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FACTORS PREDISPOSING SHORT-TUSSOCK GRASSLANDS TO *HIERACIUM* INVASION IN MARLBOROUGH, NEW ZEALAND

Summary: The effects of environment and management on the composition of short-tussock grasslands and the abundance of the invasive weed *Hieracium pilosella* were investigated in two small catchments. Species composition and site factors were recorded on a total of 182 plots and the management history of each catchment was reviewed. *H. pilosella* was present on >80% of all plots, but was at an early stage of invasion in one catchment (<5% cover) and dominant in the other (25% cover). Classification and ordination revealed strong between-catchment differences in community composition that reflected differences in environment (soil fertility and rainfall), disturbance history (animal populations and burning), and the stage of invasion by *H. pilosella*. In both catchments *H. pilosella* tended to be least abundant on the wettest, driest, and most fertile soils. However, such relationships were weak. Generalised additive models and regression showed that in the earlier stage of invasion individual site factors explained less than 20% of the variation in *H. pilosella* cover. Topographic position and slope (both indicative of soil moisture) were the most significant combined predictors, but together explained only 32% of the variation. In the later stage of invasion individual factors explained up to 33% of the variation. Topsoil sulphur, slope and topsoil calcium were the most significant combined predictors, but together explained only 53% of the variation. Between-catchment comparisons highlighted the inter-related roles of environment, disturbance history, geographic location, availability of *H. pilosella* propagules, and stage of invasion in more fully explaining the abundance of *H. pilosella*. Of five models that have been proposed for *Hieracium* invasion, the "grassland decline" model best incorporated the inter-related factors that influence spatial and temporal variation in *H. pilosella* abundance in the study area. This model concentrates on identifying predisposing and trigger factors that increase the likelihood of invasion and accounts for multiple causes and interactions by specifying five key factors that influence the ability of a plant species to invade existing vegetation: environment, disturbance, vegetation structure and composition, life history attributes of the invader, and the availability of invading propagules. The model potentially provides a comprehensive framework for evaluating the causes of *Hieracium* invasion, targeting research effort, and developing sustainable management strategies.

Keywords: Multivariate analysis; generalised additive models; plant invasion; determinants of invasion; invasibility; grazing; degradation.

Introduction

In the late 19th century, species of *Hieracium*[1] (hawkweeds) were first recorded in New Zealand. In the last 2 decades *Hieracium* species, especially *H. pilosella*, have spread dramatically in tussock grasslands where they now seriously threaten production and conservation (McMillan, 1991; Hunter, Mason and Robertson, 1992). Managed

primarily for wool production, the *c*. 1 million ha of montane-subalpine short-tussock (*Festuca novae-zelandiae*) grassland in the subhumid and humid zones have proved particularly susceptible. By 1990 *Hieracium* species were dominant in about 50% of these grasslands (Hunter, 1991). *H. pilosella* is well adapted to both low soil moisture and low soil fertility. This is usually linked to its ability to respond rapidly to pulses in available moisture, phosphate and/or nitrogen (Davy and Bishop, 1984; Makepeace, 1985; Svavarsdottir, 1995; Fan and Harris, 1996). In tussock grasslands, *H. pilosella* achieves maximum dominance in the 500 - 1200 mm rainfall zone, indicating it is relatively drought tolerant; it is less successful in both wetter and drier zones (Hunter et al., 1992). Regular applications of

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[1]Botanical nomenclature follows Cheeseman (1925), Allan (1961), Moore and Edgar (1970), Healy and Edgar (1980), Connor and Edgar (1987), Webb, Sykes and Garnock-Jones (1988), Connor (1991), Edgar and Forde (1991), and Lambrechtsen (1992).

fertiliser and oversowing with pasture species can combat *Hieracium* invasion on sites with adequate soil moisture (e.g., Scott, Robertson and Archie, 1990). However, at present there is no known means of effectively controlling *Hieracium* in the large areas of tussock grassland where such treatment is economically unsustainable.

Early explanations for this dramatic invasion centred on two hypotheses. The "invasive weed" hypothesis (e.g., Scott, 1984) implies that *Hieracium* species are aggressive invaders which are ideally suited to the tussock grassland environment, exclude other species, and are themselves a direct cause of grassland degradation. In contrast, the "symptom of degradation" hypothesis (e.g., Treskonova, 1991) contends that *Hieracium* invasion is a response to degradation of the vegetation and possibly the soils caused by burning and overgrazing. Both seem plausible. Invasion by aggressive exotic weeds is a world-wide problem of disturbed tussock grasslands, such as New Zealand's, that evolved in the absence of large, hooved, mammalian herbivores (Mack, 1989).

Researchers and land managers have presented evidence both for and against each of these hypotheses (e.g., Hunter *et al.*, 1992), suggesting neither is sufficiently comprehensive. Some of the most conflicting evidence comes from quantitative analyses of long-term vegetation change. In tall-tussock (*Chionochloa*) grassland, Treskonova (1991) considered that grazing-induced degradation (principally reduction of the tussock canopy) was the primary cause for invasion by *H. pilosella* between the 1960s and 1990s. This study was confined to grazed communities. In both grazed and retired short-tussock grasslands over a similar period, neither hypothesis proved adequate (Rose, Platt and Frampton, 1995). The rate and extent of invasion by *H. pilosella* was not uniform (contrary to the invasive weed hypothesis), but was not significantly affected by grazing history (contrary to the degradation hypothesis). The influence of possible soil degradation on *Hieracium* invasion is unclear, partly because there is little quantitative information on long-term changes in soil organic matter and nutrients. In Otago over the last *c*. 15 years there has been some evidence for declining levels of organic carbon under grazing (McIntosh, Allen and Patterson, 1994; McIntosh *et al.*, 1994, 1996). However, *H. pilosella* increased both on "unimproved" sites and on sites where oversowing and topdressing had significantly raised organic carbon levels. Further, organic carbon actually increased beneath *H. pilosella* patches that invaded sparsely vegetated sites with high proportions of bare soil (McIntosh and Allen, 1993). In Canterbury,

there was little difference in soil properties inside and outside animal-proof exclosures after 45 years (Basher and Lynn, 1996).

Three more complex, interactive hypotheses have been suggested. These share several concepts and recognise that the aggressive weed and symptom of degradation hypotheses may not be mutually exclusive. For brevity we refer to these as the "grassland decline", "site suitability/propagule rain" and "niche creation" hypotheses. The "grassland decline" hypothesis (Rose, 1992) is based on a review of available anecdotal and scientific information. It invokes three interacting factors to explain the abundance of *Hieracium* in tussock grasslands: *Hieracium* dispersal patterns, the site tolerances and strategies of different *Hieracium* species, and the inherent susceptibility of different grasslands to invasion. Grassland susceptibility reflects composition and structure, which in turn reflect site environment and site history. Grassland susceptibility is assessed from an approach commonly used in evaluating the etiology of diseases and forest declines, where complex interactions between biotic and abiotic factors are involved (Manion, 1981). Applied to invasion, the approach recognises that not all ecosystems, communities, populations or individuals will be equally susceptible to all invaders. It concentrates on identifying relevant characteristics of the vegetation and the invader, as well as predisposing and trigger factors that increase the likelihood of invasion. Predisposing factors include relatively static or long-term stresses on the vegetation, e.g., climate, soils, grazing history, genetic potential. Trigger factors include short-term stresses such as drought or heavy defoliation that provide a "window of opportunity" for invasion.

The "site suitability/propagule rain" hypothesis (Duncan, Colhoun and Foran, 1997) is closely related to the decline hypothesis. Based on quantitative analysis of *Hieracium* distribution at a regional scale (in Canterbury and Otago), Duncan *et al.* (1997) concluded that the probability that a site will be invaded by *Hieracium* is a function of the suitability of the site for *Hieracium* establishment (itself a reflection of environment and past management) and the size of the *Hieracium* propagule rain.

The "niche creation" hypothesis is based on a detailed interference experiment involving gradients in soil fertility and cutting frequency (Fan and Harris, 1996). The hypothesis stresses interactions between the characteristics of *Hieracium* species that determine their ability to compete for light, mineral nutrients and water (pre-adaptation characteristics), the predisposing influences of canopy removal by

sheep and rabbits (precursor effects), the trigger effect of low and irregular fertiliser application, and the consequential effects of *Hieracium* establishment/spread. Fan and Harris (1996) contend that the key factor leading to invasion of tussock grasslands by *Hieracium* species was increased aerial application of superphosphate fertiliser from 1960 onwards, and that invasion was triggered where the application was below the threshold required to sustain oversown legumes so that they could fix sufficient nitrogen to sustain oversown higher fertility requiring forage grasses.

Continuing debate on the basic causes for *Hieracium* invasion reflects both the complexity of the issue and a lack of quantitative data. In this study we use multivariate techniques, generalised additive models, and regression to investigate the effects of environment and past management on community composition and the abundance of *Hieracium pilosella* in two predominantly "unimproved" short-tussock grasslands that are at different stages of invasion. We posed three main questions: (1) what are the main environmental and management influences on grassland composition and *H. pilosella* abundance?; (2) do the influences vary with the stage of invasion?; and (3) how well do present hypotheses explain the observed patterns of spread

and dominance by *H. pilosella*? We also comment briefly on the distribution of two less abundant species, *H. caespitosum* and *H. lepidulum*.

Methods

Study area

Short-tussock grassland composition and *Hieracium* abundance were investigated in two small catchments located in the Awatere Valley, inland Marlborough (Fig. 1). In Andy's Gully (2.6 km^2; 42°02'S, 173°26'E) the grasslands range from 760 to 1210 m a.s.l. Limestone Stream (6.6 km^2; 41°56'S, 173°37'E) lies 18 km further down the Awatere Valley. Because Limestone Stream is characterised by higher relief, the short-tussock grasslands extend from 700 to 1650 m. In both catchments, the predominant rock types are strongly indurated sandstones and siltstones (Challis, 1966) and the characteristically steep (> 20°) hillslopes reflect rapid uplift and high rates of geological erosion. The predominant soils include Pallic, Brown and Recent soils, each of variable depth, texture and horizonation (Lynn and Basher, 1994; L.R Basher and I.H. Lynn, unpubl. data; soil classes after
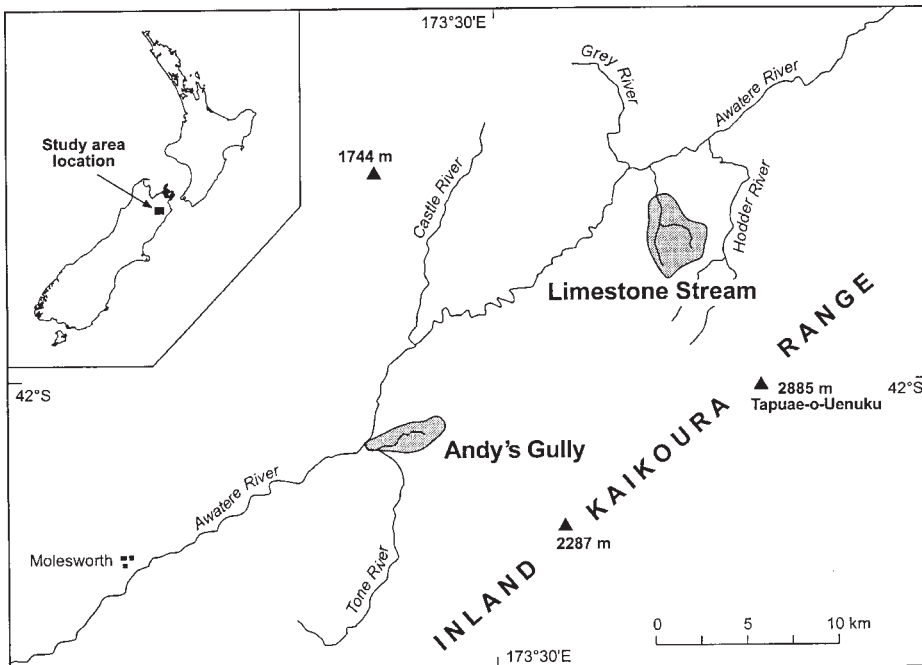

Figure 1: *Study area location.*

Hewitt, 1992). Rainfall records from within 9 km of each catchment (1951-80 normal rainfalls) suggest that Andy's Gully receives 11% less annual precipitation than Limestone Stream (676 and 762 mm, respectively; New Zealand Meteorological Service, 1985). Both catchments are characterised by a high frequency of dry periods (>60 days) especially in summer and autumn, low mean annual temperatures (*c.* 8°C) and a wide annual and diurnal range of temperatures, frequent ground frosts (average of >200 per year), and frequent strong, dry winds.

Vegetation history

The present vegetation of the Awatere Valley (Williams, 1989; Courtney and Arand, 1994) reflects human-induced disturbances over the last 750 years (McGlone and Basher, 1995). Between 10 000 and 750 years B.P., the area was clothed in indigenous conifer and conifer/broad-leaved forest below 1600 m a.s.l. Between 750 and 600 years B.P, most of this was burnt by Polynesians and was replaced by fern, grass, and scrub. By the 1860s, the arrival of European pastoralists led to increased burning, extensive grazing by sheep, and the spread of exotic species. As for much of the South Island high country (O'Connor, 1982, 1986), by the 1900s grassland stature and density would have been reduced because of regular burning, high stock numbers and rabbit (*Oryctolagus cuniculus* L.) plagues. Remnant trees (*Podocarpus hallii*, *Hoheria lyallii)* and tall-tussocks (*Chionochloa flavescens*) are now rare in the vicinity of the study catchments, where the present vegetation consists of semi-natural short tussock (*Festuca novae-zelandiae*, *Poa cita*) grassland. Exotic grasses and herbs often dominate (*Agrostis capillaris*, *Anthoxanthum odoratum*, *Hieracium* spp.). Patches of scrub and shrubland (*Rosa rubiginosa*, *Discaria toumatou*, *Cassinia leptophylla*, *Coprosma* spp.) are frequent.

Local farmers consider that *Hieracium* species are progressively invading down the Awatere Valley. For Andy's Gully, *H. pilosella* was probably present by the 1960s (it was recorded on nearby Molesworth Station in 1953; Moore, 1976). It has increased noticeably since the mid 1980s (R. and W.P.J. Stevenson, pers. comm.) and is now dominant. Limestone Stream is in an earlier stage of invasion. *H. pilosella* was locally present by 1963, but remained uncommon until 1989 (A.S and E.G. Pitts, pers. comm.). It is now widespread, locally dominant, and is increasing rapidly. For example, on permanent plots established in 1992 and 1994, *H. pilosella* had doubled in cover by 1996 (A.B. Rose, *unpubl. data*).

Management and feral animal history

Domestic animals, mainly merino sheep, have grazed the study catchments for at least 140 years (Kennington, 1978) but, as for most high country runs, the exact history of grazing is not recorded. In both catchments, average stock numbers have been reduced over time and are presently estimated at 0.8 - 1.2 stock unit/ha/yr. Until 1974, Limestone Stream was grazed all year by 700 wethers. Subsequently this number has been reduced to 100 for 4 months in spring-early summer (September or October to December or January) to promote vegetation regrowth and seeding. Usually most stock are also removed over winter (May or June to September), depending on the availability of feed on improved lower country (A.S and E.G. Pitts, pers. comm.). In Andy's Gully, between 1950 and 1990 stock numbers were about twice as high as at present and the catchment was grazed all year. Since 1990, the catchment has carried 100 ewes, which are removed in winter (May - July) and again for up to 6 weeks in spring (September-October) for lambing. It also carries 15 cattle for 10 months per year (R. and W.P.J. Stevenson, pers. comm.).

By the 1880s rabbit populations had reached very high densities in the upper Awatere (Kennington, 1978). Other feral animals have also had a significant impact on the vegetation, but numbers have generally declined since the 1960s because of hunting. For Limestone Stream (A.S and E.G. Pitts, pers. comm.), in the 1940s and 1950s the number of feral ungulates shot per year exceeded the number of sheep present. Goats have been the main feral browsers. However, until 1963 feral sheep were also numerous, and until the 1970s pigs were common and caused considerable soil disturbance. At present, the catchment contains low to moderate numbers of goats and low numbers of hares, pigs, possums and deer. Historically, rabbits have been confined to two small localised populations that have required only sporadic control. In contrast, Andy's Gully is one of the most rabbit-prone areas in the upper Awatere and has been subjected to intensive rabbit poisoning operations about every 5 years since the 1970s. The catchment also contains low populations of possums and hares. Goats, deer, and pigs are uncommon (R. and W.P.J. Stevenson, pers. comm.).

Although both catchments were burned in the past, they have not been burnt since 1963 for Limestone Stream and since 1970 for Andy's Gully. When sampled, a small area in the upper part of Andy's Gully was the only part of the study area that had been fertilised: in 1981 with sulphur super phosphate, and in 1984 and 1989 with sulphur. This

area had also been oversown with cocksfoot (*Dactylis glomerata*) and red clover (*Trifolium pratense*).

Sampling

In 1993 we sampled 93 sites in Limestone Stream and 89 in Andy's Gully after extensive reconnaissance. The sites were located in homogeneous grassland on representative slope positions of the main landforms, and covered the range of elevations and aspects. Standard vegetation plot size was 100m^2, reduced occasionally to meet homogeneity criteria. For each plot, the vegetative cover of all vascular species present was estimated in six classes (<1%; 1-5%; 6-25%; 26-50%; 51-75%; 76-100% cover) and three height tiers (<0.3 m; 0.3-1 m; 1-2 m). Ground cover was estimated to the nearest 5% for vascular vegetation, moss, litter, bare soil, broken rock and bedrock. Aspect, slope, and elevation were recorded. Potential solar radiation was calculated from aspect and slope angle (Frank and Lee, 1966) using the program SOLRAD (G.M.J. Hall, *pers comm.*). Drainage was scored as good (3), medium (2), or poor (1) as an estimate of the time that water remained on the soil surface. Sheep camps (areas where sheep congregate) were identified from evidence of heavy defecation. Landform and slope position were recorded according to Whitehouse, Basher and Tonkin (1991) and were then combined to form eight topographic position classes that reflected an assumed gradient of decreasing moisture: 1 = swale, 2 = terrace, 3 = alluvial fan, 4 = debris mantled toeslope, 5 = debris mantled footslope, 6 = debris mantled backslope, 7 = bedrock backslope, 8 = bedrock shoulder and crest. A soil pit was dug to bedrock or to at least 1 m depth under the dominant plant species near the centre of each plot and the soils were described according to Milne *et al*. (1991) and classified according to Hewitt (1992). Available water capacity was calculated after Griffiths (1985). To estimate topsoil fertility for each plot, 10 randomly located soil cores were taken (0-10 cm depth), then bulked and analysed for pH, total organic C, total N, exchangeable cations (Ca, Mg, K, Na), CaCl$_2$-extractable Al, Olsen-P, and phosphate-extractable S (Blakemore, Searle and Daly, 1987).

Analyses

Vegetation composition and vegetation-environment relationships

Plant communities and vegetation gradients were identified by classification and indirect ordination.

Importance values for each species in each plot were calculated by summing their cover classes (1 = < 1% to 6 = 76-100%, see above) across height tiers.

Plots were classified using the program TWINSPAN (Hill, 1979b) in the computer package PC-RECCE (Hall, 1992) with default options, except that cover classes were used as pseudo-species cut levels. Plot-groups were then identified at two levels, using a minimum group-size of 4 plots (the minimum number needed to adequately analyse their composition, cover, and site factors). Groups defined at the first two TWINSPAN dichotomies were termed "community groups". Within each group, further dichotomies defined "communities". The composition of the plot-groups and their site-factor distributions were summarised, and mean cover values for each species were calculated from the mid points of the cover classes (Hall 1992). Community groups and communities were named after species present with at least 10% mean cover. Those species markedly more frequent in one community group or community than in any other were determined. These "indicator species" were defined as species present on > 40% of plots in one community group or community which were also at least 20% more frequent there than in any other plot group at the same level of comparison (Rose, Harrison and Platt, 1988).

To understand vegetation gradients at different levels, ordinations were performed on the full data set and on subsets of plots identified from the classification (see Peet 1980). Ordinations were carried out using detrended correspondence analysis (DCA; Hill, 1979a) in the computer package CANOCO (ter Braak, 1991). Vegetation/environment relationships were inferred from (1) Spearman rank correlations between site factor values and DCA plot scores, (2) site factor comparisons between plot groups using Kruskal-Wallis one way ANOVA, and (3) vectors and environmental biplot scores generated by DCA. SYSTAT software was used for correlations and ANOVAs (Wilkinson, 1990). A Bonferroni-corrected significance level of < 0.05 was used to determine the significance of correlations (Kleinbaum, Kupper & Muller 1988).

Hieracium pilosella site preferences

The distribution of *H. pilosella* was broadly determined in relation to communities, catchments, and ordination axes. All plots were used in these analyses, including those on oversown and topdressed sites.

At a more detailed level, generalised additive models and regression models were then developed.

These used site factors to predict the cover of *H. pilosella* on individual plots in each catchment independently. The main aim of these detailed analyses was to develop and compare models for unimproved tussock grassland at different stages of invasion, therefore the 15 oversown and topdressed sites within a restricted part of Andy's Gully were excluded. *H. pilosella* cover classes were treated as a continuous dependent variable. Altitude, slope, potential solar radiation, available water capacity, topsoil depth, and topsoil P, S, C, Ca, N, Mg, K, Na, pH and Al were specified as continuous predictors. Topographic position, drainage class, landform class, and sheep camps were specified as categorical predictors using dummy variables.

Relationships between site factors and cover were first explored using the generalised additive model extension of multiple normal-theory linear regression models (Hastie and Tibshirani, 1990). GAMs are non-parametric in contrast to standard parametric regression approaches which assume a specific relationship (e.g. linear) between predictor and response variables. GAMs use a smoothing function to interpolate the response curve that best fits the predictor variables; here cubic splines were used. The degrees of freedom (d.f.) of the predictor variable can be set to allow the fitted response curve to be increasingly complex; d.f. = 1 specifies a linear response, higher d.f. allow for more complex responses (e.g. polynomial, skewed, bimodal etc.). GAMs are well suited to exploring the nature of plant distributions along environmental gradients, which may take a range a forms (see Austin 1985, Yee and Mitchell 1991). The GAM analogue of normal regression is based on a gaussian model with an identity link function, i.e., where errors are normally distributed with a mean of zero and constant variance. Standard analysis of residuals were used to verify that this was a suitable model for our data.

The GAM analyses proceeded in two stages (GAIMS software; Almudevar and Tibshirani, 1991). The first stage examined the strength of the relationship between each individual predictor and *H. pilosella* cover. For each continuous predictor, models with d.f. of 1,2,3 and 4 were progressively fitted. F-tests were used to compare the models and more complex functions were accepted only if they resulted in a significant change in residual deviance over simpler (e.g., linear) functions. For categorical variables, models were calculated using *d.f.* = n-1, where *n* = the number of categories present.

The second stage GAM analyses determined which combinations of variables most strongly predicted *H. pilosella* cover. The best combination of predictors was selected using forward selection and an F-test with a Bonferroni-corrected threshold

significance value of 0.05. The most suitable d.f. for each continuous predictor was chosen as described above. Interactions were tested between all significant predictors.

Although GAMs were useful to determine the nature of the relationships between predictor variables and *H. pilosella* cover, standard regression models have the advantage of allowing a predictive equation to be calculated and currently allow the use of more sophisticated software for detailed analysis of residuals. After each second-stage GAM based model was developed, we used the same variables with appropriate transformations (if required) to develop the standard regression model that best approximated the form of the GAM curve (SYSTAT Version 5 software; Wilkinson, 1990). To assess whether the equivalent regression model predicted *H. pilosella* cover as adequately as the GAM, the final deviances of the two models were compared. To ensure that individual observations had not unduly influenced the parameter estimates, the regressions were refitted after deleting observations with the highest residuals, highest Cook's D influence statistics, and extreme predictor values (see Nicholls, 1989).

Results

Vegetation composition

Three community groups were identified from the TWINSPAN classification. Within these groups, seven communities were distinguished by different combinations of dominant species (Table 1) and up to 16 indicator species that were uncommon in other communities (Table 2a). Several other species were common in more than one community and indicated affinities between communities (Table 2b-e). Community group 1 was characteristic of poorly drained sites and contained only 9 plots, precluding finer subdivision. Community groups 2 and 3 were characteristic of well-drained sites, and each contained three communities. *Hieracium pilosella* was common in six communities and attained > 80% frequency overall (Table 2d).

1. *Carex secta-Juncus articulatus-Trifolium repens* community group.

This minor community group, restricted to wet swales in both catchments, was the only group dominated by sedges and rushes. Other distinguishing features included 16 indicator species (e.g., *Festuca arundinacea*, *Juncus effusus*), the absence of *Hieracium* species, and low proportions of bare soil and rock (Tables 1, 2).

Table 1: *Cover of dominant species (> 10% mean cover) and* Hieracium *species, and ground-cover for each community. Values are means to the nearest 5%: + = <2.5% , . = absent. Community symbols as in the text: 1 =* Carex secta-Juncus articulatus-Trifolium repens; *2a =* Festuca novae-zelandiae-Anthoxanthum odoratum-Cassinia leptophylla; *2b =* Festuca novae-zelandiae-Anthoxanthum odoratum-Rytidosperma clavatum; *2c =* Poa cita-Dactylis glomerata-Poa compressa; *3a =* Hieracium pilosella; *3b =* Agrostis capillaris-Hieracium pilosella; *3c =* Hieracium pilosella-Dactylis glomerata.

Community	1	2a	2b	2c	3a	3b	3c
Number of plots	9	38	45	11	24	44	11
Juncus articulatus	20	+	.	+	.	.	.
Carex secta	20	+	.	.	.	.	.
Trifolium repens	20	5	+	15	+	+	10
Festuca rubra	10	.	+	+	+	5	+
Festuca arundinacea	10	.	.	.	+	+	.
Carex coriacea	10	.	.	.	.	+	.
Stellaria graminea	10	.	.	.	.	+	.
Vignea inversa	10	.	.	.	.	.	.
Holcus lanatus	10	5	5	+	5	5	+
Festuca novae-zelandiae	.	20	20	5	+	+	5
Cassinia leptophylla	.	10	+	+	+	+	.
Anthoxanthum odoratum	.	15	20	5	+	+	+
Rytidosperma clavatum	.	+	20	5	10	5	5
Poa compressa	.	+	+	15	+	+	+
Poa cita	+	5	5	20	5	+	+
Dactylis glomerata	+	+	+	20	+	+	25
Rosa rubiginosa	+	+	+	+	10	5	+
Agrostis capillaris	10	+	+	.	5	35	5
Trifolium pratense	+	.	+	5	+	+	15
Hieracium pilosella	.	5	5	+	25	30	40
H. caespitosum	.	5	+	+	+	+	5
H. lepidulum	.	+	+	.	+	+	+
H. praealtum	.	.	+	.	.	.	.
Vegetation	85	65	70	80	55	75	85
Bare soil	5	5	10	5	15	5	5
Rock	.	20	15	10	20	10	+
Litter	+	5	5	5	10	10	10
Moss	5	+	+	.	.	+	.

2. *Festuca novae-zelandiae* community group.
Of the 94 plots in this community group, all except three were from Limestone Stream. The group was distinguished by moderately abundant *Festuca novae-zelandiae* or *Poa cita* tussocks (25% combined cover), low overall cover of *Hieracium pilosella* (<5%), and high frequencies of *Uncinia divaricata*, *Cassinia leptophylla*, *Epilobium alsinoides*, and *Anthoxanthum odoratum* (Tables 1, 2).

2a. *Festuca novae-zelandiae-Anthoxanthum odoratum-Cassinia leptophylla* community.
Festuca novae-zelandiae, Anthoxanthum odoratum, and the shrub *Cassinia leptophylla* together accounted for 45% average cover in this community. It contained five indicator species (e.g., *Luzula rufa, Blechnum penna-marina, Rytidosperma setifolium*). *Hieracium pilosella* and *H. caespitosum* each accounted for 5% cover and *H. lepidulum* was widespread, at lower cover values (Tables 1, 2).

2b. *Festuca novae-zelandiae-Anthoxanthum odoratum-Rytidosperma clavatum* community.
Festuca novae-zelandiae and the grasses *Anthoxanthum odoratum* and *Rytidosperma clavatum* each accounted for 20% cover in this community, which contained three indicator species (*Pteridium esculentum, Vittadinia australis, Gnaphalium audax*). *Hieracium pilosella* accounted for 5% cover. *H. lepidulum* and *H. caespitosum* were widespread at lower cover values (Tables 1, 2).

2c. *Poa cita-Dactylis glomerata-Poa compressa* community.
Poa cita, Dactylis glomerata, Poa compressa, and *Trifolium repens* accounted for 70% cover in this community, which contained three indicator species (*Bromus mollis, Arenaria serpyllifolia, Bromus diandrus*). *Hieracium pilosella* was less abundant than in communities 2a and 2b, and *H. lepidulum* was absent.

3. *Hieracium pilosella - Agrostis capillaris* community group.
All 79 plots in this community group were from Andy's Gully. Distinguishing features included abundant *Hieracium pilosella* (25% mean cover), low combined cover of *Festuca novae-zelandiae* and *Poa cita* tussocks (< 5%), and high frequencies of *Agrostis capillaris, Rosa rubiginosa,* and *Hypericum perforatum* (Tables 1, 2).

3a. *Hieracium pilosella* community.
This community contained abundant *Hieracium pilosella* (25% cover), high proportions of bare soil and rock (35% combined ground cover), and the indicator species *Raoulia australis* and *Verbascum thapsus* (Tables 1, 2). *H. caespitosum* and *H. lepidulum* were widespread at low cover values (<5%).

3b. *Agrostis capillaris-Hieracium pilosella* community.
Agrostis capillaris (35% cover) and *Hieracium pilosella* (30% cover) were codominant in this community, which was also distinguished by high frequencies of *Poa pratense. H. caespitosum* and *H. lepidulum* were widespread at low cover values (<5%).

3c. *Hieracium pilosella-Dactylis glomerata* community.

Hieracium pilosella was more abundant in this community than in any other (40% cover), despite a moderately dense, taller canopy of oversown *Dactylis*

glomerata (25% cover) and *Trifolium pratense* (15%). Other distinguishing features included low proportions of bare soil or rock (<5%) and high frequencies of *Orobanche minor*. *H. caespitosum* and *H. lepidulum* were present at low cover values (<5%).

Table 2: *Floristic relationships between the 7 communities showing (a) indicator species most common in one community, and (b-e) species common in more than one community. Values represent the frequency of occurrence of each species in 6 classes: . = absent, 1 = 1-20%, 2 = 21-40%, 3 = 41-60%, 4 = 61-80%, 5 = 81-100%. Community symbols as in the text and Table 1.*

Community	1	2a	2b	2c	3a	3b	3c
Number of plots	9	38	45	11	24	44	11
(a) Indicator species							
Festuca arundinacea	5	.	.	.	1	2	.
Juncus articulatus	4	1	.	1	.	.	.
Juncus effusus	4	1	.	.	.	1	.
Ranunculus cheesemani	4	1	.	.	.	.	.
Eleocharis acuta	4	1	.	.	.	.	.
Stellaria graminea	4	.	.	.	.	2	.
Myosotis laxa	4	.	.	.	.	.	.
Gnaphalium limosum	3	1	1	.	.	.	.
Sagina procumbens	3	1	.	1	.	.	.
Ranunculus glabrifolius	3	1	.	.	.	.	.
Prunella vulgaris	3	1	.	.	.	.	.
Epilobium chionanthum	3	1	.	.	.	.	.
Phleum pratense	3	.	.	.	1	1	.
Poa trivialis	3	.	.	.	.	1	.
Carex coriacea	3	.	.	.	.	1	.
Ranunculus repens	3	.	.	.	.	.	.
Luzula rufa	1	4	1	1	.	1	1
Scleranthus uniflorus	.	3	1	1	1	1	.
Blechnum penna-marina	.	3	1	1	1	1	.
Rytidosperma setifolium	.	3	1	.	1	1	.
Deyeuxia avenoides	.	3	1	.	.	1	1
Pteridium esculentum	1	.	3	.	1	.	.
Vittadinia australis	.	2	5	1	3	1	.
Gnaphalium audax ssp. *audax*	.	2	5	1	2	1	.
Bromus mollis	2	1	2	5	.	1	2
Arenaria serpyllifolia	.	2	3	5	2	1	1
Bromus diandrus	.	.	1	4	.	1	.
Raoulia australis	.	2	1	.	4	1	.
Verbascum thapsus	.	.	2	2	4	1	1
Poa pratense	1	1	.	1	1	3	1
Trifolium pratense	2	.	1	2	1	1	5
Orobanche minor	.	.	1	.	1	1	3
(b) Species most common in community group 2							
Uncinia divaricata	.	5	5	1	3	3	.
Cassinia leptophylla	.	5	4	2	1	1	.
Epilobium alsinoides	.	4	4	1	3	1	.
Anthoxanthum odoratum	.	5	5	4	3	3	1

Community	1	2a	2b	2c	3a	3b	3c
Number of plots	9	38	45	11	24	44	11
(c) Species most common in community group 3							
Rosa rubiginosa	1	1	2	1	5	5	4
Agrostis capillaris	2	2	1	.	5	4	4
Hypericum perforatum	.	1	1	.	5	4	4
Discaria toumatou	.	1	1	.	4	3	2
Arrhenatherum elatius	.	1	.	1	4	3	3
(d) Species most common in community groups 2 and 3							
Dactylis glomerata	2	4	4	5	5	4	5
Elymus rectisetus	1	5	5	4	4	3	4
Rumex acetosella	.	5	5	5	5	4	3
Festuca novae-zelandiae	.	5	5	5	3	4	5
Hieracium pilosella	.	5	5	3	5	5	5
Geranium sessiliflorum	.	5	5	3	5	3	1
Acaena caesiiglauca	.	5	5	3	4	2	1
Wahlenbergia albomarginata	.	5	5	2	2	4	5
Dichelachne crinita	.	4	5	3	3	1	2
Hieracium caespitosum	.	4	4	2	5	4	4
Acaena agnipila	.	1	4	2	4	1	.
Trifolium arvense	.	3	5	2	4	3	2
Rytidosperma clavatum	.	2	5	4	4	2	3
Echium vulgare	.	1	2	5	4	2	3
Poa compressa	.	1	1	4	1	2	3
Hieracium lepidulum	.	4	3	.	3	2	1
Poa colensoi	.	4	1	2	1	2	3
(e) Others							
Trifolium repens	5	4	5	5	5	4	5
Holcus lanatus	4	5	5	3	5	5	5
Hypochoeris radicata	3	5	5	4	4	4	1
Cerastium fontanum	3	5	4	5	3	4	2
Festuca rubra	3	.	1	1	3	4	1
Poa cita	2	5	5	5	5	3	4
Crepis capillaris	2	4	5	5	5	4	2
Trifolium dubium	2	2	4	4	2	2	4
Taraxacum officinale	3	2	1	2	1	2	2
Cirsium vulgare	2	3	3	3	2	1	.
Viola cunninghamii	2	3	1	1	.	1	.
Vicia hirsuta	.	2	3	1	3	1	1
Linaria arvensis	.	2	3	.	1	.	.
Lachnagrostis filiformis	.	3	2	1	1	1	.
Melicytus alpinus	.	3	3	2	2	1	1
Pimelea sericeo-villosa	.	3	3	.	.	1	.

Vegetation-environment relationships

Five successive DCA ordinations were used to explore vegetation-environment relationships. The first ordination, using all plots, only separated those in community group 1 from all others along the first axis. The ordination reflected the strong influence of soil moisture on the vegetation, with community group 1 restricted to poorly-drained swales, where soils had high available water capacity and high levels of organic C, cations, and S (Table 3).

After excluding all plots in community group 1 and three other plots in moderately-drained swales (separated in a second ordination), a third ordination clearly separated community groups 2 and 3 along Axis 1. The three communities within each group were poorly distinguished. As the two community groups were virtually restricted to separate catchments, site-factor comparisons between community groups or catchments yielded very similar results. On average, plots in Limestone Stream occurred on steeper slopes, at higher

elevations, and at higher topographic positions (drier sites) than in Andy's Gully (Table 4). In Limestone Stream, soils had lower available water capacity, and topsoils were about 3 cm deeper and contained higher levels of C and Al. Soil characteristics were again compared between catchments after excluding 15 plots on oversown and topdressed sites in Andy's Gully. Unfertilised topsoils were lower in S and slightly less acidic in Andy's Gully than in Limestone Stream; for other soil variables, exclusion had negligible effect on mean values and significance levels (Table 4).

A fourth ordination restricted to all plots within community group 2 separated the three communities characteristic of Limestone Stream, where grassland composition mainly reflected potential solar radiation and the influence of sheep camps on topsoil fertility (Fig. 2a). DCA Axis 1 was most strongly correlated with potential solar radiation, topsoil magnesium and topsoil phosphate ($r_S = 0.55$,

Table 3: *Mean site factor values for plots in community group 1 (*Carex secta-Juncus articulatus-Trifolium repens*) compared with community groups 2 and 3 combined (*Festuca novae-zelandiae and Hieracium pilosella-Agrostis capillaris*). The Bonferroni-corrected probabilities are derived from Kruskal-Wallis rank sum tests (** = P < < 0.01, * = P < 0.05, ns = not significant). Topographic position scores range from 8 (high) to 1 (low); drainage scores range from 3 (good) to 1 (poor).*

Site factor	Group 1 (n = 9)	Groups 2 & 3 (n = 173)	P
Organic C (%)	5.94	3.02	**
Ca (me%)	18.73	10.91	**
Mg (me%)	5.09	2.48	**
K (me%)	0.43	1.01	**
Na (me%)	0.60	0.10	**
S (µg/g)	26.11	3.05	**
Available water capacity (mm)	145.11	79.60	**
Topographic position	2.44	4.84	**
Slope (°)	5.11	24.68	**
Drainage score	1.33	2.96	**
Potential solar radiation (Langleys/yr)	236.52	226.01	ns
Topsoil depth (cm)	14.22	17.59	ns
pH	5.96	5.94	ns
N (%)	0.38	0.25	ns
Al (µg/g)	0.17	0.32	ns
P (µg/g)	8.44	15.14	ns
Elevation (m a.s.l.)	833	993	ns

Table 4: *Mean site factor values for plots in Limestone Stream (mainly community group 2) and Andy's Gully (mainly community group 3), excluding community group 1 (n = 9). The Bonferroni-corrected probabilities are derived from Kruskal-Wallis rank sum tests (** = P < < 0.01, * = P < 0.05, ns = not significant). Topographic position scores range from 8 (high) to 1 (low); drainage scores range from 3 (good) to 1 (poor). [1]For Andy's Gully these values exclude 15 fertilised plots; for all other soil factors, exclusion had negligible effect on means and significance.*

Site factor	Limestone Stream (n = 91)	Andy's Gully (n = 82)	P
Topsoil depth (cm)	19.03	16.00	**
Organic C (%)	3.65	2.33	**
Al (µg/g)	0.49	0.12	**
Available water capacity (mm)	69.70	90.59	**
Topographic position	6.33	5.29	**
Elevation (m a.s.l.)	1069	909	**
Slope (°)	28.30	20.66	**
pH	5.99	6.00	ns
pH[1]		6.07	*
S (µg/g)	3.65	2.39	ns
S (µg/g)[1]		1.67	*
N (%)	0.29	0.22	ns
Ca (me%)	11.12	10.67	ns
Mg (me%)	2.33	2.64	ns
K (me%)	1.05	0.97	ns
Na (me%)	0.10	0.09	ns
P (µg/g)	18.29	11.66	ns
Potential solar radiation (Langleys/yr)	231.26	226.01	ns
Drainage score	2.92	3.00	ns

0.55 and 0.44, respectively; $P < 0.01$). Community 2a, at low positions on Axis 1, was more common than the other communities on shady slopes. For example 66% of plots in community 2a, and only 9% in the other two communities, occurred on sites facing south-east to south-west. Community 2c, at high positions on Axis 1, was typical of sunny, relatively fertile sheep camps. On sheep-camps, slope angles were typically less ($< 30^o$) than for other communities ($30-40^o$) and copious manuring appeared to have boosted topsoil fertility. For example, mean topsoil phosphate and magnesium levels for community 2c were higher than for communities 2a or 2b (P = 45.8, 16.5, 11.8; Mg = 3.4, 2.4, 2.1; respectively). Similar, but less marked trends were also apparent for total nitrogen, calcium, and potassium. The three plots from Andy's Gully that were within community group 2, were also from sheep camps and/or had been fertilised. DCA Axis 2 mainly reflected a gradient of decreasing elevation ($r_S = -0.74$, $P < 0.01$) and community 2b was typical of lower elevations than communities 2a and 2c (mean elevations 984, 1148 and 1153 m, respectively). This axis also reflected decreasing topsoil levels of aluminium ($r_S = -0.50$, $P < 0.01$) and organic carbon ($r_S = -0.37$, $P < 0.05$), and increasing pH ($r_S = 0.33$, $P < 0.05$), possibly reflecting reduced precipitation and soil leaching at lower elevation.

Hieracium pilosella, *H. lepidulum* and *H. caespitosum* occurred at only low mean cover ($\leq 5\%$) in communities 2a-2c (Table 1). All were least frequent on sheep camps (community 2c; Table 2). *H. pilosella* attained lowest cover values on these sites, but there was no significant correlation between cover and plot scores on the first two axes of the fourth ordination. For *H. caespitosum* and *H. lepidulum*, generally greater cover on shady slopes (community 2a) than on sheep camps was reflected in significant negative correlations between cover and Axis 1 plot scores ($r_S = -0.38$ and -0.46, respectively, $P < 0.01$).

A fifth ordination restricted to all plots within community group 3, separated the three communities characteristic of Andy's Gully. Grassland composition mainly reflected elevation, topsoil pH and organic carbon, and whether the site had been oversown and topdressed (Fig. 2b). Because mean elevation increased from community 3b to 3a to 3c (839, 953 and 1039 m, respectvely), DCA Axes 1 and 2 were both correlated with elevation ($r_S = 0.43$, $P < 0.01$ and $r_S = -0.40$, $P < 0.05$, respectively). Axis 1 separated community 3c, on oversown and topdressed sites at high mean elevation, from the two communities on unimproved sites. Axis 2 was positively correlated with topsoil organic carbon ($r_S = 0.42$, $P < 0.01$) and negatively correlated with pH (r = -0.48, $P < 0.01$). Community 3a was typical of
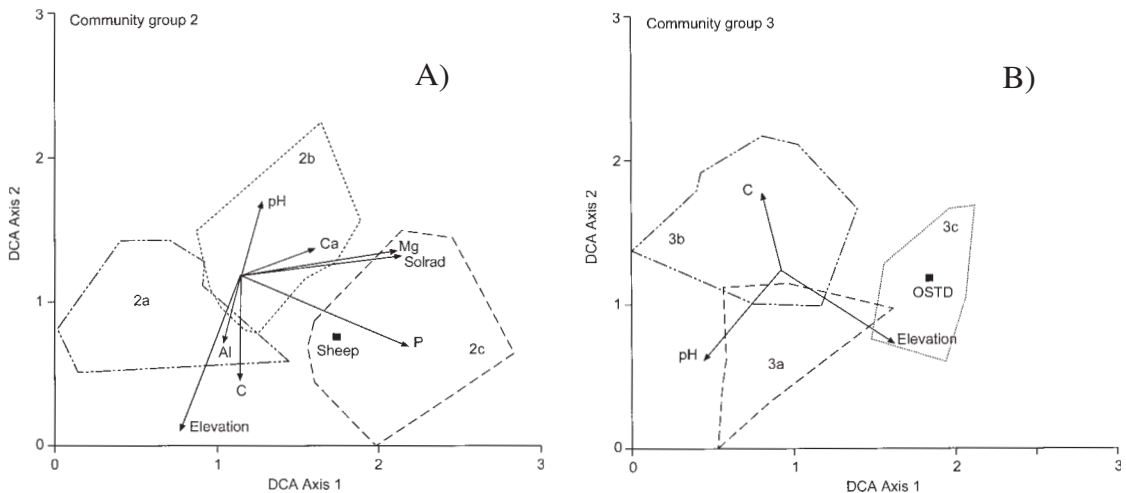

Figure 2: *Separate DCA ordinations of plots in (A) community group 2 (predominantly Limestone Stream, n = 94) and (B) community group 3 (Andy's Gully, n = 79), showing the three communities in each group. Community symbols (2a-2c, 3a-3c) are the same as in the text. Also shown are the centroids for plots located on sheep camps (SHEEP) and on oversown and topdressed sites (OSTD), and the vectors for site factors that are significantly correlated (P < 0.05) with the ordination axes, i.e., elevation, potential solar radiation (SOLRAD), and topsoil magnesium (Mg), calcium (Ca), aluminium (Al), phosphate (P), organic carbon (C) and pH.*

topsoils with lower mean organic carbon and higher pH than for communities 3b or 3c (organic carbon = 1.6, 2.7 and 2.4; pH = 6.3, 5.9 and 5.6; respectively).

Hieracium pilosella was abundant in communities 3a - 3c (25-40% cover; Table 1). Both *H. pilosella* and *H. caespitosum* attained highest cover on oversown and topdressed sites (community 3c). However, for these species and *H. lepidulum* there were no significant correlations between cover and plot scores on the first two axes of the fifth ordination.

Predictive models for *Hieracium pilosella*

Limestone Stream
For Limestone Stream, the first-stage non-parametric generalised additive models (GAMs) showed that *Hieracium pilosella* cover was significantly but weakly related to four of the 19 individual site factors tested ($P < 0.05$; Table 5a). Topographic position, an index of soil moisture, was the most significant factor but explained only 19% of the variation. *H. pilosella* tended to be least abundant on moist sites at low

Table 5: *Summary statistics for generalised additive models using individual site variables to predict* Hieracium pilosella *cover in each catchment (the 15 fertilised plots in Andy's Gully are excluded). For each variable the most significant model is given, allowing up to 4* d.f. *for continuous variables and* d.f. = n-1 *for categorical variables (n = number of categories). Significance assessed by F-tests, ns indicates P ≥ 0.05. The most significant response curves are illustrated in Fig. 3.*

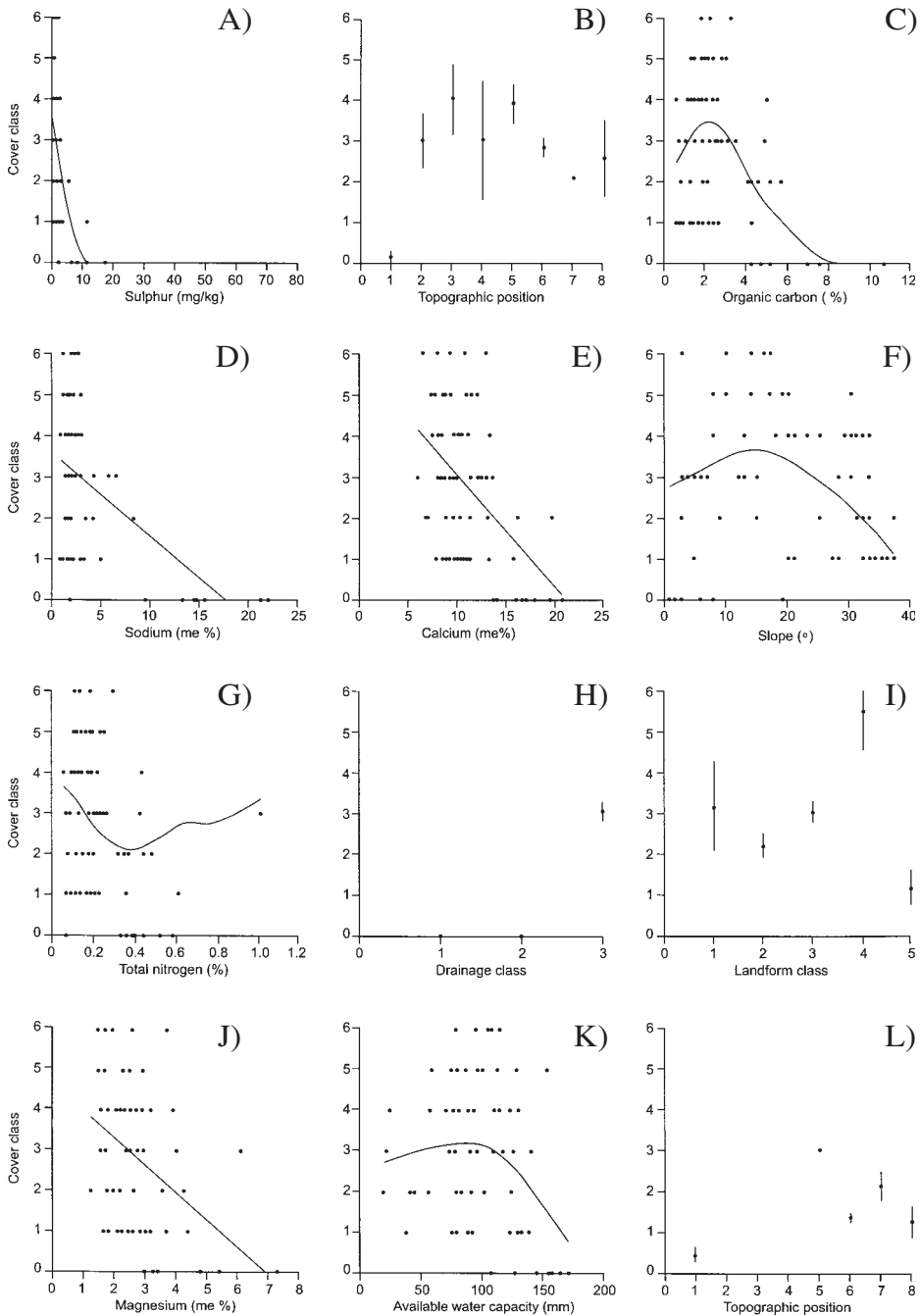| Variable	Δ deviance	d.f.	r²(%)	F	P
(a) Limestone Stream: null deviance = 103.0, total d.f. = 93					
Topographic position	19.7	4	19.1	5.19	0.001
Potential solar radiation	10.9	2	10.6	5.32	0.007
pH	9.6	2	9.3	4.64	0.012
Mg	4.6	1	4.5	4.29	0.041
S	8.5	3	8.3	2.67	ns
K	8.7	4	8.4	2.02	ns
N	7.7	4	7.5	1.77	ns
Al	6.4	3	6.2	1.96	ns
Slope	6.1	2	5.9	2.84	ns
Drainage score	4.9	2	4.7	2.23	ns
P	4.3	2	4.2	1.97	ns
Landform class	3.3	1	3.2	3.00	ns
Elevation	3.2	1	3.1	2.90	ns
Na	2.8	1	2.8	2.58	ns
Ca	1.8	1	1.8	1.66	ns
C	1.5	1	1.4	1.30	ns
Available water capacity	1.4	1	1.4	1.25	ns
Sheep camp	1.2	1	1.1	1.06	ns
Topsoil depth	0.2	1	0.2	0.21	ns
(b) Andys Gully: null deviance = 227.0, total d.f. = 74					
S	75.5	3	33.2	11.59	<0.001
Topographic position	74.2	7	32.7	4.58	<0.001
C	66.9	4	29.5	7.23	<0.001
Ca	57.4	1	25.3	24.43	<0.001
Na	57.4	1	25.3	24.39	<0.001
Slope	54.9	3	24.2	7.45	<0.001
N	52.9	4	23.3	5.25	0.001
Drainage score	52.1	2	23.0	10.59	<0.001
Landform class	49.3	4	21.8	4.80	0.002
Mg	42.2	1	18.6	16.46	<0.001
Available water capacity	37.5	2	16.5	7.04	0.002
K	35.8	2	15.8	6.65	0.002
Topsoil depth	30.1	2	13.3	5.44	0.006
pH	22.8	2	10.0	3.96	0.023
Elevation	9.4	2	4.1	1.53	ns
Potential solar radiation	5.3	4	2.4	0.42	ns
P	3.3	1	1.4	1.06	ns
Al	2.7	1	1.2	0.86	ns
Sheep camp	0.7	1	0.3	0.22	ns

Figure 3: *Smoothed response curves for* Hieracium pilosella *cover in relation to the most significant individual predictor variables as determined by first-stage generalised additive models for Andy's Gully (A-K) and Limestone Stream (L). The individual variables account for 17-33% of the variation in cover (Table 5).* H. pilosella *cover classes (1-6, respectively) are <1; 1-5; 6-25; 26-50; 51-75 and 76-100%. For categorical variables, means and standard errors are shown. Topographic position scores range from 1 (low/moist) to 8 (high/dry), drainage scores range from 1 (poor) to 3 (good), and landform classes are 1 = alluvial fan, 2 = bedrock slope, 3 = debris mantled slope; 4 = high terrace; 5 = low terrace.*

topographic positions (swales) and on dry sites at high topographic positions (e.g., bedrock shoulders and crests; Fig. 3). However, interpretation was hampered by a lack of sites at intermediate and low topographic positions in the catchment. Relationships with solar radiation, topsoil pH and topsoil magnesium were significant, but each explained only 5-11% of the variation (Table 5a).

The second-stage GAM analysis showed that variation in *H. pilosella* cover was more fully explained by combinations of site factors than by single factors (Table 6). Topograhic position and slope were the best combined predictors, together accounting for most of the variation explained by other site factors. With topographic position already in the model, inclusion of slope as a negative linear function accounted for a further 13% of the variation, but the combined relationship still only accounted for 32% of the variation. No additional variables resulted in a significant change in deviance. As slope influences water retention, the model reinforced the conclusion that soil moisture was important. There were no significant interactions between the two predictor variables. Because the GAM was adequately fitted with linear and categorical predictors, it was identical to the standard regression model.

Andy's Gully

H. pilosella cover was more predictable in Andy's Gully than in Limestone Stream. The first-stage GAMs showed that *H. pilosella* cover was significantly related to 14 of the 19 individual site factors ($P < 0.05$; Table 5b). However, no factor accounted for more than 34% of the variation. *H. pilosella* cover tended to decline with increasing topsoil fertility as shown by relationships with sulphur, organic carbon, calcium, and sodium, which were the most significant soil variables ($R^2 = 25$-33%; Fig. 3). Trends for magnesium ($R^2 = 19$%) and total nitrogen ($R^2 = 23$%) were weaker, and there were no significant relationships with phosphate or aluminium. Additionally, *H. pilosella* cover tended to peak on sites with intermediate soil moisture, as indicated by a tendency for high cover values on intermediate topographic positions ($R^2 = 33$%; Fig. 3). Weaker relationships with drainage, available water capacity, slope and landform class ($R^2 = 17$- 23%; Fig. 3) supported this conclusion. For example, a unimodal relationship with slope indicated *H. pilosella* cover peaked on slopes of about 15°, with lower values for very gentle slopes (typically wet swales or dry bedrock crests) and very steep slopes (typically dry bedrock backslopes).

Table 6: *Predictive models for* Hieracium pilosella, *Limestone Stream. (a) Stages of the forward selection non-parametric generalised additive model (GAM) for predicting* H. pilosella *cover from the most significant combination of site variables, and statistics for the equivalent standard regression model. At the first stage of the GAM, topographic position (topos) was the best predictor of* H. pilosella *cover. At the second stage, adding slope to the model resulted in the most significant change in deviance. No additional predictor variables resulted in a change of deviance with a probability < 0.05 (assessed with an F test). (b) coefficients and standard errors for the regression model.*

(a) Model development

Model	Residual deviance	d.f.	Δ deviance	d.f. of added predictor	P	R²(%)
GAM:						
intercept	102.99	92		1		
intercept + topos	83.34	88	19.65	4	0.001	19.1
intercept + topos + slope	70.36	87	12.98	1	<0.001	31.7
Regression:						
intercept + topos + slope	70.36	87		6	<0.000	31.7
				(full model including intercept)		

(b) Regression parameter estimates

Variable	Coefficient	s.e.
intercept	1.420	0.387
topos (class 5)	2.450	0.704
topos (class 6)	2.030	0.435
topos (class 7)	2.530	0.454
topos (class 8)	0.340	0.426
slope	-0.065	0.016

Second-stage GAM analysis again showed that variation in *H. pilosella* cover could be explained more fully by combinations of site factors than by single factors. The best combined predictors were sulphur, slope and calcium, which together accounted for 53% of the variation (Table 7). Sulphur was the most significant predictor; a polynomial function with d.f. = 3 accounted for just over 33% of the variation (as in the first-stage GAM, see Fig. 3). Progressive inclusion of a unimodal function of slope and a negative linear function of calcium accounted for an additional *c.*10% of the variation at each step. There were no significant interactions between the three predictors. There was close agreement between the GAM and the parametric regression model (Table 7); final deviances were 107 and 104 respectively (from a null deviance of 227) and R^2 values were 53% and 52%.

Discussion

Influences on grassland composition

At a wide range of scales, tussock grassland composition reflects the effects of environment and disturbance (Scott, 1979; Rose *et al.*, 1988; McKendry and O'Connor, 1990). Environmental influences include moisture, temperature, soil fertility, and stresses such as drought and fertilising. Disturbance factors include grazing, burning, and geomorphic events. Additionally, short-tussock grasslands are undergoing widespread and rapid vegetation change (Scott, Dick and Hunter, 1988; Connor, 1992; Rose *et al.* 1995; Duncan *et al*, 1997). Therefore, explanations for variation in short-tussock grassland composition also need to integrate information on vegetation change. Predominant among such changes are the effects of invasion by exotic species, particularly *Hieracium pilosella*.

By identifying seven distinct communities within three broader community groups, all within two catchments totalling only 9.2 km², our study highlights fine-scale variation in the composition of short-tussock grasslands. Vegetation composition strongly reflected site moisture and fertility. One community group was restricted to the few wet and relatively fertile swales in the area. In contrast, the two predominant tussock grassland groups occurred almost exclusively on well drained, less fertile sites. These groups showed strong spatial separation, with the *Festuca novae-zelandiae* group virtually

Table 7: *Predictive models for* Hieracium pilosella, *Andy's Gully (the 15 fertilised plots are excluded). (a) Stages of the forward selection non-parametric generalised additive model (GAM) for predicting* H. pilosella *cover from the most significant combination of site variables, and statistics for the standard regression model that best approximated the GAM. At the first stage of the GAM, topsoil sulphur (S) was the best predictor of* H. pilosella *cover; cover showed a polynomial response to S (d.f. = 3). At the second stage, adding slope to the model resulted in the most significant change in deviance; the response was unimodal (d.f. = 2). At the third stage, topsoil calcium (Ca) resulted in the most significant change in deviance; the response was linear (d.f. = 1). No additional predictor variables resulted in a change of deviance with a probability < 0.05 (assessed with an F test). (b) coefficients and standard errors for the regression model.*

(a) Model development

Model	Residual deviance	d.f.	Δ deviance	d.f. of added predictor	P	R²(%)
GAM:						
intercept	226.72	72		1		
intercept + S	151.50	69	75.22	3	0.001	33.2
intercept + S + slope	127.25	67	24.25	2	0.003	43.7
intercept + S + slope + Ca	106.56	66	20.69	1	<0.001	53.0
Regression:						
intercept + S + slope + Ca	104.21	68		5	<0.000	52.3
				(full model including intercept)		

(b) Regression parameter estimates

Variable	Coefficient	s.e.
intercept	4.549	0.743
$\log_{10}S$	-1.770	0.609
slope	0.197	0.064
slope²	-0.006	0.002
Ca	-0.197	0.059

restricted to Limestone Stream and the *Hieracium pilosella - Agrostis capillaris* group restricted to Andy's Gully. Such between-catchment variation in the tussock grasslands partly reflects overall differences in environment. The higher mean elevation of Limestone Stream (1069 m) than Andy's Gully (909 m) could explain the greater abundance of native species in Limestone Stream (e.g., *Luzula rufa*, *Rytidosperma setifolium*) and of exotics in Andy's Gully (e.g., *Poa pratense*, *Arrhenatherum elatius*). In Canterbury short-tussock grasslands, native species have been found to be more abundant above 1000 m elevation and exotics below (Rose *et al*. 1995). Higher annual rainfall for Limestone Stream (*c*. 762 mm) than for Andy's Gully (*c*. 676 mm) may also partly explain the greater abundance of *Cassinia leptophylla* and *Pteridium esculentum* in Limestone Stream and of *Rosa rubiginosa* in Andy's Gully. Higher rainfall would also cause higher rates of biomass production and soil weathering in Limestone Stream, contributing to the significantly deeper topsoils with higher levels of organic carbon, sulphur, and aluminium compared to Andy's Gully.

Between-catchment differences in tussock grassland composition also reflected differences in disturbance history. The history of burning and of domestic and feral animal populations suggest Andy's Gully has been subjected to higher overall rates of disturbance than Limestone Stream. This has probably contributed to the greater abundance of fire and grazing-tolerant exotic species in Andy's Gully, and of tussocks and other native species in Limestone Stream.

It is likely that present differences in composition between Limestone Stream and Andy's Gully have been accentuated by the more extensive spread of *H. pilosella* in Andy's Gully. Although there are no quantitative long-term records of former composition or vegetation change for either catchment, until *H. pilosella* erupted Andy's Gully was considered highly productive tussock grassland (R. and W.P.J. Stevenson *pers comm*.). Near Andy's Gully, quantitative data on grassland composition collected in 1951-52 from Molesworth Station (681 mm annual rainfall; Moore, 1976) also suggest the grasslands were, at least structurally, more similar to those of Limestone Stream than at present. On Molesworth, for example, *Festuca novae-zelandiae* was abundant, and the grasslands contained many minor native species (Moore, 1976). The present vegetation differences between Andy's Gully and Limestone Stream predominantly involve differential species abundances, as the two tussock grassland community groups share most species and no indicator species are restricted to only one group.

Several species that are now less abundant in Andy's Gully than in Limestone Stream have been shown to decline as *H. pilosella* increases, e.g., *Festuca novae-zelandiae*, *Uncinia divaricata*, *Epilobium alsinoides*, *Luzula rufa*, and *Anthoxanthum odoratum* (Rose *et al*., 1995). Within the catchments, interpretation of tussock grassland composition is largely limited by a lack of detailed information on disturbance.

Influences on the abundance of *Hieracium pilosella*

Hieracium pilosella was present on over 80% of sites sampled, indicating this species has a wide niche breadth. Nevertheless its cover was not uniform. Soil moisture and fertility are widely considered to be important influences on the success of *H. pilosella* (see Introduction). In the study area, *H. pilosella* tended to be least abundant on the wettest, the driest and the most fertile soils at all levels of analysis. However, relationships were weak. In Limestone Stream, soil moisture variables (topgraphic position and slope) together explained only 32% of the variation in *H. pilosella* cover. Soil fertility variables explained even less of the variation, and most were not significant. On unfertilised sites in Andy's Gully, significant soil moisture and fertility variables individually explained less than 34% of the variation, while the most significant factors (topsoil sulphur, slope, and topsoil calcium) together explained only 53%. At a regional scale, Duncan *et al*. (1997) also found that *Hieracium* cover was more predictable in the later stages of invasion. Cover-environment relationships might have been enhanced by more detailed site information, but our results clearly indicate that factors other than soil moisture and fertility explain much of the variation in *H. pilosella* cover.

In addition to soil moisture and fertility, comparisons between Andy's Gully and Limestone Stream highlight the potential roles of disturbance history, geographic location, availability of *H. pilosella* propagules, and stage of invasion in explaining the abundance of *H. pilosella*. Lower rainfall, lower mean levels of topsoil carbon and sulphur, and higher rates of disturbance have probably predisposed Andy's Gully to heavier infestation. Irregular fertilising in the upper part of Andy's Gully may have triggered expansion of *H. pilosella* (see Svavarsdottir, 1995; Fan and Harris, 1996). Seedling establishment is important in the early phase of *H. pilosella* invasion at Limestone Stream: in six stands examined along an elevational gradient, seedling (single rosette) densities averaged 26 per 100m^2 (A.B. Rose, *unpubl. data*). Andy's

Gully is located 18 km further up the Awatere Valley. *H. pilosella* tends to decrease in dominance down-valley (Hunter, 1991; *pers. obs.*), a gradient which runs contrary to the prevailing wind direction. This suggests that Andy's Gully may have been subjected to inherently higher inputs of wind-borne *H. pilosella* seed. However, it remains to be seen whether between-catchment differences in such predisposing factors have affected the eventual magnitude, or merely the rate of invasion. In Limestone Stream, *H. pilosella* is already present at low cover values on most sites and is rapidly expanding (see Introduction). Both catchments lie within the rainfall zone where *H. pilosella* achieves maximum dominance elsewhere in the short-tussock grasslands.

Models for *Hieracium* invasion

Many factors have been shown to affect the ability of a plant species to invade existing vegetation (Crawley, 1987; Drake et al., 1989; Burke and Grime, 1996). These can be incorporated within five broad headings: environment (including stress), disturbance, vegetation structure and composition, the availability of invading propagules, and life-history attributes of the invader. Such factors interact to cause vegetation change by affecting population dynamics (Peet and Christensen, 1980). This study shows that, even within a small area, combinations of such factors are required to adequately assess reasons for spatial variation in both *H. pilosella* abundance and grassland composition. Additionally, relationships can vary with time.

Both the invasive weed and symptom of degradation hypotheses (e.g., Scott, 1984; Treskonova, 1991; Hunter *et al*. 1992) invoke few factors to explain *Hieracium* success. In the study area, they only partly account for spatial variation in the abundance of *H. pilosella*, and do not specifically account for temporal differences in abundance. Although *H. pilosella* was clearly invasive, it was not uniformly abundant, partly because of environmental heterogeneity. In Andy's Gully, generally negative correlations between soil fertility and abundance suggest *H. pilosella* would be favoured by soil degradation, but soil fertility variables explained less than half the variation, and soil moisture was also involved. *H. pilosella* was positively associated with higher levels of disturbance, but other factors were also involved.

The "grassland decline", "niche creation", and "site suitability/propagule rain" models (see Introduction; Rose, 1992; Fan and Harris, 1996; Duncan *et al*., 1997) can all account for complex causes and interactions. Nevertheless, the niche creation hypothesis attributes the widespread success of *Hieracium* to one trigger factor (low and irregular fertiliser inputs) and does not specifically account for differences in vegetation structure and composition or the availability of propagules. Although our soil analyses may not have detected the effects of past nutrient pulses, there is evidence that irregular fertilising contributed to the greater abundance of *H. pilosella* in Andy's Gully than in Limestone Stream. However, other factors are also involved. Further, *H. pilosella* is widespread and increasing in Limestone Stream and in other tussock grasslands that have never been fertilised. Therefore, the hypothesis relies on the untested assumption that unintentional nutrient inputs from fertilised lands, by long-distance aerial drift of fertiliser or by nutrient transfer by stock, have been sufficient to trigger expansion of *H. pilosella*.

Our study indicates the need to allow for broader interpretations of *Hieracium* invasion, as provided by the "grassland decline" and "site suitability/propagule rain" hypotheses. Both can account for temporal variation in *Hieracium* abundance. We believe the advantage of the grassland decline model is that it is more comprehensive, because: (1) it specifically addresses interactions between environment, disturbance, vegetation structure and composition, the availability of invading propagules, and life-history attributes of the invader; (2) it forces formulation of hypotheses involving both long-term predisposing and short-term trigger factors; (3) it allows for different interpretations depending on the particular species of *Hieracium* involved; and (4) it predicts that there may be instances where vegetation composition/ structure confer high susceptibility regardless of management. While a detailed review is beyond the scope of this study, using this approach a simple model can begin to be developed for *H. pilosella* in short-tussock grasslands (Table 8). No doubt the model can be refined and expanded, but it can clearly incorporate the several factors that contribute to present differences in the abundance of *H. pilosella* between Andy's Gully and Limestone Stream. For example, it predicts that Andy's Gully is more highly predisposed to invasion because of lower rainfall, lower soil fertility, higher rates of disturbance, and because of its location. Likely trigger factors include more frequent drought stress, irregular fertilising, and rabbit population outbreaks. The model also predicts future increases in *H. pilosella* in Limestone Stream because, like Andy's Gully, it is predisposed to invasion by low rainfall, high past rates of disturbance, and because the composition and structure of short-tussock grasslands confers low resistance to invasion.

Table 8: *A preliminary "grassland decline" model for* Hieracium pilosella *invasion of short-tussock grasslands. The rate and extent of invasion are determined by interactions between the five main factors. Some possible predisposing and trigger factors are indicated that may increase the likelihood of invasion.*

1. Environment:
Predisposing: Low rainfall, low soil moisture and fertility.
Trigger: Drought, irregular/inadequate fertilising.

2. Disturbance:
Predisposing: Long history of anthropogenic disturbance (grazing/browsing, burning).
Trigger: Pest population outbreaks (e.g., rabbits, invertebrates), heavy grazing, fire.

3. Vegetation Structure and Composition:
Predisposing: Low stature, low canopy cover, abundant safe sites for *Hieracium* establishment, many native species poorly adapted to grazing and trampling.
Trigger: Heavy defoliation/mortality.

4. Availability of *H. pilosella* Propagules:
Predisposing: Proximity and location in relation to invasion fronts/established populations (external seed rain), stage of invasion (local seed rain, degree of vegetative spread).
Trigger: Wet growing seasons or grazing flower heads may trigger vegetative spread.

5. Life-History Attributes of *H. pilosella*:
Drought tolerant, tolerant of low soil fertility, rapid response to nutrient and moisture pulses, well adapted to long-range dispersal, rapid vegetative spread, light demanding.

A clear implication of the present study and those of Rose *et al*., 1995 and Duncan *et al*., 1997 is that interpretation of *Hieracium* invasion, and management response to it, should focus on multiple causes and interactions rather than single-factor explanations. The grassland decline model potentially provides a comprehensive and testable framework for assessing the limits of interpretation of existing research and for targeting future research. The model may resolve apparently conflicting interpretations of *Hieracium* invasion, e.g., vegetation structure may prove to be a key factor explaining the different responses of *H. pilosella* to grazing in tall and short-tussock grasslands (Treskonova, 1991; Rose et al., 1995). The model may also resolve the frequently conflicting impressions of *Hieracium* invasion held by land managers, e.g., differences in environment, vegetation structure, or availability of propagules (stage of invasion) may explain why a management technique is apparently successful in one area but not in another. We suggest that without such a framework, the interpretation of research, and the sustainable management of grasslands prone to *Hieracium* invasion, can only be partially successful.

Acknowledgements

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