Rapid short-tussock grassland decline with and without grazing, Marlborough, New Zealand

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Abstract: Species abundance, species richness, and ground cover were measured over 10 years on nine paired grazed and exclosure plots in short-tussock grassland in the early stages of invasion by *Hieracium* species. With and without grazing, *H. pilosella* and *H. caespitosum* increased markedly and *H. lepidulum* increased locally. In contrast, 50% of all other common species and species groups, and total, native, and exotic species richness declined significantly. Exclusion increased or had no effect on rates of increase in *Hieracium* species and rates of decline in short tussocks, and did not reduce rates of decline in other species. Exclusion had no effect on decline in native species richness, but mainly accelerated declines in total and exotic richness. Declines in 13 key vegetation variables were significantly predicted by increase in *Hieracium* abundance, suggesting competitive exclusion. With or without grazing, *Hieracium* species will become more dominant and other species will continue to decline. The effects of large herbivores on plant species diversity can often be predicted from site productivity. Our results indicate the need also to account for species origin, spatial scale, time, and exotic invasion.

Keywords: exclosures, herbivore impacts, *Hieracium caespitosum*, *Hieracium lepidulum*, *Hieracium pilosella,* plant invasion, species richness, vegetation change

Introduction

New Zealand's tussock grasslands have been widely altered by 150 years of grazing by sheep, cattle, and feral mammals. Concerns over soil erosion prompted retirement of grassland from grazing between the 1940s and 1970s, while later initiatives have been more focused on protection of indigenous biodiversity (Mark 1993). In the last decade, over 225 000 ha of the 2.2 million hectares of tussock grassland in Crown Pastoral Leases have been removed from grazing or are being assessed (Land Information New Zealand, unpubl. data 2006). Such grasslands will be managed formally for protection of indigenous biodiversity (Mark & McLennan 2005).

Short-tussock grassland dominated by *Festuca novae-zelandiae* and *Poa cita* is one of the main vegetation types currently being retired from grazing (Mark & McLennan 2005). Occupying c. 1 million hectares, these grasslands are typical of montane–subalpine mountain slopes, valley floors and basins of the eastern South Island rain shadow, often where forest has been removed by Māori or European fires (McGlone 2001). These mainly seral grasslands, induced by fire and grazing, are compositionally unstable, as predicted for grasslands that evolved without large mammalian herbivores (Milchunas et al. 1988), and pose severe problems for conservation (Mark 1993). 'Passive' management through removal of grazing is presently the main conservation strategy, but the long-term effects on grassland biodiversity are highly uncertain.

Erratic rainfall can inhibit recovery (Allen et al. 1995) and colonisation of bare ground is slow because of frost heave and wind erosion (Whitehouse 1984). Exotic grasses or conifers may respond more rapidly and preclude slower growing natives (Lord 1990; Rose et al. 2004; King & Wilson 2006). As grazing pressure declines, formerly dominant native woody species and tall tussocks (*Chionochloa* spp.) begin to recover and spread, but seed sources may have been lost over extensive areas (Rose & Platt 1992; Lee et al. 1993; Duncan et al. 2001; Mark & Dickinson 2003; Rose et al. 2004). Ungrazed short-tussock grassland will still be subjected to ongoing invasion by aggressive and potentially dominant exotic weeds, particularly *Hieracium pilosella* (Rose et al. 1995; Meurk et al. 2002; Walker et al. 2003b).

In this paper we address two issues posing strong challenges to effective conservation and grazing management of short-tussock grassland: compositional instability and high susceptibility to invasion by perennial exotics. If removal of grazing is to be used as a management tool for protecting short-tussock grasslands it may be

most successful where there are low populations of invasive exotics such as *Hieracium pilosella*. We therefore compared temporal trends over 10 years in grazed and ungrazed short-tussock grasslands with <5% *Hieracium* cover at the beginning of the study. We asked two main questions: does removal of grazing prompt vegetation recovery and inhibit further invasion by *Hieracium* species; and do temporal changes in species richness and abundance reflect changes in *Hieracium* abundance?

Methods

The study area is in Limestone Stream, Awatere Valley, inland Marlborough (41°56' S, 173°37'E), and is described in detail by Rose et al. (1998). The area is steep (20–40°) and underlain by Pallic, Brown, and Recent soils on strongly indurated sandstones and siltstones (limestone is not present). Annual rainfall is estimated at 760 mm, with frequent dry periods of >60 days, especially over the growing season. The short-tussock grasslands (*Festuca novae-zelandiae*, *Poa cita*) contain a wide range of exotic and native herbs and scattered woody species.

The area is managed for extensive sheep farming without any added fertiliser or oversown pasture species (Rose et al. 1998). Domestic animals, mainly merino sheep, have grazed the area as part of a wider management block for c. 150 years, but the exact history of grazing is not recorded. Until 1974, the area was grazed all year by 700 merino wethers. Since then this has been reduced to 100 wethers for 4 months in spring to early summer to promote vegetation recovery. Most stock are usually removed over winter, depending on the availability of feed on lower country. Present stock numbers average 0.8–1.2 stock units per hectare annually. No direct estimates of grazing were made during this study.

Feral animals have also had a significant impact on the vegetation, but numbers have declined since the 1960s because of hunting. Over the study period these included low populations of goats, pigs and hares. Although introduced rabbit populations had reached very high densities in the upper Awatere by the 1880s, in the study area they have been confined to very low numbers for at least the last four decades (Rose et al. 1998) and we saw only one rabbit during the study.

In 1994 nine representative grassland sites were selected between 780 and 1250 m a.s.l. on north-, south-, east-, and west-facing slopes, reflecting the important influences of elevation and potential solar radiation on composition (Table 1; Rose et al. 1998). Adjacent sites were 200–500 m apart and all had <5% estimated cover of *Hieracium pilosella*, reflecting the early stage of invasion in the catchment (Rose et al. 1998). Less abundant *H. caespitosum* and *H. lepidulum* were also present. At each site, a 25 × 25-m plot was fenced to exclude sheep and feral herbivores, and a similar-sized grazed control plot was established in visually similar vegetation on the same landform and slope position.

The vegetation was measured in summer (mid-January to mid-March) from 1994 to 2004. At each exclosure and control plot we established three parallel, permanent 20-m transects (5 m apart), and three permanent 50 × 50-cm quadrats (at the centre of each transect). Along each transect, 50 circular subplots of 15-cm diameter were spaced at 40-cm intervals. Annually, *Hieracium* cover was estimated within each subplot as 0, <1, 1–5, 6–25, 26–50, 51–75, or 76–100% using reference cards, and ground cover was recorded as vascular vegetation, bryophytes, lichen, litter, topsoil, subsoil, or rock, using a point intercept at the centre of each subplot. At 5-year intervals, the shoot frequency of all vascular species was recorded from their presence in each subplot. For each

Table 1. Site factor summary for paired control and exclosure plots at nine sites in Awatere Valley, Marlborough, New Zealand, in 1994. * $P = 0.05$.

	Mean		Range
	Control	Exclosure	
Elevation (m a.s.l.)	1005	1003	795–1240
Potential solar radiation (Langleys yr^{-1})	0.420	0.421*	0.203–0.597
pH	5.78	5.83	5.30–6.40
Organic C (%)	2.29	2.05	1.24–4.92
N (%)	0.17	0.16	0.10–0.34
Ca (me%)	10.14	9.84	6.32–13.42
Mg (me%)	2.59	2.42	1.37–3.81
K (me%)	0.89	0.89	0.65–1.20
Na (me%)	0.05	0.07	0.02–0.11
Al (µg g^{-1})	0.20	0.24	0.00–0.82
P (µg g^{-1})	14.50	14.30	6.54–27.19
S (µg g^{-1})	2.02	2.29	0.77–7.87

quadrat, the cover of all vascular species and ground cover was estimated annually in the above classes. Quadrats were gridded into 10×10-cm squares to aid estimation. Transect and quadrat cover estimates were converted to % cover using the midpoints of the cover classes and summarised for each species, for 10 species groups sufficiently large for analysis and representing all species present, and for each ground cover category (Table 2). Total, native, and exotic species richness (number of vascular species present) were calculated annually per quadrat and 5-yearly per subplot, transect (50 subplots), and plot (3 transects).

Site factors recorded for each plot included elevation, slope, aspect, and potential solar radiation (calculated from

latitude, slope, and aspect; SOLRAD software, G.M.J. Hall pers. comm., 1996). In 1994, 10 randomly located soil cores (0–10 cm) were taken from each plot, then bulked and analysed for pH, total organic C, total N, exchangeable Ca, Mg, K and Na, Ca-Cl$_2$ extractable Al, Olsen P, and phosphate-extractable S (Blakemore et al. 1987).

Rainfall data were available from Upcot, 5 km north of the study area (National Institute of Water and Atmospheric Research, unpubl. data, 2004). The 1994–1997 sampling period recorded average to above-average rainfall and was generally moister than 1998–2004. For example, in the 12 months preceding the 1998 and 2004 samples Upcot received only 61% and 66% of normal annual rainfall

Table 2. Changes in mean % quadrat and transect (t) cover of the main vegetation components measured annually on paired control and exclosure plots at nine sites in Awatere Valley, Marlborough, New Zealand, 1994 to 2004. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns not significant. [a]Indicates treatment means significantly different in 2004 ($P < 0.05$). Rain6 = overall effects of preceding 6-monthly rainfall. Overall temporal effects in parentheses are not significant when Rain6 is included in the model.

	Mean in 1994 Control	Exclosure	Mean net change/10 yr Control	Exclosure	Std error of net change Control	Exclosure	Overall net change/10 yr	Annual comparisons Time	Grazing × Time	Rain6
Exotic species										
Total *Hieracium* spp.	4.7	3.5	+17.9	+26.3	3.94	4.74	***	***	**	ns
Total *Hieracium* spp. (t)	3.9	3.3[a]	+12.8	+19.9**	3.28	2.58	***	***	**	***
H. pilosella	2.7	1.8	+14.6	+17.5	2.94	4.92	**	***	ns	ns
H. pilosella (t)	2.6	1.9	+10.3	+14.8	2.36	2.40	***	***	*	***
H. caespitosum	0.7	0.5	+0.7	+4.3	1.25	1.73	*	***	**	ns
H. caespitosum (t)	0.6	0.6	+0.6	+2.3*	0.26	0.66	**	***	***	**
H. lepidulum	1.3	1.3	+2.6	+4.4	2.21	2.99	ns	***	ns	ns
H. lepidulum (t)	0.3	0.7	+1.9	+2.9	1.73	2.33	ns	***	ns	ns
Non-Hieracium perennial herbs	15.7	18.4[a]	−10.0	−16.7	2.54	4.01	**	***	*	*
Grasses	11.9	13.2	−7.9	−11.8	2.27	3.33	**	***	ns	*
Anthoxanthum odoratum	6.5	8.9	−3.6	−7.9	1.57	2.59	**	***	**	ns
Holcus lanatus	5.3	2.9	−5.0	−2.7	1.52	1.18	**	***	*	ns
Forbs	3.8	5.2	−2.1	−4.9	1.13	1.32	**	***	***	ns
Hypochaeris radicata	2.4	1.7	−1.9	−1.5	0.79	0.70	*	***	ns	ns
Annual/biennial herbs	2.4	1.3	−1.6	−1.0	0.66	0.33	**	(**)	ns	*
Native species										
All perennial herbs	29.5	37.9	−8.0	−18.2	3.84	6.08	*	***	**	*
Tussocks	10.8	18.2*	−1.7	−12.6*	3.10	3.77	*	***	***	ns
Festuca novae-zelandiae	7.6	11.0[a]	0.0	−7.5*	2.56	2.42	*	***	***	ns
Poa cita	3.2	7.2	−1.7	−5.1	0.91	2.10	*	***	ns	ns
Other grasses	9.9	8.1	−1.0	+2.8	1.69	2.83	ns	ns	ns	*
Rytidosperma clavatum	9.0	6.2	−0.8	+3.5	1.58	2.73	ns	ns	ns	ns
Forbs	8.8	11.6	−5.2	−8.4	2.42	1.87	**	***	ns	*
Acaena caesiiglauca	2.4	3.7	−2.1	−3.6	0.97	1.27	**	***	ns	ns
Woody perennials	4.9	2.4	−2.7	+2.2	1.58	2.18	ns	ns	*	ns
Ozothamnus leptophyllus	3.4	1.7	−2.2	+0.4	1.06	1.45	ns	ns	ns	ns
Ground cover										
Vascular vegetation	43.9	53.0	+1.9	−7.0	5.66	6.21	ns	(*)	ns	***
Vascular vegetation (t)	41.3	46.4	+1.1	−3.7	5.10	3.08	ns	(*)	ns	***
Litter	21.2	15.6[a]	−4.3	+16.9**	3.32	3.18	*	(**)	***	***
Litter (t)	27.7	26.4	+3.6	+13.9*	5.37	2.10	*	(**)	**	***
Bare ground	32.7	28.3[a]	+5.5	−12.0	3.85	5.01	ns	ns	***	*
Bare ground (t)	30.7	26.4[a]	+4.8	−12.3***	2.76	2.11	ns	ns	***	***
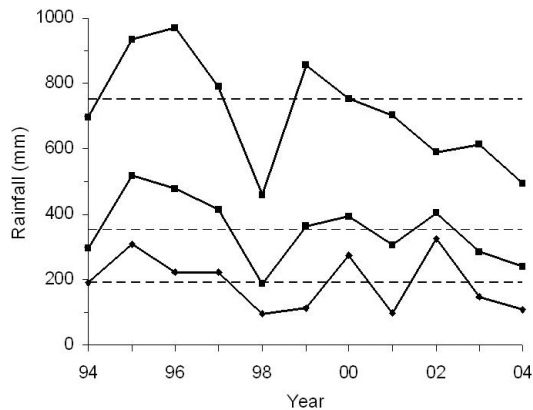
Figure 1. Total rainfall at Upcot recording station, Marlborough, New Zealand, in the 12, 6 and 3 months preceding each sampling year (upper, middle and lower lines, respectively). Horizontal lines represent the 12-month long-term average and the 6- and 3-month averages for the study period (1994-2004).

(respectively) and in the 3 or 6 months preceding the 1998, 1999, 2001 and 2004 samples it received only 50–68% of average for the study period (Fig. 1).

Analysis

Mixed-model analysis of variance (ANOVA) was used to analyse temporal changes between 1994 and 2004, with site (the paired exclosure and control plots) as a random factor and time and grazing treatment as fixed effects. We analysed changes in total, native, and exotic species richness and all cover, ground cover, and frequency components with >1% overall mean. These models tested the effects of time, grazing treatment, and appropriate interaction terms, using all annual or 5-yearly measurements over the 10 years. For annually measured cover, ground cover, and species richness variables, the strength of rainfall effects was estimated by including in the models the total rainfall for the 6 months preceding sampling (the approximate growing season). Because of the paired-plot design, however, the key interaction between time and grazing treatment was not confounded by possible temporal variation in rainfall or other site factors. We also analysed net changes in mean cover, frequency, and species richness over the 10 years using mixed-model ANOVA, which tested the effects of time and grazing treatment and their interactions. These analyses compared only the initial (1994) and final (2004) measurements. Paired *t*-tests were used to compare initial or final means for site and vegetation variables.

Factors potentially affecting vegetation change were examined by comparing net changes in 20 key vegetation variables with initial site factors and net changes in *Hieracium* cover. All exclosure and control plots were used ($n = 18$). Rainfall could not be included because variation between plots was unknown. Dependent variables included net change in the cover of major species groups, and total, native, and exotic species richness per plot, transect, quadrat, and subplot. For the quadrats, because we measured the cover of all species we also used net change in Shannon–Weiner diversity index as a dependent variable. Correlation coefficients were first calculated between all variables, allowing for the paired-plot design. For each of the 21 dependent variables, stepwise backward mixed-model regressions were then used to determine the most significant independent predictors of change among all site factors and *Hieracium* cover variables that had univariate associations significant at $P < 0.1$.

Results

Initial composition and site factors

In 1994 the vegetation was dominated by native perennial herbs (34% mean total cover), mainly comprising *Festuca novae-zelandiae* and *Poa cita* tussocks, the sward-forming grass *Rytidosperma clavatum*, and the forb *Acaena caesiiglauca* (Table 2). Non-*Hieracium* perennial exotic herbs (17% cover) mainly included the grasses *Anthoxanthum odoratum* and *Holcus lanatus* and the forb *Hypochaeris radicata*. Bare ground (soil + rock) accounted for about one-third of the ground cover and mean total *Hieracium* cover was 4% (mainly *H. pilosella*). Only 11 species were present at >1% mean quadrat cover (Table 2), but 46 were present at >1% mean transect frequency (Table 3). The exclosures and controls were well matched, with few significant differences in site and vegetation variables (paired *t*-tests, $P < 0.05$; Tables 1–4).

Changes in species cover and frequency

The vegetation changed markedly inside and outside the exclosures between 1994 and 2004. Annual quadrat comparisons showed that 17 of the 21 main species and species groups changed in overall mean cover over time (ANOVA, $P < 0.05$; Table 2). Among these, 16 species and groups showed a significant net change in cover over the full 10 years (ANOVA, $P < 0.05$; Table 2). Five-yearly transect comparisons showed that 27 of the 46 most frequent species changed in overall mean frequency, with 21 species (46%) showing a net overall change (ANOVA, $P < 0.05$; Table 3). Temporal patterns of change in cover or frequency often differed between treatments (grazing × time interaction; Tables 2, 3). Over the full 10 years, however, there were few significant differences in net change or in mean cover between treatments, indicating that the resulting vegetation was similar inside and outside the exclosures in 2004. For perennial species and groups,

Table 3. Changes in mean % transect frequency of the main species (measured 5-yearly) on paired control and exclosure plots at nine sites in Awatere Valley, Marlborough, New Zealand, 1994 to 2004. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns not significant.

	Mean in 1994		Mean net change/10 yr		Std error of net change		Overall net change/10 yr	Five-yearly comparisons	
	Control	Exclosure	Control	Exclosure	Control	Exclosure		Time	Grazing × Time
Exotic species									
Hieracium spp.									
H. pilosella	13.6	10.2	+30.7	+47.8**	5.26	3.90	***	***	**
H. caespitosum	3.3	7.2	+4.6	+10.4	1.53	3.42	*	***	ns
H. lepidulum	5.3	7.9	+6.3	+5.9	4.70	3.16	ns	**	ns
Non-*Hieracium* perennial herbs									
Grasses									
Anthoxanthum odoratum	64.5	68.4	−13.2	−16.1	8.70	9.18	**	**	ns
Holcus lanatus	36.0	36.1	−28.6	−31.6	5.19	6.72	**	***	ns
Agrostis capillaris	2.2	5.6	+0.8	−0.9	2.14	2.73	ns	ns	ns
Dactylis glomerata	4.0	5.0	−1.1	+1.0	0.90	1.61	ns	ns	ns
Forbs									
Hypochaeris radicata	19.3	24.7	−12.4	−18.8	4.64	3.69	**	***	ns
Rumex acetosella	21.6	20.1	−11.6	−18.3	2.30	3.21	***	***	ns
Trifolium repens	11.4	17.4*	−8.0	−15.7**	3.16	4.80	*	***	ns
Cerastium fontanum	3.8	7.6*	−2.3	−7.3*	2.43	3.49	ns	**	ns
Acaena agnipila	0.9	1.8	+2.9	+1.0	2.54	1.08	ns	ns	ns
Annual/biennial herbs									
Crepis capillaris	28.9	32.0	−23.7	−30.7	7.09	5.70	**	***	ns
Trifolium arvense	17.2	15.3	−4.1	−9.2	8.44	2.47	ns	ns	ns
Trifolium dubium	4.4	5.8	−3.0	−5.2	1.40	1.57	**	***	ns
Linaria arvensis	3.4	5.9	+6.7	−2.0	2.99	1.76	ns	ns	*
Vicia sativa	3.5	3.5	−1.8	−1.7	1.74	0.73	ns	ns	ns
Arenaria serpyllifolia	1.6	1.7	−0.4	−1.6	0.88	0.67	*	*	ns
Torilis arvensis	1.9	3.3	−0.5	−2.8	1.00	1.67	ns	*	ns
Native species									
Tussocks									
Festuca novae-zelandiae	26.7	31.1	−9.0	−10.3	3.75	3.45	**	***	ns
Poa cita	19.4	20.2	−9.2	−15.2**	1.24	1.59	***	***	*
Other grasses									
Rytidosperma clavatum	29.2	40.4	+10.3	+3.0	5.74	2.93	ns	ns	ns
Elymus solandri	16.6	20.4	−1.9	−7.0	2.41	3.39	ns	ns	ns
Lachnagrostis lyallii	4.3	2.4	−2.9	−1.9	1.27	0.89	ns	**	ns
Poa colensoi	4.2	3.6	+0.1	−0.3	0.72	0.45	ns	ns	ns
Dichelachne crinita	3.6	3.9	−1.2	−0.1	0.86	0.57	ns	ns	ns
Deyeuxia avenoides	1.5	1.9	0.0	+2.8	0.9	1.12	*	ns	ns
Forbs									
Wahlenbergia albomarginata	37.8	49.0	−15.8	−25.4	5.67	4.86	**	***	ns
Geranium sessiliflorum	34.6	31.1	−26.4	−25.7	5.66	3.81	***	***	ns
Acaena caesiiglauca	28.2	31.1	−22.2	−27.2	4.06	5.08	***	***	ns
Uncinia divaricata/ Carex breviculmis	11.9	12.4	−3.4	−5.8	1.11	2.11	**	**	ns
Epilobium alsinoides	4.8	5.6	−4.0	−4.9	1.46	2.46	*	***	ns
Helichrysum spp.	2.6	6.6	−2.0	−5.9	1.39	5.84	ns	ns	ns
Viola cunninghamii	2.4	4.0	−2.1	−2.7	2.07	1.51	ns	*	ns
Raoulia subsericea	1.9	2.4	−1.3	−2.3	0.96	1.02	*	**	ns
Dichondra repens	1.4	1.5	−0.9	−0.9	0.50	0.43	**	*	ns
Gnaphalium audax	1.7	5.1	+0.2	−3.4	0.92	2.61	ns	ns	ns
Pteridium esculentum	2.4	1.0	−1.2	+0.1	0.91	0.07	ns	ns	ns
Luzula rufa	1.2	1.6	−0.1	−0.8	0.34	0.48	ns	ns	ns
Raoulia australis	4.2	1.1	−2.4	−0.4	1.97	0.59	ns	ns	ns
Woody species									
Ozothamnus leptophyllus	11.5	10.2	−5.4	−3.2	2.23	2.87	ns	**	ns
Leucopogon fraseri	6.1	7.8	−2.1	−2.7	2.15	2.52	ns	ns	ns
Vittadinia australis	4.8	8.5	−2.9	−7.4	0.83	2.62	*	***	*
Muehlenbeckia spp.	1.6	3.0	+0.4	+1.8	0.56	1.38	ns	ns	ns
Pimelia spp.	1.2	0.8	−0.1	+0.3	0.17	0.51	ns	ns	ns
Coprosma propinqua	0.7	0.6	+1.2	+0.7	0.78	0.30	ns	*	ns
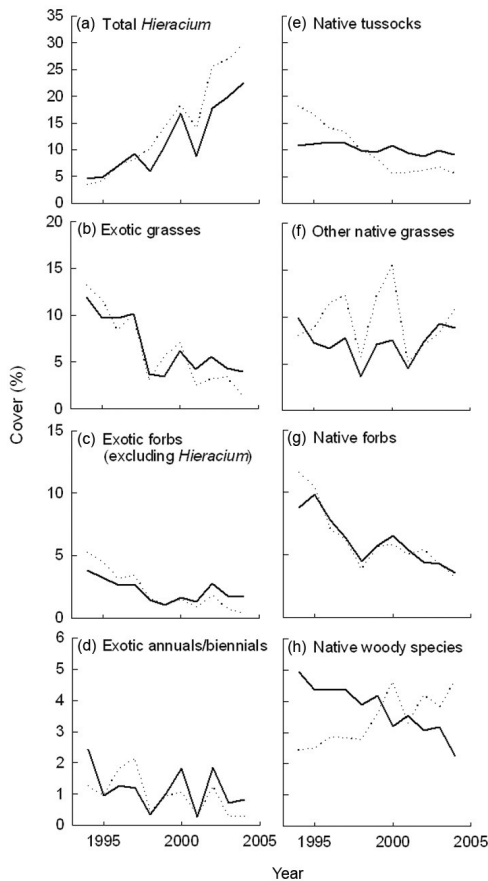
Figure 2. Annual trends (1994-2004) in mean quadrat (0.25 m²) cover on nine grazed (solid line) and ungrazed plots (broken line), Awatere Valley, inland Marlborough, New Zealand. Note the different *y*-axis scales.

short-term fluctuations in cover partly reflected rainfall, e.g. several groups declined in the dry seasons of 1998 or 2001 and increased in the moist season of 2000 (Figs 1, 2). Despite this, overall temporal trends in cover persisted when 6-month rainfall was included in the ANOVA models (Table 2). In contrast, temporal variation in the total cover of annual/biennial herbs was largely explained by 6-month rainfall (Table 2; Figs 1, 2).

Species of *Hieracium* increased markedly in overall cover and frequency between 1994 and 2004 (exclosures plus controls combined; Tables 2, 3). Overall, total *Hieracium* cover increased from 4% to 26% on the quadrats and 4% to 20% on transects ($P < 0.001$; Table 2; Fig. 2A). This largely reflected an overall increase in *H. pilosella*, e.g. on transects it increased from 2% to 15% mean cover and from 12% to 51% mean frequency ($P < 0.01$). The less abundant *H. caespitosum* also increased in overall

cover and frequency ($P < 0.05$), but similar trends for *H. lepidulum* were not significant. Exclusion of grazing did not significantly reduce the net rate of increase in *Hieracium* species in total or individually compared with grazed plots (Tables 2, 3). On ungrazed transects the mean net rates of increase in total *Hieracium* cover, *H. pilosella* frequency, and *H. caespitosum* cover were at least 1.5 times greater than on grazed transects ($P < 0.05$). Otherwise there were no significant differences in the net rate of change in cover or frequency between treatments.

Exotic non-*Hieracium* perennial herbs declined markedly inside and outside the exclosures. Overall, their mean total quadrat cover declined from 17% in 1994 to 4% in 2004 ($P < 0.01$; Table 2), reflecting large net declines in both grasses (13% to 3%; Fig. 2A) and forbs (5% to 1%; Fig. 2C). On transects, five of the nine most common exotic grasses and non-*Hieracium* forbs declined in frequency and none increased ($P < 0.05$; Table 3). Among these, *Trifolium repens* and *Cerastium fontanum* were initially more frequent inside the exclosures, but then also declined at a greater rate inside the exclosures (Table 3) and in 2004 there were no significant differences between treatments (paired *t*-tests; $P < 0.05$). For all exotic non-*Hieracium* perennial herb species and species-groups, exclusion of grazing did not result in any significant recovery or lower net rates of decline compared with the grazed plots over 10 years ($P < 0.05$; Tables 2, 3).

Annual and biennial exotic herbs declined from 2% to <1% overall cover over the 10 years (Table 2; Fig. 2D), and the frequency of the main species, *Crepis capillaris*, declined significantly (Table 3). There were no significant net effects of excluding grazing on total cover or individual species.

Native perennial herbs declined overall. Overall total quadrat cover of the group declined from 34% in 1994 to 20% in 2004 ($P < 0.05$; Table 2). This reflected significant net declines in the total cover of tussocks (15% to 7%; Fig. 2E) and forbs (10% to 3%; Fig. 2G), but there was no significant change in the total cover of other native grasses (mainly *Rytidosperma clavatum*; Fig. 2F). On transects, 11 of the 22 most frequent native herbs declined significantly in overall frequency and only the relatively minor grass *Deyeuxia avenoides* increased (Table 3). There were no significant net effects of excluding grazing on the quadrat cover or transect frequencies of native perennial herbs, forbs, or non-tussock grasses (Tables 2, 3). For tussocks, however, the net effects of exclusion were negative; both total tussock and *F. novae-zelandiae* cover declined more rapidly inside the exclosures, and *P. cita* was the only native perennial to decline more rapidly in frequency inside the exclosures (Tables 2, 3; $P < 0.05$).

Native woody perennials remained at less than 5% total cover inside and outside the exclosures (Fig. 2H). There were no significant net changes in cover or frequency and no significant responses to exclusion of grazing (Tables 2, 3).

Changes in species richness

All measures of species richness varied over time and declined over the full 10 years ($P < 0.05$; Table 4). For example, over 10 years total species richness for the exclosures and controls combined declined by 14% per plot, 21% per transect, 26% per quadrat, and 38% per subplot. Temporal trends in all annually measured variables (total, native, and exotic richness per quadrat) persisted with 6-month rainfall in the ANOVA models ($P < 0.001$). Short-term effects of rainfall included a decrease in total richness in the dry seasons of 1998 and 2001 (Fig. 3A, B). There were no significant effects of excluding grazing on native species richness ($P < 0.05$). In contrast, exotic richness was generally adversely affected by exclusion, with significantly greater net declines in richness per plot, transect, and quadrat compared with grazed plots ($P < 0.05$). Although total plot and transect richness and exotic transect richness were initially significantly higher inside the exclosures, they also declined more rapidly inside the exclosures (Table 4), and by 2004 there were no significant differences between treatments (paired t-tests; $P < 0.05$).

Changes in ground cover

Overall, temporal trends in the proportions of vascular vegetation, litter, and bare ground largely reflected 6-month rainfall (Table 2; Figs 1, 3). There was no significant net change in the percentage cover of vegetation, which was not significantly affected by the removal of grazing. A significant net overall increase in the percentage cover of litter ($P < 0.05$) reflected a 1.5-fold increase on transects and a 2-fold increase on quadrats inside the exclosures, with little net change under grazing (Fig. 3C). On both quadrats and transects inside the exclosures the mean percentage cover of bare ground almost halved over the 10
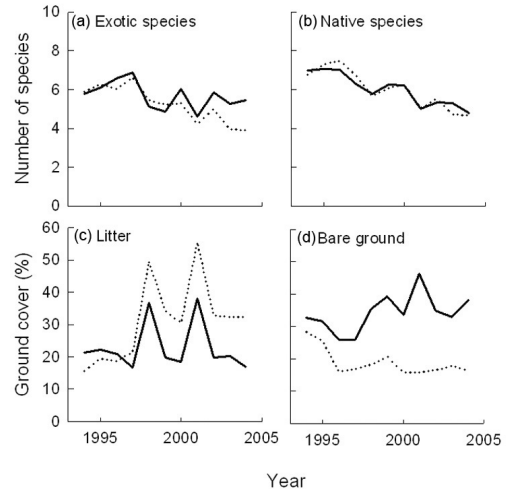
Figure 3. Annual trends (1994-2004) in mean quadrat (0.25 m²) species richness and ground cover on nine grazed (solid line) and ungrazed plots (broken line), Awatere Valley, inland Marlborough, New Zealand. Note the different *y*-axis scales.

years, but under grazing it increased slightly and showed greater fluctuation (Fig. 3D; Table 2). The treatment effect was highly significant for transects ($P < 0.001$) and almost significant for the quadrats ($P = 0.052$).

Factors affecting vegetation change

Net change in *Hieracium* cover was negatively correlated with net change in 13 of the 21 vegetation variables assessed and there were no positive correlations (Table

Table 4. Changes in mean species richness on paired control and exclosure plots at nine sites in Awatere Valley, Marlborough, New Zealand, 1994 to 2004. Means are for transect subplots (0.02 m²), quadrats (0.25 m²), transects (50 subplots, 0.88 m²), and plots (3 transects, 2.65 m²). Quadrats were measured annually, all others 5-yearly. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns not significant. Rain6 = overall effects of preceding 6-monthly rainfall.

	Mean in 1994		Mean net change/10 yr		Std error of net change		Overall net change/10 yr	Annual or 5-yearly comparisons		
	Control	Exclosure	Control	Exclosure	Control	Exclosure		Time	Grazing × Time	Rain6
Total plot richness	37.2	41.4*	−2.3	−8.8*	1.95	1.60	**	***	**	.
Total transect richness	28.2	31.6**	−3.4	−8.8**	1.33	1.27	**	***	**	.
Total quadrat richness	12.8	12.7	−2.6	−4.1	0.96	0.68	***	***	*	***
Total subplot richness	6.2	6.2	−2.4	−2.4	0.48	0.38	***	***	ns	.
Native plot richness	20.8	22.8	−2.4	−3.3	1.12	0.55	**	***	ns	.
Native transect richness	15.7	16.7	−2.7	−3.6	0.70	0.34	***	***	ns	.
Native quadrat richness	7.0	6.8	−2.2	−2.1	0.78	0.63	**	***	ns	***
Native subplot richness	3.3	3.2	−1.5	−1.5	0.23	0.29	***	***	ns	.
Exotic plot richness	16.4	18.7	+0.1	−5.4*	1.33	1.30	*	**	**	.
Exotic transect richness	12.4	14.8**	−0.7	−5.2**	0.82	1.05	**	***	***	.
Exotic quadrat richness	5.8	5.9	−0.3	−2.0**	0.38	0.46	*	***	**	***
Exotic subplot richness	3.0	3.0	−1.0	−0.9	0.35	0.37	**	***	ns	.

5; $P < 0.05$). Increase in total *Hieracium* was associated with declines in nine vegetation variables ($r = -0.48$ to -0.80), and each *Hieracium* species was associated with declines in three or four variables ($r = -0.48$ to -0.76). In multiple regressions, net increase in *Hieracium* cover alone or in combination with initial site factors significantly predicted net decline in the 13 vegetation variables ($r^2 = 0.23–0.75$; Table 6). Changes in four vegetation variables were significantly predicted from initial site factors alone and there were no significant models for a further four variables. Increase in total *Hieracium* was a significant predictor in three models of total species decline, including plot and transect richness and quadrat diversity ($r^2 = 0.23–0.56$). Increases in total *Hieracium* or *H. pilosella* were significant predictors in six models of exotic species decline, including plot, transect and quadrat richness, and perennial herb, grass, and forb cover ($r^2 = 0.27–0.64$). *H. caespitosum* or *H. lepidulum* were significant predictors in four models of native species decline, including subplot richness and perennial herb, tussock and forb cover ($r^2 = 0.30–0.75$). For native species there were no significant relationships with total *Hieracium* or *H. pilosella* (the most abundant species). Among site factors, altitude and potential solar radiation were the most frequent predictors of vegetation change, with greatest decline at low altitude and on shady sites.

Discussion

Short-tussock grassland decline

In the study area, the composition of both grazed and ungrazed short-tussock grasslands changed markedly and the direction of change was independent of grazing treatment. Overall increases in the abundance of *Hieracium pilosella* and *H. caespitosum* and local increases in *H. lepidulum* were accompanied by overall declines in 50% of all other common herbs and declines in total, native, and exotic species richness at all spatial scales measured. Such compositional instability and directional change are common results from temporal studies in unfertilised, non-oversown short-tussock grassland over the last 30 years (e.g. Rose 1983; Scott et al. 1988; Rose et al. 1995, 2004; Duncan et al. 1997, 2001; Jensen et al. 1997; Meurk et al. 2002; Walker et al. 2003b). The rate and extent of species declines in our study are among the highest reported for such grasslands and partly reflect the frequent growing season droughts recorded during the study period.

The rise in *Hieracium* species and declines in other species confirm earlier predictions. In 1993, comparisons with communities in a more heavily infested catchment nearby suggested that the low abundance of *Hieracium* species in the study area reflected an early stage of invasion

Table 5. Significant correlation coefficients between net change over 10 years (Δ) in key vegetation variables and cover of *Hieracium* spp. on paired control and exclosure plots at nine sites in Awatere Valley, Marlborough, New Zealand, 1994 to 2004. ** $P < 0.01$; * $P < 0.05$.

	ΔTotal *Hieracium* spp.	Δ*H. pilosella*	Δ*H. caespitosum*	Δ*H. lepidulum*
All species				
ΔPlot richness	-0.48*			
ΔTransect richness	-0.70**	-0.51*		
ΔQuadrat richness				
ΔQuadrat diversity	-0.52*			
ΔSubplot richness				
Non-*Hieracium* exotic species				
ΔPlot richness	-0.52*			
ΔTransect richness	-0.69**			-0.48*
ΔQuadrat richness	-0.61**			-0.48*
ΔSubplot richness				
ΔNon-*Hieracium* perennial herb cover	-0.80**	-0.76**		
ΔPerennial grass cover	-0.67**	-0.74**		
ΔPerennial forb cover	-0.66**			-0.56*
ΔAnnual/biennial herb cover				
Native species				
ΔPlot richness				
ΔTransect richness				
ΔQuadrat richness				
ΔSubplot richness			-0.65**	
ΔPerennial herb cover			-0.53*	
ΔTussock cover			-0.51*	
ΔOther perennial grass cover				
ΔPerennial forb cover			-0.55*	

rather than inherently low susceptibility to invasion (Rose et al. 1998). In 1995, *Hieracium* seedlings were widespread (38 seedlings per 100 m^2) despite low cover values, and were establishing among vegetation, litter, and bare soil in proportion to the availability of these substrates – indicating none conferred significant resistance to invasion (Rose & Frampton 1999). The large increase in *Hieracium* species (especially *H. pilosella*) since 1994 conforms to the 'grassland decline' model, which integrates long-term predisposing factors and short-term trigger factors to predict the likely magnitude of invasion (Rose et al. 1998). For Limestone Stream, suggested predisposing factors include the ongoing rain of *Hieracium* propagules from outside the catchment and increasing availability from within, combined with a long history of anthropogenic disturbance, a stressful environment characterised by low soil fertility and low growing-season rainfall, and a vegetation structure and composition that confers little resistance to invasion because of low stature, low canopy cover, low tussock density, shallow litter layers, abundant safe sites for seedling establishment, and the presence of many native species that are poorly adapted to grazing or trampling (Rose et al. 1998; Rose & Frampton 1999). Trigger factors that probably accelerated *Hieracium* invasion and grassland decline in the present

study include the two very dry seasons of 1998 and 2001, which had obvious negative impacts on the vegetation but from which *Hieracium* species recovered rapidly to continue increasing.

Does removal of grazing induce recovery?

The removal of grazing had few beneficial effects on indigenous biodiversity or pastoral production over 10 years. There were no instances where it slowed the increase in *Hieracium* species or the declines in any other species. Without grazing, the rates of increase in *Hieracium* species and rates of decline in native tussocks (*Festuca novae-zelandiae*, *Poa cita*) and exotic species richness were greater than or equal to grazed grassland. The only potential benefits we found were a decline in bare ground and an increase in plant litter (see also McIntosh & Allen 1998), but these may have partly reflected greater *Hieracium* increase and tussock death inside the exclosures. An increase in litter can also have a negative effect on species richness, although this is most marked in more productive grasslands (Tilman 1993; Foster & Gross 1998).

A comparison of existing *Hieracium* cover inside and outside exclosures at several sites in the early stages of invasion led to the conclusion that sheep could be

Table 6. Significant regression models using initial site factors and change in *Hieracium* cover to predict changes in 21 key vegetation variables (Δ = net change over 10 yr) on paired control and exclosure plots at nine sites in Awatere Valley, Marlborough, New Zealand, 1994 to 2004. Site variables include topsoil sodium (Na), sulphur (S) and nitrogen (N), potential solar radiation (PSR), and altitude (ALT). *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns not significant.

	R^2	P
All species		
ΔPlot richness = −0.38 − 0.32(ΔTotal *Hieracium*)	0.23	*
ΔTransect richness = 3.00 − 0.31(ΔTotal *Hieracium*) − 64.58Na	0.56	**
ΔQuadrat richness = −6.84 + 8.35PSR	0.27	*
ΔQuadrat diversity = −1.96 − 0.02(ΔTotal *Hieracium*) + 0.001ALT	0.41	**
ΔSubplot richness	-	ns
Non-*Hieracium* exotic species		
ΔPlot richness = 1.67 − 0.27(ΔTotal *Hieracium*)	0.27	*
ΔTransect richness = 3.35 − 0.23(ΔTotal *Hieracium*) − 49.95Na	0.61	***
ΔQuadrat richness = −0.33 − 0.08(ΔTotal *Hieracium*)	0.37	**
ΔSubplot richness = −4.96 + 0.003ALT	0.32	*
ΔNon-Hieracium perennial herb cover = 0.31 − 0.62(ΔTotal *Hieracium*)	0.64	***
ΔPerennial grass cover = −1.34 − 0.53(Δ*H. pilosella*)	0.54	***
ΔPerennial forb cover = 1.70 − 0.14(ΔTotal *Hieracium*) − 1.00S	0.58	***
ΔAnnual/biennial herb cover = −6.47 + 0.005ALT	0.37	**
Native species		
ΔPlot richness	-	ns
ΔTransect richness	-	ns
ΔQuadrat richness = −1.91 + 40.18Na − 16.76N	0.50	**
ΔSubplot richness = −2.47 − 0.19(Δ*H. caespitosum*) + 3.01PSR	0.75	***
ΔPerennial herb cover = −27.80 − 1.43(Δ*H. caespitosum*) + 43.54PSR	0.47	**
ΔTussock cover = −0.98 − 1.41(Δ*H. caespitosum*) − 0.75(Δ*H. lepidulum*)	0.50	**
ΔOther perennial grass cover	-	ns
ΔPerennial forb cover = −4.93 − 0.75(Δ*H. caespitosum*)	0.30	*

used to graze flower heads and control the establishment and increase of *H. caespitosum* and *H. lepidulum*, but that light grazing would increase the rate of spread of the more prostrate *H. pilosella* by stimulating stolon production (Espie 1994). However, that study did not track changes in abundance over time to determine the subsequent rate and magnitude of invasion. Temporal studies over periods of 10 or more years indicate that total *Hieracium* abundance has increased markedly with and without grazing in unfertilised short-tussock grassland (Scott et al. 1988; Rose et al. 1995, 2004; Meurk et al. 2002; Walker et al. 2003b). In the study area there was noticeable removal of *H. pilosella*, *H. caespitosum* and *H. lepidulum* flower heads by sheep and trampling damage to seedlings and stolons, but these are unlikely to make much difference to the eventual magnitude of invasion. Grazing did slow the rate of increase in *H. caespitosum* on the transects, but not on the quadrats. There was no significant grazing effect for *H. lepidulum*. For *H. pilosella* the effects of grazing were either adverse (on transects) or not significant (on quadrats).

The density of the dominant short tussocks *Festuca novae-zelandiae* and *Poa cita* has been lowered by long-term pastoral impacts, and the removal of grazing combined with irrigation or fertiliser may induce their recovery (Scott 2000; Walker et al. 2003b). However, as at Limestone Stream, most quantitative studies indicate that reduced grazing alone is not effective for inducing widespread recovery of *F. novae-zelandiae* and *P. cita* in unfertilised short-tussock grassland. The response of short tussocks to reduced grazing has been examined in temporal studies, as well as in synchronous comparisons of vegetation with different grazing histories.

Most temporal studies in unfertilised grassland indicate that reduced grazing pressure alone has been ineffective over periods of almost 40 years. In six semi-arid to humid montane systems in Otago, Canterbury and Marlborough, *F. novae-zelandiae* and *P. cita* declined with and without grazing over 10–25 years (Rose et al. 1995; Meurk et al. 2002; this study), declined under a wide range of grazing histories (including removal of grazing) over 10–34 years (Scott et al. 1988; Duncan et al. 2001), or at best showed non-significant declining trends over 37 years of reduced grazing pressure (Rose et al. 2004). In a 12-year study, without fertiliser there were no significant differences in final tussock cover or trends in tussock cover between grazed and ungrazed treatments (Walker et al. 2003b). In a semi-arid area, 4 years after removal of grazing there had been a non-significant increase in the frequency of *F. novae-zelandiae*, but the study period had higher than average rainfall and trends on comparable grazed sites were not examined (Walker 2000).

Synchronous comparisons of fencelines, exclosures, and management blocks can generate useful hypotheses on past impacts (e.g. Lord 1990; Gibson & Bosch 1996; Rose et al. 1998; Walker et al. 2003a; Norton et al. 2006), but they assume there were no differences in past composition and provide no information on current trends in abundance. Predictions and recommendations from synchronous comparisons seldom have been tested by temporal studies (Duncan et al. 2001; this study), but overall they also provide little evidence for short tussock recovery prompted by reduced grazing alone. Ordination of semi-arid and sub-humid short-tussock stands using synchronous comparisons of fenceline effects and different management blocks suggested *F. novae-zelandiae* decreased with increasing 'pastoral impact' (Gibson & Bosch 1996). However, this does not necessarily imply that *F. novae-zelandiae* will recover after removal of grazing.

The limitations of such comparisons are highlighted by a combined synchronous and temporal study in humid montane grassland (Rose et al. 1995). In 1988 the cover of *F. novae-zelandiae* was 50% lower on grazed northern slopes than on equivalent slopes that had been retired from grazing for 22 years, suggesting recovery after retirement. However, temporal data from permanent transects measured regularly between 1965 and 1990 showed that *F. novae-zelandiae* was declining irrespective of grazing management. Fenceline comparisons in a mesic low-altitude grassland showed that after 4–24 years the cover of *P. cita* was lower on ungrazed than on grazed sites, probably because competing exotic grasses responded more rapidly to release from grazing (Lord 1990). In semi-arid montane grassland, after 16 years there was little difference in the cover of *F. novae-zelandiae* inside and outside four exclosures (McIntosh & Allen 1998). In a synchronous comparison of five blocks in sub-humid grassland subjected to different grazing, oversowing, and topdressing regimes it was concluded that oversowing and topdressing resulted in greater tussock cover compared with nil inputs and lower stocking rates (Norton et al. 2006). However, there was at most only a 1.3% difference in the mean cover of the minor tussock *Poa colensoi* between blocks (0.1 to 1.4% mean cover) and there were no significant differences in the mean cover of *F. novae-zelandiae* or any other tussock species (cover data were not presented). By far the main differences were in the cover of *H. pilosella* (39–87%). Fenceline and exclosure comparisons over a wide range of intermontane valley-floor and basin short-tussock sites showed no consistent effect of reduced grazing on the total biomass of native grasses, but *F. novae-zelandiae* and *P. cita* were not listed separately and for many sites the date of divergence in management was unknown (Walker et al. 2003a).

Is *Hieracium* causing short-tussock-grassland decline?

The spread of low-growing *H. pilosella* in disturbed tall-tussock (*Chionochloa*) grassland reflects past degradation and opening up of dense, closed-canopied communities through burning and grazing (Treskonova 1991; Rose &

Frampton 1999). After removal of disturbance, tall tussocks can recover and inhibit further spread of *H. pilosella* for 10–30 years (Meurk et al. 2002; Mark & Dickinson 2003). Resistance to the more erect and shade tolerant *H. lepidulum* is less certain (Rose & Frampton 1999). The pastoral conversion of closed tall-tussock grassland to more open short-tussock grassland represents a threshold in invasibility, and the rapid spread of *Hieracium* species in both grazed and ungrazed short-tussock grasslands reflects their naturally low resistance to invasive plants (Rose et al. 1998; Rose & Frampton 1999).

Our study supports the interpretation that competition from *Hieracium* species is a direct cause of further vegetation degradation and species declines in unfertilised short-tussock grassland. *Hieracium* invasion is not restricted to unvegetated substrates. *Hieracium* seedlings establish within all types of vegetation substrate present and even the physiognomically dominant short tussocks pose few barriers to establishment (Rose & Frampton 1999). It is unlikely that further vegetative expansion or dense seedling establishment would not be directly at the expense of that vegetation. Once dense patches are established, *H. pilosella* can effectively capture soil resources including moisture and mineral N, probably outcompeting resident plants and further promoting the spread of *Hieracium* (McIntosh & Allen 1998; Scott et al. 2001). In the study area, *Hieracium* species were the only plants to show large increases in abundance while half of all other species declined over the 10 year study period. It is likely that the rapid rates of increase in *Hieracium* and decline in other species were partly the result of drought, but *Hieracium* species recovered more rapidly than others.

Quantitative correlations between the rise in *Hieracium* and declines in other species have been difficult to demonstrate in individual temporal studies (Duncan et al. 2001; Walker et al. 2003b; Rose et al. 2004), but a comparison between several studies showed that the proportion of decreasing species increased with the extent of invasion (Rose et al. 2004). In the study area, net declines in key species cover and richness variables were significantly predicted by the net increase in cover of *Hieracium* species, regardless of grazing treatment.

Effects of grazing on species diversity

The effects of large herbivores on species diversity often fit within a site productivity framework. Effects are most intense in high-productivity grasslands, where reduced grazing (including exclusion) generally causes a decline in species diversity. In unproductive grasslands, reduced grazing either promotes diversity or has little effect (Gibson & Kirkpatrick 1989; Virtanen et al. 2002; Bakker et al. 2006). However, grazing effects are not always as accurately predicted. Both the direction and rate of change in species abundances can vary with productivity (Pakeman 2004) and the relationship between diversity

and productivity can vary over time (Tilman 1993). Additionally, a simple productivity framework does not readily account for displacement of species by invading exotics. For the relatively unproductive grasslands of the study area, the effects of exclusion on species richness varied with species origin and spatial scale, and we also suggest they may be time dependent. Partly in response to *Hieracium* invasion, species richness was declining both with and without grazing. As predicted by the productivity framework, there were no significant effects of exclusion on the ongoing decline in native species richness. In contrast, however, exotic richness generally declined more rapidly in response to exclusion than under grazing. Additionally, the adverse effects of exclusion on total and exotic richness were more pronounced for plots and transects than for the smaller quadrats and subplots. Over the first 10 years, exclusion has promoted decline in the number of disturbance-adapted exotics, but this partly reflects greater invasion by *Hieracium* species. Over the next 10 years this may well be followed by a more rapid decline in native richness, especially if *Hieracium* species continue to become more dominant inside than outside the exclosures.

Future trends and management

The abundance curves for *Hieracium* species in the study area show no signs of levelling off in the near future and we would therefore expect further declines in a wider range of species. The clear implications of this and all other recent studies of temporal change in short-tussock grassland are that successful future management for conservation of indigenous biodiversity or for pastoral production will not be able to rely solely on removal or manipulation of grazing pressure, will need to reduce the abundance of at least one species of *Hieracium*, and will need to be able to drive vegetation change in an acceptable direction. To maintain short-tussock grassland, both conservation and pastoral management will rely on the successful establishment and spread of *Hieracium* biocontrol agents (Morin & Syrett 1996; Syrett et al. 1996). In appropriate areas, conservation management will need to encourage succession to communities capable of more effectively resisting *Hieracium* invasion, such as native shrubland or forest. Continued pastoral production will rely on ongoing inputs of fertiliser and oversowing with exotic herbaceous species that can outcompete *Hieracium* at higher soil nutrient levels.

Acknowledgements

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