NH_4^+; Tanentzap et al. 2013). Surface leaching and changes in water table depth associated with fluctuation in lake levels may transport this nitrogen to soil-depth levels not sampled in our study, but still available to plants.

Herbivory can affect community composition by increasing plant mortality, modifying competitive interactions between species by reducing plant vigour, changing the nutrient balance, creating fresh surfaces for seed establishment through scarification, and the grazers acting as vectors for plant propagules, and modifying seed-bank germination patterns (Crawley 1983). We tested the latter two of these factors and found no effect of geese faeces on the composition of seedlings germinating from the seed bank. Faecal addition did increase the total number of seeds that germinated, but with no effect on the species composition among the seedlings. The introduction of substantial numbers of seeds in the faeces would have had a homogenising effect on the species germinating across communities; instead we found a clear community effect regardless of faecal addition. Moreover, no seeds germinated from moist goose faeces. All this suggests that rather than the faeces increasing the size of the seed bank, faeces increased germination rates of the existing seed bank, probably via their nitrogen content. Moderate concentrations of nitrates break seed dormancy in many species (Vleeshouwers et al. 1995; Finch-Savage & Leubner-Metzger 2006).

While the seedlings germinating from the seed bank was specific to each community, it had very little relationship to the composition of the community it came from, as with many other communities (e.g. Pugnaire & Lázaro 2000; Romo & Bai 2004). For instance, *Cotula coronopifolia* was more than twice as common in the seed bank of the Leptinella community than in that of the Leptinella-Potentilla community, the only community where *C. coronopifolia* was recorded above ground. *Leptinella dioica*, which was very common in vegetation plots from turf communities but absent in sedge communities, was relatively common in the seed bank of sedge communities. These results suggest that community structure at this site was more strongly driven by factors such as competition and grazing than propagule pressure.

Grazing appears to be the major factor maintaining the compositional differences between the Leptinella-Potentilla and Leptinella turf communities and their distinction from the Carex communities. The two turf communities showed large shifts in species composition shortly after grazing was prevented (i.e. 2007), with dramatic increases in *Agrostis stolonifera* by 2008 (285 g of dry matter per square metre compared with 8.9 ± 2.8 g and 33.2 ± 23.7 g respectively for 2007 and 2008 in the controls), and the two communities became more similar (Fig. 4). We expect that in the absence of grazing the two turf communities would revert to a taller-statured community similar to the Carex communities, which were found further away

from the water margins but dominated by *Agrostis stolonifera*. There were already weak trends in this direction (Fig. 4b, c), with *Carex sinclairii* establishing by 2008.

Grazing appears to have a similar but less distinct effect on the Carex-Eleocharis community. Biomass and species compositional change after cessation of grazing were modest, though by 2008 ungrazed plots showed similar levels of *Agrostis stolonifera* to the other ungrazed communities (Figs 3–5).

We can only speculate on the role that extinct native waterfowl and other native avian herbivores might have had in structuring the plant communities in these lacustrine environments in prehuman times. However, there is no reason to suspect that their impact would have been qualitatively different from the current assemblage of avian species. Some indigenous plant species (e.g. *Leptinella*) because of their long evolutionary associations with birds may have become dependent on this avian nutrient source and regulator of competitive dominance. Current assemblages of birds fill a significant role in maintaining indigenous plant diversity, and future management of turf communities should provide for avian grazing.

Acknowledgements

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