Two decades of vegetation change across tussock grasslands of New Zealand's South Island

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Executive Summary

This report summarises changes that have occurred in plant community structure in tussock grasslands since the 1980s, and is an update to a study published by Duncan et al. (2001). We used data from 125 permanently-marked vegetation transects, which were set up on 29 properties in areas of tussock grassland across Canterbury and Otago in the South Island of New Zealand between 1982 and 1986 (first measurement), were re-measured between 1993 and 1998 (second measurement) and again between 2005 and 2007 (third measurement). The number of transects on each property ranged from one to ten. The transects were set-up by the Department of Lands and Survey, placed to be representative of the general vegetation in the area (C. Jensen, personal communication), and ranged in elevation from 370 m to 1880 m. The transects are on land that is in both conservation and pastoral tenure, and some of these areas have changed in tenure over the 24 year period of monitoring.

We present the results of an investigation into the effects of tenure on change in community structure for these transects. These changes are investigated in terms of species composition (the identities of the species that coexist in an area) and species richness (the number of species that coexist). Changes in species composition and species richness were investigated between the first and second measurements (first period) and between the second and third measurement (second period).

Each transect was 100 m long and comprised 50 square $0.25m^2$ quadrats placed at regular two metre intervals. At the first measurement, the presence of each vascular plant species inside each quadrat, including overhanging vegetation, was recorded. Vascular plants include all those species that have differentiated tissue, and do not include mosses or liverworts. At the second and third measurements, each vascular species was given a cover score within the quadrat (<1%, 2-5%, 6-25%, 26-50%, 51-75%, 76-100%). Plant species identifications were consistent across measurements because the same botanist, Carol Jensen, was involved in identifications at each measurement. Seasonal effects in species identifications were mitigated by always re-measuring each transect in summer, and during the same month that it was originally set up, as much as possible. A range of environmental data was collected using the GPS locations recorded for each transect.

There were 375 species encountered over the 125 transects and three measurement times. There was a great deal of variation among transects in species

composition; the sampling encompassed a wide variety of vegetation types and environmental conditions. A cluster analysis, using a reduced dataset that excluded rare species (194 species), classified each transect into one of six community groups, which were characterised by their species composition: (1) Alpine vegetation dominated by low-growing and mat-forming species, (2) Short-tussock grasslands dominated by native species, (3) Tall-tussock grasslands with herbaceous inter-tussock species, (4) Tall-tussock grasslands with woody inter-tussock species, (5) Short-tussock grasslands dominated by exotic species, and (6) Weedy, highly-modified grasslands.

Groups (1) and (6) were then excluded to investigate changes in composition on transects that were characteristic of "tussock grasslands" (194 species on 103 transects). Change in composition was quantified by calculating a measure of both the amount that transects changed, and the nature or direction of compositional change during each period. This analysis showed that the particular high country property that a transect was on influenced the amount that it changed in composition, i.e. some properties changed more in composition than others. The property that a transect was on also affected the way that it changed in composition, i.e. transects on some properties were more likely to change towards becoming more dominated by native species than others. This suggests that land management at the property level is important in determining changes in tussock grassland plant species composition. Tenure category was not related to either the amount or nature of compositional change in these tussock grasslands.

For all 125 transects, species richness declined during the first period, and increased during the second period, at both the small (quadrat) and large (transect) scales. Both native and exotic species declined in mean quadrat species richness during the first period, and then increased during the second period. Small herbs, large herbs, ferns, and rushes/sedges all declined significantly in mean quadrat species richness during the first time period, and then increased significantly during the second time period. *Hieracium* species richness increased at both the quadrat and transect scales during both time periods. Changes in *Chionochloa* species richness over time was negligible at the quadrat and transect scales. Changes in species richness were similar on transects in both conservation and pastoral tenure.

Although the changes in mean quadrat species richness differed for each time period, soil alkalinity and rock type were significant predictors of these changes for both periods. Soil fertility was a significant predictor for the first period, and this was replaced by tenure during the second period. Soil alkalinity was correlated with elevation.

In general, transects in conservation tenure did not change in composition or species richness differently from transects in pastoral tenure, which indicates that removing grazing alone does not necessarily enhance native biodiversity. However, considering that plants in tussock grasslands are slow growing, and that these areas have been grazed and burned for more than a century, we may expect it to take some time for dynamics in conservation land to become different to those in pastoral land.

The changes in species richness and composition in this study are not directly attributable to changes in exotic species in either conservation or tenure. The observed, consistent increase in *Hieracium* spp. supports the idea that *Hieracium* invades and increases in areas regardless of original species composition or management.

Overall, the changes in the community structure of these tussock grasslands are related to a combination of environmental factors, such as soil chemistry and climate, and management factors. The inconsistent changes that have occurred on these 125 transects over the past 24 years, and the nature and complexity of the variables that explain those changes, make it difficult for us to be able to make any clear predictions about future changes that may occur. However, we can conclude from this research that of these permanent transects that the conversion of pastoral lease land to conservation tenure has not, so far, had a large impact on changes in plant species composition or species richness in these tussock grasslands. This highlights the importance of continued monitoring of these permanent transects and a range of other High Country sites for many years into the future if we are to obtain a good understanding of the effects of land use on vegetation change.

Introduction

The Tenure Review process is resulting in large areas of South Island high country passing into the conservation estate. The government is responsible for maintaining biodiversity, cultural, and other values of this land. Many of these values may be indicated by aspects of plant community structure, such as species richness and composition. It is therefore relevant to investigate past trends in the effects of land tenure on vegetation change.

We know from the literature that the important ecological factors determining the community structure of tussock grassland vegetation are: temperature and precipitation (slope, aspect, elevation), soil conditions, invasion by exotic species, such as *Hieracium* spp., and grazing by introduced mammals, such as sheep, rabbits and deer (Hubbard and Wilson 1988, Rose et al. 1995, Allen et al. 1997, Walker and Lee 2000, Mark and Dickinson 2003). The important management factors are grazing by stock, burning, topdressing, and over-sowing with pasture species (Cockayne 1921, Zotov 1938, Mark and McLennan 2005, Norton et al. 2006). These management factors are often confounded with ecological factors; for example, grazing, topdressing and over-sowing are more intense at lower elevations, which also have higher temperatures than areas at higher elevations.

How land tenure explicitly impacts on these ecological and management factors, and consequently their effect on plant community structure, is unknown. We can predict, however, that these effects in a given location are likely to be idiosyncratic, simply because human decisions regarding land management are often inconsistent, especially across large geographic areas. An additional and important consideration is that considering the short period of time (relative to the timescales over which we might expect tussock grasslands to respond to changes in environmental and management conditions) over which most land tenure change has occurred in the South Island, tenure is more likely to indicate differences in initial conditions than how vegetation will change over time. This is because land that is put into the Department of Conservation (DoC) estate is, at least historically, usually very different than the land that stays or gets given over to pastoral use.

An analysis by Duncan et al. (2001) compared small-scale species richness for 142 permanent transects on 33 high country properties across Otago and southern

Canterbury, which were measured in the 1980s and remeasured in the 1990s. Their analysis suggested that there was widespread decline in species richness over this ten to fifteen year period. This study is a reanalysis of the data for 125 of these transects on 29 properties that were resampled for a third time between 2005 and 2007 (Figure 1).

In this report, we present the results of an investigation into the effects of tenure on change in community structure for these transects. These changes are investigated in terms of species composition (the species that coexist in an area) and species richness (the number of species that coexist). The 125 transects were placed on land in both conservation and pastoral tenure, and some of the properties changed tenure throughout the 24-year period of measurements (Table 1). Grouping the transects by tenure is a coarse method of classifying by management, with transects in conservation tenure assumed to have been ungrazed by domestic stock. However, records of stock numbers were not obtained for the transects in pastoral tenure, meaning that no inferences can made about the effects of grazing intensity on species composition or richness in tussock grasslands in this study.

This dataset is of very high quality in terms of consistency in species identifications across the 24 years and is well-suited to the landscape-level analysis of vegetation change because it spans a long period of time and a wide geographic range.

Methods

Study area

A total of 125 permanently-marked vegetation transects, which were set up on 29 properties in areas of tussock grassland across Canterbury and Otago in the South Island of New Zealand between 1982 and 1986 (first measurement), were re-measured between 1993 and 1998 (second measurement) and again between 2005 and 2007 (third measurement) (Figure 1). The number of transects on each property ranged from one to ten. The transects were set-up by the Department of Lands and Survey, and placed to be representative of the general vegetation in the area (C. Jensen, personal communication), and range in elevation from 370 m to 1880 m.

Data collection

Each transect was 100 m long and comprised 50 square $0.25m^2$ quadrats placed at regular two metre intervals. At the first measurement, the presence of each vascular plant species inside each quadrat, including overhanging vegetation, was recorded. Vascular plants include all those species that have differentiated tissue, and so does not include mosses or liverworts. At the second and third measurements, each vascular species was given a cover score within the quadrat (<1%, 2-5%, 6-25%, 26-50%, 51-75%, 76-100%). Plant species identifications were consistent across measurements because the same botanist, Carol Jensen, was involved in identifications at each measurement. Seasonal effects in species identifications were mitigated by always re-measuring each transect in summer, and during the same month that it was originally set up, as much as possible.

A range of environmental data was collected using the GPS locations recorded for each transect. Rock type (greywacke or schist) was obtained from mapped data from general soil surveys of the South Island (New Zealand Soil Bureau 1968). The software ArcGIS 9.1 (ESRI 2005) was used to extract elevation, slope, aspect, and temperature and precipitation data from available national spatial datasets at each site location. Elevation was extracted from a 25×25 m resolution digtial elevation model (DEM) provided by Landcare Research. Slope and aspect surfaces were derived from the DEM data using spatial analysis functions in the GIS, from which values were subsequently extracted for site locations. The climate-related data were extracted from 500×500 m resolution interpolated climate surfaces provided by NIWA. Mean monthly temperature and mean monthly precipitation taken over thirty years for each transect location were used. An index of solar radiation, which is the potential amount of radiation from the sun that a transect may receive, was calculated from latitude, aspect, and slope (Kaufmann and Weatherred 1982).

The tenure of each transect (pastoral or conservation) was obtained from Land Information New Zealand and Department of Conservation records. To assess whether a transect had been burned between the first and second measurements the current lessee was asked and/or the vegetation was assessed for signs of burning. This was not done at the third measurement due to time restrictions. At the third measurement five soil samples were taken at regular 20 m intervals along each transect and then pooled. Samples were dried and analysed to obtain their cation exchange capacity,

total base saturation, pH, calcium, phosphorus, potassium, sulphate sulphur, magnesium, sodium, and bulk density by New Zealand Labs using standard techniques (Kay and Hill 1998).

Data analysis

Patterns in species composition

To identify transects of similar species composition, a cluster analysis was performed using PC-ORD version 4 (McCune and Mefford 1999) on species' abundances at all three measurements using the relative Sorenson distance measure and Ward's linkage method. The abundance of a particular species was the number of quadrats that species occurred in on a given transect. To reduce the effects of rare species, the dataset used included only the 194 species that occurred at on at least one transect at all three measurements. Indicator species analysis was used to identify the species that were characteristic of each community type. Indicator species analysis is a method that identifies the species that are characteristic of a particular group of sites and is based on both their occupancy across those sites and their relative abundances within those sites (Dufrene and Legendre 1997). The indicator value is the product of these two values taken as percentages (McCune and Mefford 1999). The appropriate number of groups to be identified by the cluster analysis was determined by selecting the grouping that resulted in the highest mean indicator value across all species.

A Principal components analysis (PCA) was performed using PC-ORD version 4 (McCune and Mefford 1999) on the soil characteristics because many were highly correlated with each other. The variables included were base saturation, cation exchange capacity, bulk density, soil calcium, magnesium, pH, phosphorus, potassium, sodium and sulphur. This process created variables that represent gradients in soil chemistry that can be used as environmental variables.

An ordination by detrended correspondence analysis (DCA) using CANOCO, version 4.5 (ter Braak and Smilauer 2002) was conducted on the above dataset. This analysis allows us to quantify turnover in species composition using the calculated gradient lengths, which are in 'species turnover units' (Leps and Smilauer 2003, pg. 160). DCA is recommended for situations where gradient lengths are greater than three, as was the case with this dataset (ter Braak and Smilauer 2002).

An indirect gradient analysis by DCA is used to show the relationship between gradients in species composition and measured environmental variables without constraining the compositional axes (ter Braak and Smilauer 2002). This analysis was performed for those transects classified by the cluster analysis as "tussock grasslands" (see Results). The environmental variables used were: rock type, tenure, whether or not a transect had been burnt prior to the second measurement time, mean monthly temperature, mean monthly precipitation, soil PCA axes 1 and 2 (see Results), elevation, and solar radiation. Mean monthly precipitation was log-transformed to approximate normality. For both DCAs, detrending by 26 segments and Hill's scaling was used.

Analysis of temporal patterns

Changes in composition over time for the 103 'tussock grassland' transects (see Results) was displayed on the DCA diagram by plotting trajectories of each transect for the first time period (between the first and second measurements), and for the second time period (between the second and third measurements). This method has been used previously to investigate changes in composition over time (e.g. Collins and Adams 1983, Leps 1987, Kahmen et al. 2002, Meurk et al. 2002). The distance between the points on each transect was used as a measure of the amount of compositional change that has occurred during the time periods. For each transect, the Euclidean distance (D) between points on the DCA ordination diagram at each measurement was calculated using Pythagoras' theorem as

$$D = \sqrt{d_1^2 + d_2^2},$$

where, for the first time period, d_n is the distance between the first and second measurements on DCA axis n. Similarly, for the second time period, d_n is the distance between the second and third measurements on DCA axis n. Three analysis of variance tests (ANOVAs) were used to test if the distance moved by a transect was related to property, tenure, or tussock grassland community type.

A direction category for each transect describing how that transect had changed in composition during the two time periods was generated by classifying the direction of change on the DCA graph into one of four categories: (1) changed negatively on the first axis and positively on the second axis, (2) changed positively

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on the first axis and positively on the second axis, (3) changed negatively on the first axis and negatively on the second axis, (4) changed positively on the first axis and negatively on the second axis. Chi-square tests for goodness of fit (Zar 1999) were performed to investigate whether the direction of change was related to property, tenure or community type (defined by the cluster analysis). Because there were low sample sizes in some categories, *P* values were estimated by Monte Carlo simulations based on 2000 replicates (Gotelli and Ellison 2004). All temporal analyses were performed in R version 2.5.1 (R Core Development Team 2007).

Changes in mean quadrat species richness

Species richness analyses were performed using all 375 species on all 125 transects. For each transect at each measurement, mean quadrat species richness was calculated by summing the total number of quadrats that each species occurred in, and then dividing by 50 (the number of quadrats on a transect). Change in mean quadrat species richness during the first time period was calculated for each transect by subtracting mean quadrat species richness at the first measurement from mean quadrat species richness at the second measurement. Changes in mean quadrat species richness for each transect were standardised to a rate of change per ten years by dividing the change in species richness by the interval between measurements (in years) and then multiplying by ten. This was repeated for the second time period.

A significant change in mean quadrat species richness (*P* < 0.05) for all species was tested for by performing a two-tailed one-sample *t*-test on the change in mean quadrat species richness per ten years between the first and second measurements, and then between the second and third measurements.

Each vascular plant species encountered was classified by its life history characteristics in three ways, following Duncan et al. (2001):

1) Growth form: in terms of woody, grasses excluding *Chionochloa* spp., small herbs less than 2 cm tall, large herbs greater than 2 cm tall, ferns, rushes and sedges, *Hieracium* spp., or *Chionochloa* spp.. *Hieracium* spp. and *Chionochloa* spp. were considered separately because they may have disproportionate effects on species richness (Treskonova 1991, Scott 1993).

2) Longevity: whether plants were annual or perennial.

3) Origin: whether plants were native or introduced. Analyses using origin excluded *Hieracium* spp. because they have large impacts on changes in tussock grasslands,

and the effect of *Hieracium* alone could overshadow the effects of other exotic species (Duncan et al. 2001)

Significant changes in mean quadrat species richness for each of these groups, were tested for using two-tailed one-sample *t*-tests ($P < 0.05$) on the change in mean quadrat species richness per ten years during the first period, and the second period, with Bonferonni corrections for multiple tests on the same data.

Significant changes in mean quadrat species richness for each tenure category were calculated using one-sample *t*-tests ($P < 0.05$) on the change in mean quadrat species richness per ten years for the first and second time periods. A two-tailed two-sample *t*-test was used to assess whether transects in different tenure categories showed similar changes in mean quadrat species richness between measurements. Tenure at the second measurement was used so that the number of transects in each category was the same for each test. To investigate whether changes in native and exotic species richness differed according to tenure, two-tailed one-sample *t*-tests were performed on changes in mean quadrat species richness in native and exotic species along transects under conservation and pastoral tenure.

Predictors of mean quadrat species richness change for each time period: linear mixed-effects models

To find the best environmental predictors of change in mean quadrat species richness, two models were built that predicted change, one for each of the two time periods. The response variable was change in mean quadrat species richness. This richness measure excluded *Chionochloa* and *Hieracium* species because these species groups were included in the model as potential predictor variables (following Duncan et al. 2001).

Transects clustered together in space are likely to be more similar to each other than those further apart because they experience the same environmental conditions, i.e., they are spatially autocorrelated (Legendre 1993). To account for this, "property" was included as a random effect in the model. This means that the variation in transects within a property is taken into account in assessing the amount of variation that is explained by other variables in the model. The remaining explanatory variables that are explicitly tested for are called fixed effects (Crawley 2002), which are the environmental variables recorded at each transect.

For all 125 transects, 11 variables were considered as potential predictors of change in mean quadrat species richness between measurements: tenure at the second measurement, elevation, soil alkalinity (PCA axis 1), soil fertility (PCA axis 2), mean monthly temperature and precipitation, rock type, change and presence of *Hieracium* spp and *Chionochloa* spp., solar radiation, and whether or not the site had been burnt prior to the second measurement time. One alpine bog transect had high outlying values for soil chemistry variables and was removed from the analysis. The assumption of normality of the response variables demanded by mixed-effects models (Crawley 2002) were met without needing to transform the response variable for either time period. These models were run using the nlme package in R version 2.5.1 (Pinheiro et al. 2006, R Core Development Team 2007).

Results

A total of 375 species were encountered over the three sampling periods on the 125 sampled transects (Appendix I). Only 194 species occurred more than once on more than one transect at all three times (the reduced dataset).

Data reduction and environmental variables

Principal components analysis resulted in two principal axes that accounted for 62% of the variation in soil characteristics (Table 2). The first principal axis reflected soil alkalinity. Sites with high base saturation and pH had high values on the axis. The second principal axis reflected soil fertility. Sites with high cation exchange capacity, bulk density and sodium had high values on the axis. The amounts of other cations and elements in the soil were partially correlated with both these axes.

Many of the environmental variables were correlated with each other. Pearson correlations among the continuous environmental variables showed that in particular, elevation, soil alkalinity, mean monthly temperature, and mean monthly precipitation were correlated (Table 3). Boxplot and table analyses (results not included) showed also that elevation, temperature, and precipitation were related to the presence of *Chionochloa* on transects; *Chionochloa* tended to be present on transects that had soils of greater alkalinity, were at higher elevations, and experienced lower temperatures and higher precipitation.

Cluster analysis and indicator species analysis

Six distinct community types were identified by the cluster and indicator species analyses (Figure 2). Percent chaining in the cluster analysis was 0.51 percent showing that the selected method was appropriate in that it generated clusters without having to add transects to clusters arbitrarily (McCune and Mefford 1999). Indicator species analysis showed that six clusters were appropriate; indicator values were highest for most clusters at this level. The six communities are described below.

(1) Alpine vegetation dominated by low-growing and mat-forming species

Indicator species: *Dracophyllum muscoides, Luzula pumila, Raoulia hectorii, Agrostis muelleriana*

This community contained only native species adapted to high alpine environments. Mean elevation for these transects was 1428 m, and 88% of the transects were in pastoral tenure. It included mat-forming species such as *Dracophyllum muscoides* and *Raoulia hectorii*, small herbs such as *Celmisia laricifolia* and *Kelleria dieffenbachii*, and the small native grass *Agrostis muelleriana*. All species in this community were perennial.

(2) Short-tussock grasslands dominated by native species

Indicator species: *Aciphylla aurea, Raoulia subsericea, Viola cunninghamii, Festuca novae-zelandiae*

Mean elevation for these transects was 1193 m, and 78% of the transects were in pastoral tenure. Native species were abundant in this community, including *Festuca novae-zelandiae* and *Poa colensoi*. Some exotic weed species were abundant, such as *Hypochaeris radicata* and *Rumex acetosella*. Native species that were abundant in this community were small herbs such as *Leptinella pectinata*, *Lagenifera cuneata* and *Wahlenbergia albomarginata*, as well as woody species including *Pimelea oreophila* and *Leucopogon fraserii*.

(3) Tall-tussock grasslands with herbaceous inter-tussock species

Indicator species: *Gnaphalium mackayii, Chionochloa* spp*., Celmisia lyallii, Uncinia* spp.

Native species were abundant in this community, where *Chionochloa* spp. were dominant and *Poa colensoi* was abundant. Mean elevation was 1358 m, and 72% of the transects were in pastoral tenure. These communities were in moist soils, as shown by the abundance of sedges such as *Unicina* spp., *Carex* spp., and the rush *Schoenus pauciflorus*. Small native herbs were abundant in this community, including *Gnaphalium mackayii, Anisotome flexuosa* and *Epilobium* spp.

(4) Tall-tussock grasslands with woody inter-tussock species

Indicator species: *Celmisia spectabilis, Blechnum penna-marina, Dracophyllum uniflorum, Gaultheria depressa*

Mean elevation was 1011 m, and 48% of the transects were on pastoral tenure. This community contained the highest number and proportion of transects in conservation tenure. *Chionochloa* spp. were abundant in this community, as well as other, mainly native, species that were characteristic of areas of tall-tussock grassland that have been retired from grazing. These included the shrubs *Dracophyllum uniflorum* and *D. acerosum*, and the large and conspicuous herb *Celmisia spectabilis*. Exotic species including *Agrostis capillaris*, *Hypochaeris radicata*, and *Hieracium pilosella* were also abundant.

(5) Short-tussock grasslands dominated by exotic species

Indicator species: *Trifolium repens, Linum catharticum, Anthoxanthum odoratum, Hieracium lepidulum*

Festuca novae-zelandiae was less-abundant in this community (compared to the other short-tussock community). Mean elevation was 1041 m, and 85% transects were in pastoral tenure. There was evidence that this community had been oversown

"recently", because *Trifolium repens* and *Holcus lanatus* were abundant. Native species present were characteristic of disturbed sites, such as *Deyeuxia avenoides* and *Discaria toumatou*. The three most abundant *Hieracium* species in the data set, *H. lepidulum*, *H. pilosella* and *H. praeltum*, were strongly associated with this group.

(6) Weedy, highly-modified grasslands

Indicator species: *Trifolium arvense, Raoulia australis, Vulpia bromoides, Raoulia beauverdii*

Exotic and annual species were abundant in this highly modified community. Mean elevation for these transects was 825 m, and 93% transects were in pastoral tenure. These include the grasses *Bromus tectorum, B. hordeaceus* and *Vulpia bromoides*, and the herbs *Trifolium arvense* and *Echium vulgare*. Native species in this community were low-growing, including the hardy *Raoulia australis* and the inconspicuous grass *Poa maniototo*. The invasive exotic shrub *Rosa rubiginosa* was in this community.

Pattern in species composition

Results from the detrended correspondence analysis (DCA) for all of the 125 transects at all three times were consistent with the cluster analysis results. The cluster groups clearly separate out on the ordination diagram and the species that are close to sites within each community type are the same as those identified in the indicator species analysis (Figure 3). The gradient length of the first axis was very long (5.9) showing that there was more than complete turnover in species composition from one end of this axis to the other (Table 4). The gradient lengths for the subsequent axes were also long. Eigenvalues for the first ordination axis was high (0.62), showing that there is at least one strong gradient in species composition across these transects; however, the percent variance explained by the axes was low at less than 20% for all four axes. This is likely to be due to the large amount of variability in the data produced by the large number of species and high species turnover. Due to this, for the subsequent analysis of changes in species composition, we limited the analysis to transects that were classified as tussock grasslands (Figure 2). Interestingly, the tenure review process has resulted in a very compositionally

different set of transects being passed over to DoC tenure during the second time period than the first time period (Figure 4).

The DCA of the 194 species occurring in the 103 'tussock grassland' transects showed that there was still a reasonable degree of variation in species composition (Figure 5) and that this was well represented by the first axis of the ordination, which had an eigenvalue of 0.45 and explained about 8% of the variation in species composition (Table 5). This is reasonable given the large number of species and high variation in the dataset; the second and higher axes explained a lot less. The first axis was well-correlated with the environmental data ($r = 0.93$) showing that most of the variation in the dataset can be represented by one strong gradient in species composition. The species-environment correlation for the second axis was also high ($r = 0.78$), showing that although this axis represents a much smaller amount of the variation in species composition, this variation is strongly associated with an environmental gradient. The indirect DCA results show that soil alkalinity, temperature, elevation and precipitation are all correlated with both DCA axis 1 and axis 2 to some degree (Table 6, Figure 5). The centroids for the categorical variables, tenure, burning, and rock type are clustered near the centre of the diagram, but an examination of the correlations between the environmental variables and the site scores on the first two axes shows that tenure and rock type are correlated with DCA axis 2 (Table 6, Figure 5).

Changes in species composition

Most transects did not change to any great degree in species composition. Across both time periods only seven transects changed cluster groups and all of those transects shifted from short-tussock grasslands dominated by natives to short-tussock grasslands dominated by exotic species except one, which shifted from the tall-tussock grasslands with herbaceous inter-tussock species to short-tussock grasslands dominated by exotic species.

The distance that a transect moved between each measurement on the DCA scatterplot of site scores (Figure 6) is the equivalent of the amount that it changed in composition. Between the first and second measurements, the amount that transects changed in species composition was related to property and community type, but not to tenure. A Tukey Honestly Significant Difference Test for multiple comparisons

(Zar 1999) showed that during the first time period, many properties changed in composition in different amounts to each other. Another Tukey test revealed that transects in the short-tussock grasslands with exotic species changed more than transects in all other community types. Importantly, the differences in the amount of compositional change were still significant for both tenure and community type after removing the outlying transect, as well as the outlier in the property variable (Figure 7). During the second time period, the amount that transects changed in composition differed depending on which property they were on (Table 7). However, only one property changed significantly more than two other properties (Figure 7).

Examining the direction that transects moved in ordination space between measurements is a way of understanding the nature of compositional changes that these transects have made over time. The direction that transects changed in composition during the first time period was significantly related to the community type that it was in (Table 8). Both types of short-tussock grasslands tended to move positively on the first axis, and positively on the second axis, towards species composition dominated by *Hieracium pilosella, H. praeltum* and *Agrostis capillaris* (Figure 5). The direction of change in tall-tussock grasslands were less consistent.

The direction that transects changed in composition during the second time period was significantly related to the community type that it was in (Table 8).On three of the 26 properties that tussock grasslands occurred on, all transects moved positively on both the first and second axes, towards composition characterised by exotic species *Hieracium pilosella*, *H. praeltum*, *Anthoxanthum odoratum*, and *Agrostis capillaris* (Figure 6). There was no relationship between community type, property, or tenure and the direction of compositional change for the first time period (Table 8).

Changes in mean quadrat species richness

Mean quadrat species richness declined significantly during the first time period and then increased significantly during the second time period (Table 9, Figure 8). Most transects followed this pattern (Figure 9). Mean quadrat species richness at the third measurement was not significantly different from that at the first measurement, which shows that it had nearly recovered to pre-decline levels at the third measurement (two-sample *t*-test: $t = 0.50$, d.f. = 248, $P = 0.620$, equal variances, Figure 8).

Both native and exotic species declined in mean quadrat species richness during the first time period, and then increased during the second time period (Table 9, Figure 10). Mean quadrat native species richness declined more than mean quadrat exotic species richness during the first time period (two-sample t-test: t = -6.16, d.f. = 239, P < 0.001, unequal variances). However, mean quadrat native species richness then increased more than exotic species richness during the second period (two-sample t-test: t = 6.00, d.f. = 202, P < 0.001, unequal variances). This shows that native species richness has changed more over time than exotic species richness.

Small herbs, large herbs, ferns, and rushes/sedges all declined significantly in mean quadrat species richness during the first time period, and then increased significantly during the second time period. *Hieracium* species increased in mean quadrat species richness during both time periods, but only the increase in *Hieracium* was significant for both periods (Table 9, Figure 10). Change in mean quadrat *Chionochloa* species richness over time was negligible (Table 9, Figure 10). Note that because all *Chionochloa* species were treated as a single species in the analysis, *Chionochloa* spp., richness is actually a measure of *Chionochloa* abundance on transects. Mean perennial quadrat species richness changed more than mean annual quadrat species richness over time (Table 9, Figure 10).

Changes in mean quadrat species richness in relation to tenure

Transects in pastoral tenure had significantly greater mean quadrat species richness than transects in conservation tenure at the first measurement (two-sample t-tests: first measurement: t = 2.37, d.f. = 41, P = 0.022, unequal variances, second measurement: t = 1.98, d.f. = 123, P = 0.050, equal variances, third measurement: t = 1.31, d.f. = 123, P = 0.1941, equal variances, Figure 11).

Changes in mean quadrat species richness were similar on transects in both conservation and pastoral tenure; richness decreased during the first time period, and then increased to pre-decline levels during the second time period regardless of tenure (two-sample t-tests: conservation land: t = -0.62, d.f. = 60, P = 0.536, equal variances; pastoral land: t = 1.04, d.f. = 186, P = 0.300, equal variances, Table 10). During the

second time period mean quadrat exotic species richness increased significantly on conservation tenured transects, but not on pastoral tenured transects (Figure 11).

Significant predictors of species richness change

Results are presented for models for each time period, and models where all 11 environmental variables were added, as well as when they were put in to the model on their own (Tables 12 and 13). Although the changes in mean quadrat species richness differed for each time period, soil alkalinity and rock type were significant predictors of these changes for both periods. Transects with higher soil alkalinity declined more in species richness during each measurement (Figures 13 and 14). Soil fertility was a significant predictor for the first period, and this was replaced by tenure during the second period. Soil alkalinity and soil fertility were both correlated with elevation (Table 3). These variables continued to be significant in the models after the removal of transects with extreme values.

Changes in transect species richness

Total transect species richness declined significantly between the first and second measurements. The increase at the third measurement was not significant (Table 14). Native species declined significantly in total transect species richness during the first period, and increased during the second period. Exotic species richness did not change significantly for either period. Total transect *Hieracium* species richness increased significantly during both periods, but there was no change in total transect *Chionochloa* species richness (Table 14).

Discussion

The large amount of variation in species composition that is encompassed by these 125 was well-characterised by the division of transects into six community groups (Figure 2). The variation in species composition is primarily a reflection of the large environmental variation that is encompassed by these transects, particularly in elevation, which represents temperature, precipitation, and soil conditions.

Elevation was correlated with plant species composition in grasslands in Fiordland between 900 m and 1600 m (Rose et al. 1988), in Central Otago below 460 m (Wilson et al. 1989) and in the Harper-Avoca Valley between 700 m and 1350 m (Rose et al. 1995). Tenure has also been shown to be related to elevation, with

transects at higher elevations being more likely to be in conservation tenure than transects at lower elevations (Walker et al. 2006). However, this is not the case in this data set with all 125 transects nor the 103 transects that were in short- and tall-tussock grassland communities (Figure 12). Species composition was strongly related to elevation because a change in elevation also represents changes in other environmental variables. As elevation increases, the climate in Central Otago becomes wetter and colder (Duncan 1965); there was a strong negative correlation between elevation and temperature on these 125 transects (Table 3). Both temperature and soil moisture are important for determining patterns in species composition in tussock grasslands (Hubbard and Wilson 1988, Partridge et al. 1991, Walker and Lee 2000). Thus, the strong patterns in species composition with changing elevation are likely to be at least partially related to differences in climate.

Soil characteristics are determined by the type of parent material, local climatic conditions, the length of time for soil formation, the level and type of activity by organisms, including plants and other organisms living in the soil, and the local topography, i.e., slope, aspect, elevation, etc. We see that for this dataset that the alkalinity (PCA axis 1) and the fertility (PCA axis 2) of the soils were related to elevation, temperature, and precipitation. These variables will in turn affect the development and characteristics of the soils through determining soil depth (soils tend to get shallower as elevation increases), temperature, which declines with elevation determines the rate of soil formation through influencing the rate of decomposition and other soil-forming processes, precipitation increases leaching; soils with high precipitation are more likely to become leached and acidic over time.

Soil characteristics may also be influenced by land management in certain ways; New Zealand farmers often fertilise their soils with nitrogen, potassium, phosphorus, and by liming. Fertilisation is more likely to occur at lower elevations, where land tends to be easier to access (Walker and Lee 2002, Norton et al. 2006). Thus, all these variables are interrelated in complex ways that represent physical processes, biological processes and human choices in land management. It is therefore difficult to tease out and clearly identify causal processes of vegetation change in these tussock grasslands.

Over the 24 years of this study there was a major fluctuation in species richness that reflects complicated changes in species composition. Given that few

studies have shown increases in species richness in tussock grasslands, sampling artefacts may be responsible for the observed changes, which may lead to a "false increase" in species richness at the third measurement. This could be a result of misidentifying or inconsistently identifying plant species at any measurement time, leading to a different number of species being recorded. Misidentifications or inconsistent identifications are unlikely to have occurred in the present study, as the same botanist was involved in species identification at each measurement time.

In addition, as much as possible, transects were re-measured during the same month that they had been established and measured previously. Not only does this further mitigate the chances of incorrectly inflating or deflating species numbers, it means that species will always be identified by the same characteristics, and the probability of detecting differences between species should stay relatively constant. These methods ensured that sampling artefacts were unlikely to be responsible for the observed changes in species richness.

Overall, most transects did not change substantially in composition over time. Six of the seven transects that moved between community groups were in the short-tussock community dominated by native species, and moved in to the short tussock community dominated by exotic species. This supports the idea that short tussock grasslands are less stable than tall-tussock grasslands (Meurk et al. 2002). However, given that pastoral species such as *Trifolium repens* and *Holcus lanatus* were abundant in the community that transects moved in to, it is likely that these areas were over-sown. *Hieracium pilosella* and *H. praeltum* were also present in this community, but there is insufficient information to be able to make inferences about how management may relate to *Hieracium* abundance. This demonstrates that small-scale management inputs can have relatively large impacts on changes in species composition.

Changes in vegetation in tussock grasslands are often considered to be driven by exotic species (Rose et al. 1995, Walker 2000, Meurk et al. 2002, Rose et al. 2004, Espie and Barratt 2006). For example, exotic species have been found to increase at the expense of native species in the Harper-Avoca Valley, on Flat Top Hill, and in the Mackenzie Country (Rose et al. 1995, Walker 2000, Meurk et al. 2002). However, the changes in species richness and composition in this study are not directly attributable

to changes in exotic species richness in either conservation or tenure (Tables 9 and 11).

More species groups declined in species richness at the small scale than at the large scale (Tables 9 and 14). This is because population turnover is faster at small scales compared to large scales, and therefore species richness fluctuates more over time at small scales (Adler and Lauenroth 2003). In the present study, species richness increased during the second period at both the small and large scales. We are aware of only one other study, which was on Flat Top Hill, that has reported a recent increase in species richness over four years in tussock grasslands (Walker 2000). This is a very short period of time in these communities, and it is difficult to know how strong this trend will be over the long term (Scott et al. 1988, Mark and Dickinson 2003).

Overall, *Chionochloa* species richness was relatively stable (Tables 9 and 14). However, all *Chionochloa* species were pooled and considered as one generic species of *Chionochloa*, which means that this only represents changes in the abundance of all *Chionochloa* species. *Chionochloa* are long-lived and reproduce by mast seeding (i.e. rare, large synchronised seed events, Kelly et al. 1992), so there may have been few opportunities for *Chionochloa* to increase on these transects over the time if environmental conditions were not favourable for reproduction (Mark 1965b, Mark and Dickinson 2003). Furthermore, *Chionochloa* seedlings are highly palatable to sheep and hares, making regeneration by seed difficult where these mammals are present (Mark 1965a, Rose and Platt 1992, Lee et al. 1993). The increase in *Hieracium* species richness at both scales (Tables 9 and 14) is consistent with other studies (e.g. Treskonova 1991, Rose et al. 1998). These results are consistent with the idea that *Hieracium* invades and increases in areas regardless of original species composition or management (Rose et al. 2004).

Woody species have been shown to increase in the absence of grazing in tussock grasslands (Mark and Dickinson 2003). This may be because in the absence of grazing in pre-human New Zealand there were patches of montane vegetation that were characterised by a mixture of grass and shrub species (McGlone 2001). In the present study, of the 121 transects that woody species were present on, transects in conservation tenure increased in mean quadrat woody species richness significantly more than transects in pastoral tenure. However, this was only significant for the first time period (two-sample *t*-tests on change in mean quadrat woody species richness:

first time period: $t = 3.41$, d.f. $= 119$, $P < 0.001$, equal variances, second time period: $t = 0.70$, d.f. $= 119$, $P = 0.488$, equal variances). There is therefore no strong support for the idea that removing grazing will result in a reversion of tussock grasslands to a grassland-shrubland mosaic (Mark and Dickinson 2003); however, the relatively short time scale of this study may not have allowed us to detect such a change.

The effects of land management and tenure

Management factors are important for determining changes in species composition in tussock grasslands (O'Connor 1982, Allen et al. 1995). This is reflected here in that changes in species composition were related to property. Changes in composition at the property level are more likely to be related to management than spatial autocorrelation of environmental factors, because, each land manager has preconceived ideas about the outcomes that they aim to achieve for the land that they administer. In pastoral tenure, this will determine factors such as stocking rates, fertiliser application, burning frequency and which species will be over-sown. This has the result of directing compositional change towards that desired outcome (lessee, personal communication). Even properties within conservation tenure will be managed differently. For example, areas that have higher visitor numbers may have more weed management.

The abundance of exotic species at low elevations is consistent throughout New Zealand's South Island tussock grasslands, which emphasises the importance of management in determining species composition (Wilson et al. 1989, Lloyd et al. 2003). Management is typically more intensive at low elevations, and promotes the establishment and growth of pastorally-productive exotic species (Walker and Lee 2002, Norton et al. 2006). The effects of management on vegetation change will also differ according to the environment (Rose et al. 1995). Therefore, management can influence the environment by changing soil characteristics, and the environment can influence management, by having more favourable climate conditions for pastoral farming at certain elevations. The only way to attribute individual management practices to vegetation change in tussock grasslands is if a detailed management history of each property is known (Diaz et al. 1994), which unfortunately was not the case in this study.

Areas in the high country are subjectively chosen to either stay in pastoral tenure or to be put into conservation tenure based on their original species composition and other aesthetic and cultural values. For example, areas where native species are abundant are more likely to be transferred in to conservation tenure, because they are considered to have "significant inherent values" (Land Information New Zealand March 2003). In the present study, areas that were in pastoral tenure contained fewer native species, but this could be because they were more valuable to keep in pastoral tenure than converting to conservation tenure. In saying this, within this dataset, transects of more diverse species composition were being represented in the conservation estate as more and more properties were going through the tenure review process over time (Figure 4).

Tenure, as recorded in this study, could be thought of as a coarse measure of stock grazing intensity. However, because the initial vegetation within each tenure differed, we cannot draw any firm conclusions about how grazing removal may influence changes in species composition. Specifically, the transects in the DoC estate during the 1990s were of a certain composition, in that *Chionochloa* species and native intertussock species were abundant. However, the transects in pastoral tenure were much more variable in composition. The initial species composition of an area will influence the how composition will change, because there are only seed sources for the species that are already present in an area. This means that changes in composition in the different tenure categories are not directly comparable.

Given that a wider range of species composition will be represented within the DoC estate as more areas go through Tenure Review, in another 15 to 20 years, a comparison of these transects may allow us to directly assess the effects of tenure change on vegetation change. However, we can say from this analysis that in general, transects in conservation tenure did not change in composition or species richness differently from transects in pastoral tenure, which indicates that removing grazing alone may not necessarily enhance native biodiversity (Lord 1990, Norton 2004).

There are two potential reasons that changes in composition and species richness did not differ by tenure. Firstly, in the present study, transects had been in conservation tenure for a mean of 28 years. Mark and Dickinson (2003) also found inconsistent effects after grazing had been removed for 30 years. Considering that plants in tussock grasslands are slow growing (Sewell 1952, Rose and Platt 1992),

and that these areas have been grazed and burned for more than a century, we may expect it to take some time for dynamics in conservation land to become different to those in pastoral land.

Alternatively, changes in composition may not have differed by tenure because the different tenure categories do not represent large differences in management. Some areas in pastoral tenure are not grazed, for example, at high elevations where it is difficult to muster sheep (lessees, personal communication). This makes these areas similar to conservation tenure, in that they are not grazed by domestic stock, and are not actively managed, i.e. no fertiliser, burning or oversowing. In the present study, many of these areas were in the high alpine low-growing and mat-forming species community. At the same time, vegetation in conservation tenure may continue to be browsed by introduced herbivores, such as rabbits and deer (Jensen et al. 1997, personal observation). Over time, browsing by rabbits can have similar impacts to grazing by sheep (Wills and Beggs 1986). In light of this, the different tenure categories may not necessarily represent differences in grazing that are important for changes in plant community structure.

Conclusions

Long term studies with few measurements over large time intervals (e.g. Treskonova 1991, Connor 1992) fail to capture short-term fluctuations that may be occurring in plant community structure. The present study and Walker's (2000) study show that changes in the species richness of tussock grasslands do occur over short time intervals, which gives us a deeper understanding of the dynamics that are occurring in tussock grasslands. Although small changes in composition can occur annually (Allen et al. 1995), large changes in composition appear to take longer. This is due to population processes such as dispersal and colonisation at a landscape scale.

Overall, the changes in the community structure of these tussock grasslands are related to a combination of environmental factors, such as soil chemistry and climate, and management factors. The inconsistent changes that have occurred on these 125 transects over the past 24 years, and the nature and complexity of the variables that explain those changes, make it difficult for us to be able to make any clear predictions about future changes that may occur. However, we can conclude

from this research that of these permanent transects that the conversion of pastoral lease land to conservation tenure has not, so far, had a large impact on changes in plant species composition or species richness in these tussock grasslands. This highlights the importance of continued monitoring of these permanent transects and a range of other High Country sites for many years into the future if we are to obtain a good understanding of the effects of land use on vegetation change.

Acknowledgements

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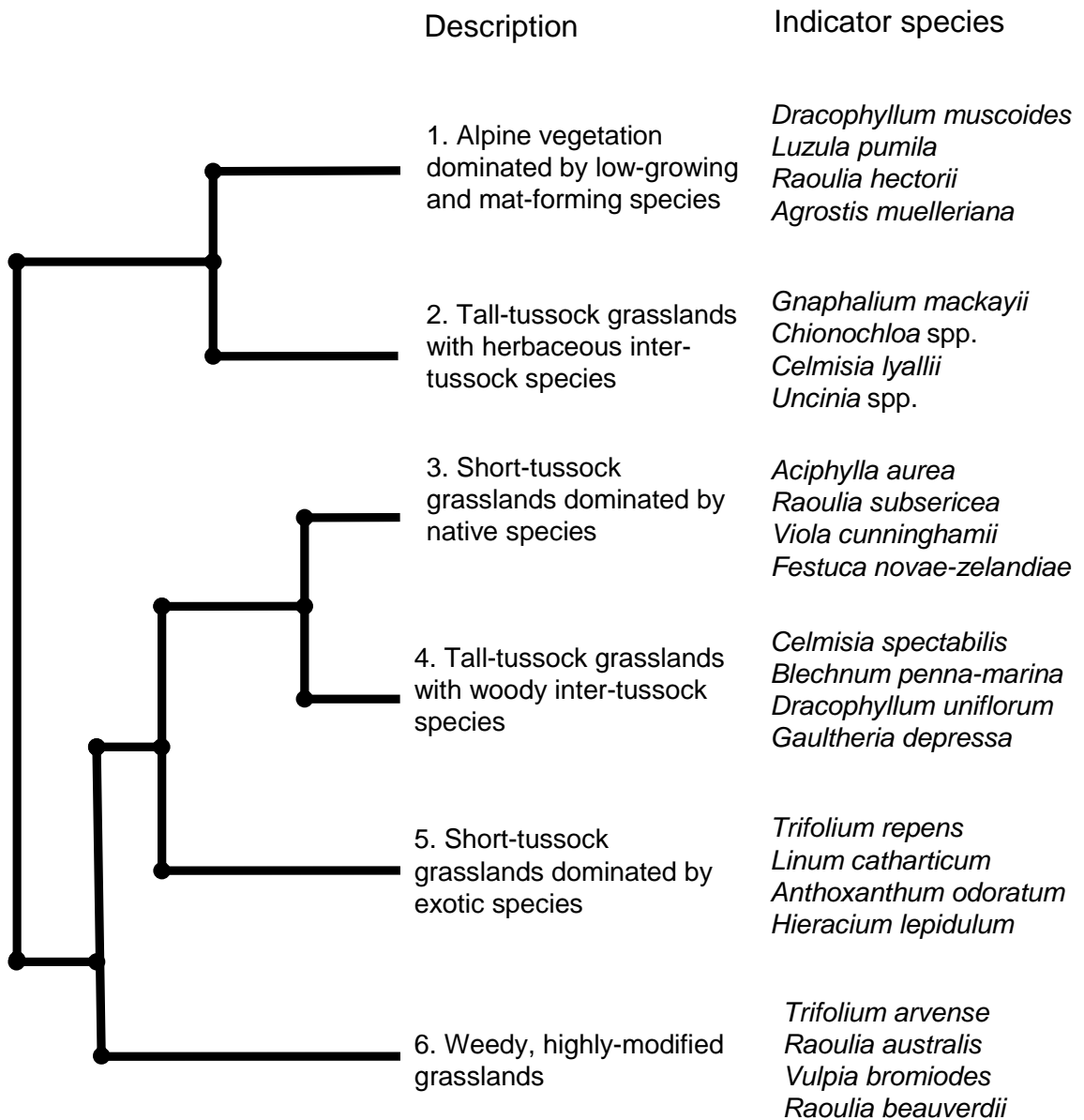
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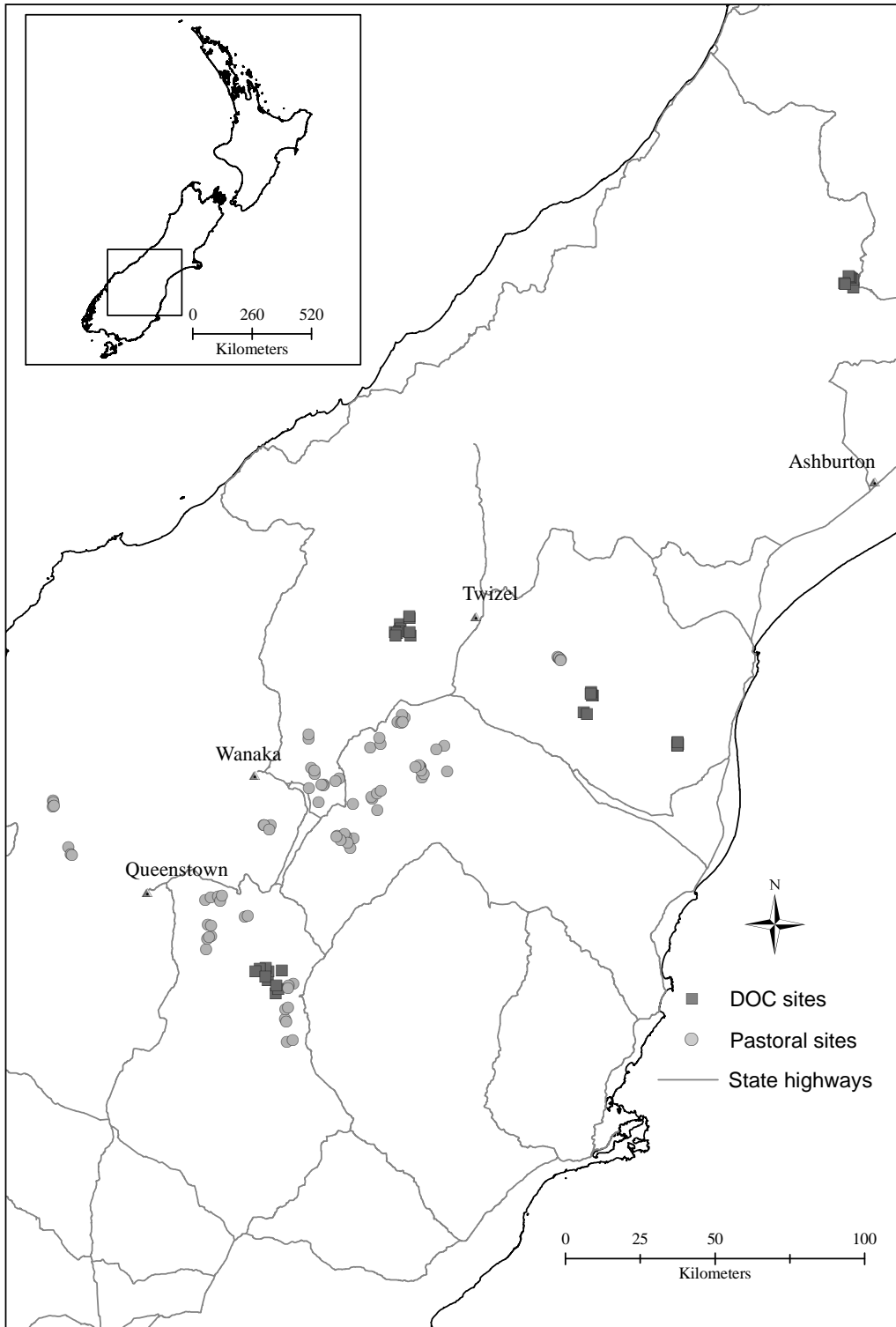
Figure 1: Location of 125 transects in tussock grasslands across Canterbury and Otago, with different symbols for each tenure category.

Description | Indicator species

1. Alpine vegetation dominated by low-growing and mat-forming species

Dracophyllum muscoides
Luzula pumila
Raoulia hectorii
Agrostis muelleriana

2. Tall-tussock grasslands with herbaceous inter-tussock species

Gnaphalium mackayii
Chionochloa spp.
Celmisia lyallii
Uncinia spp.

3. Short-tussock grasslands dominated by native species

Aciphylla aurea
Raoulia subsericea
Viola cunninghamii
Festuca novae-zelandiae

4. Tall-tussock grasslands with woody inter-tussock species

Celmisia spectabilis
Blechnum penna-marina
Dracophyllum uniflorum
Gaultheria depressa

5. Short-tussock grasslands dominated by exotic species

Trifolium repens
Linum catharticum
Anthoxanthum odoratum
Hieracium lepidulum

6. Weedy, highly-modified grasslands

Trifolium arvense
Raoulia australis
Vulpia bromiodes
Raoulia beauverdii

Figure 2: Diagram giving descriptions of the six community types identified by the cluster analysis, the indicator species for each cluster and the relationships among the communities. Photographs of examples for each of these community types are in Appendix II.
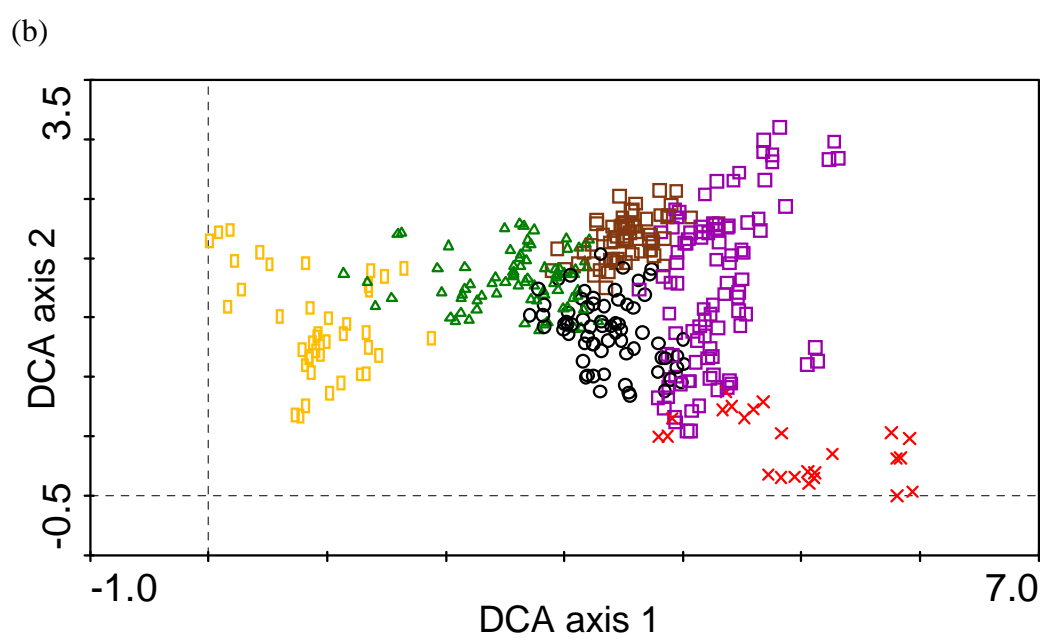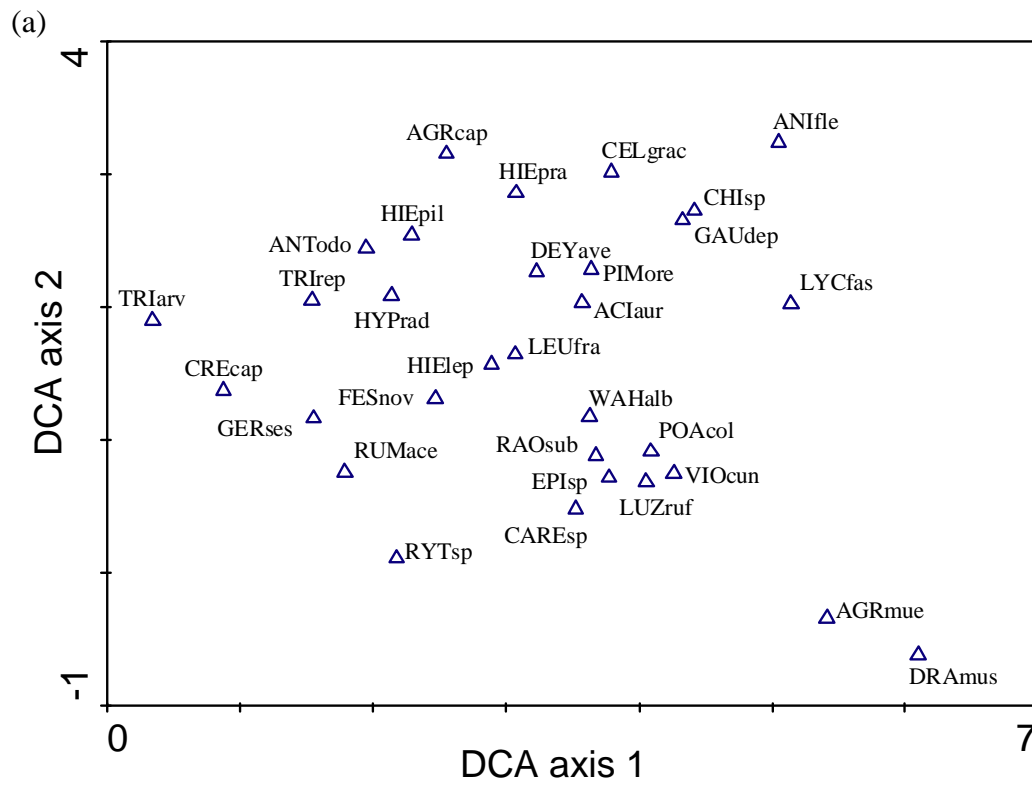
Figure 3: Ordination diagrams from detrended correspondence analysis showing (a) species scores and (b) site scores on DCA axes 1 and 2 for the 194 vascular plant species that occurred at least once in 125 transects across three measurement times. Site scores are labelled by cluster group: alpine vegetation dominated by low-growing and mat-forming species (red crosses), tall-tussock grasslands with woody inter-tussock species (purple squares), tall-tussock grasslands with herbaceous inter-tussock species (brown squares), short-tussock grasslands dominated by native species (black circles), short-tussock grasslands dominated by exotic species (green triangles), ,and weedy, highly-modified grasslands (yellow rectangles). For clarity, only scores for species that had weights higher than 10% are plotted on the ordination diagram. Species that are close together on the graph are likely to occur on the same transect. Sites that are close together are similar in species composition. See appendix I for definition of species codes.
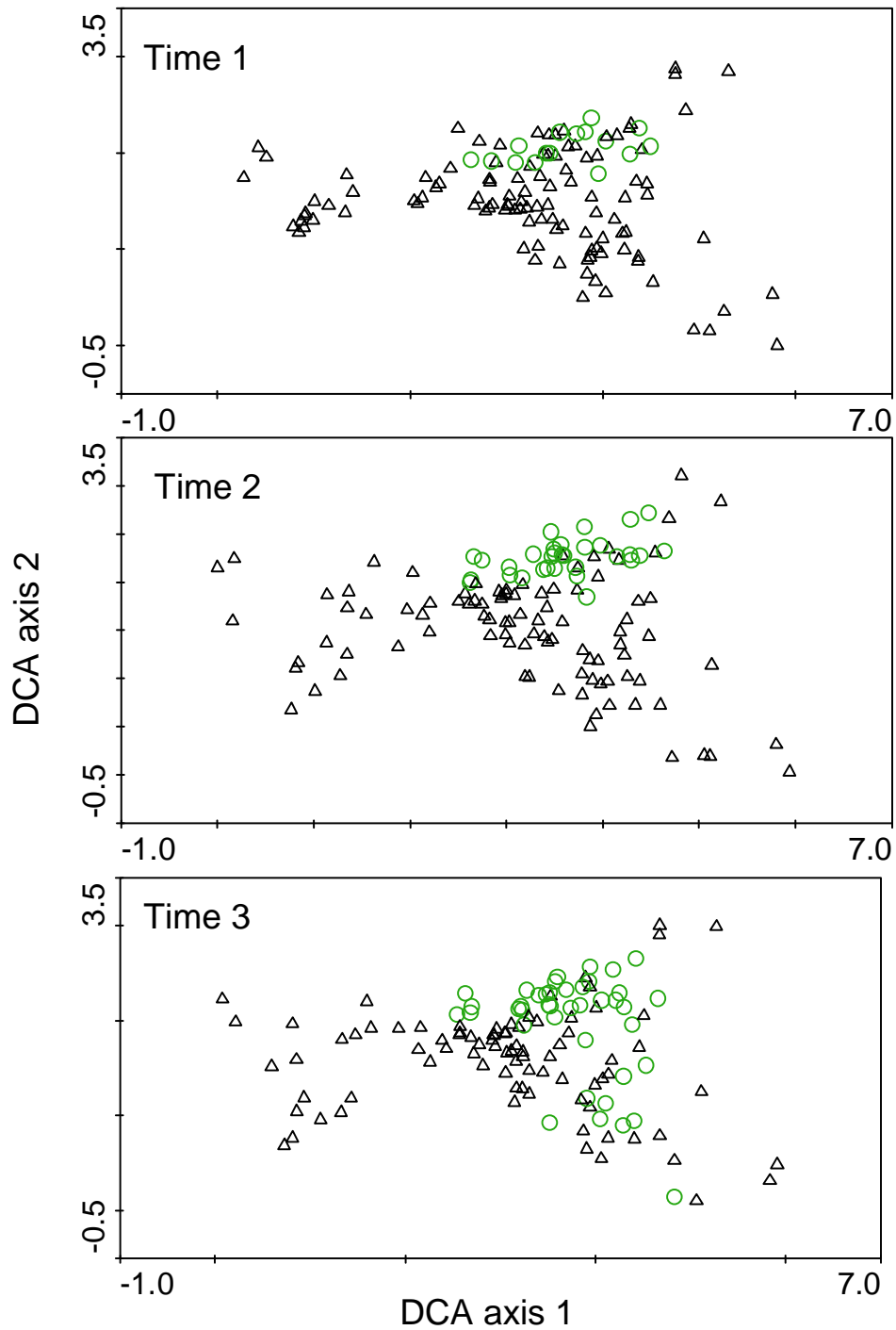
Figure 4: Tenure at each measurement time for 125 transects showing site scores on DCA axes 1 and 2. Sites that are close together are similar in species composition. Green circles represent transects in conservation tenure, black triangles represent transects in pastoral tenure at each measurement.
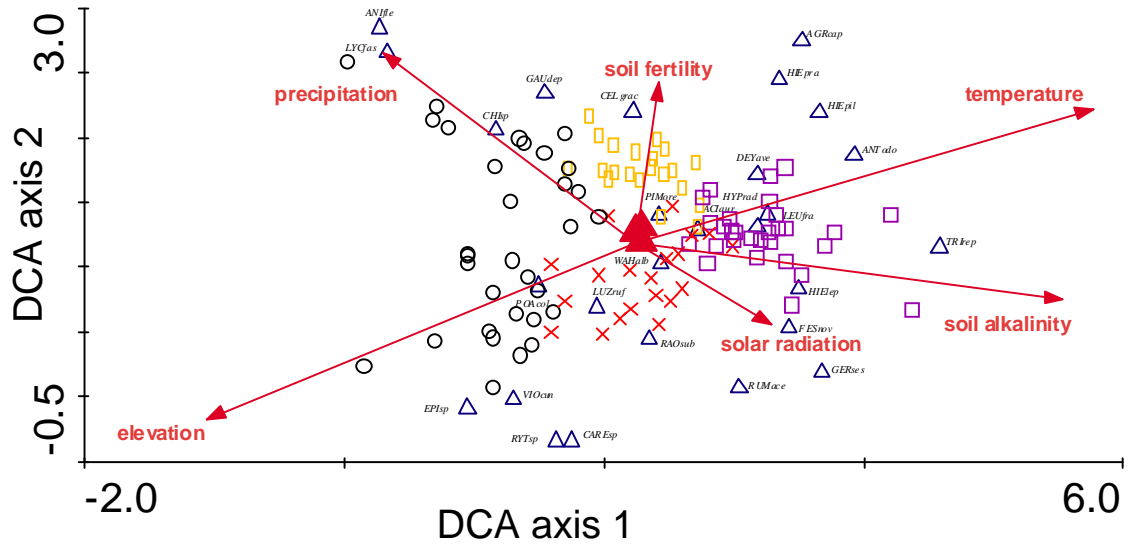
Figure 5: Ordination diagram from detrended correspondence analysis showing species scores, site scores, and environmental variable vectors on DCA axes 1 and 2 for the 194 vascular plant species that occurred at least once in 103 transects across three measurement times. Site scores are labelled by tussock cluster group: Short-tussock grasslands dominated by native species (red crosses), short-tussock grasslands dominated by exotic species (purple squares), tall-tussock grasslands with herbaceous inter-tussock species (black circles), and tall-tussock grasslands with woody inter-tussock species (yellow rectangles). For clarity, only scores for species that had weights higher than 10% were included in the ordination diagram (open blue triangles). The three nominal environmental variables clustered in the centre of the diagram are not labelled for clarity, but are rock type, tenure, and burning (filled red triangles).
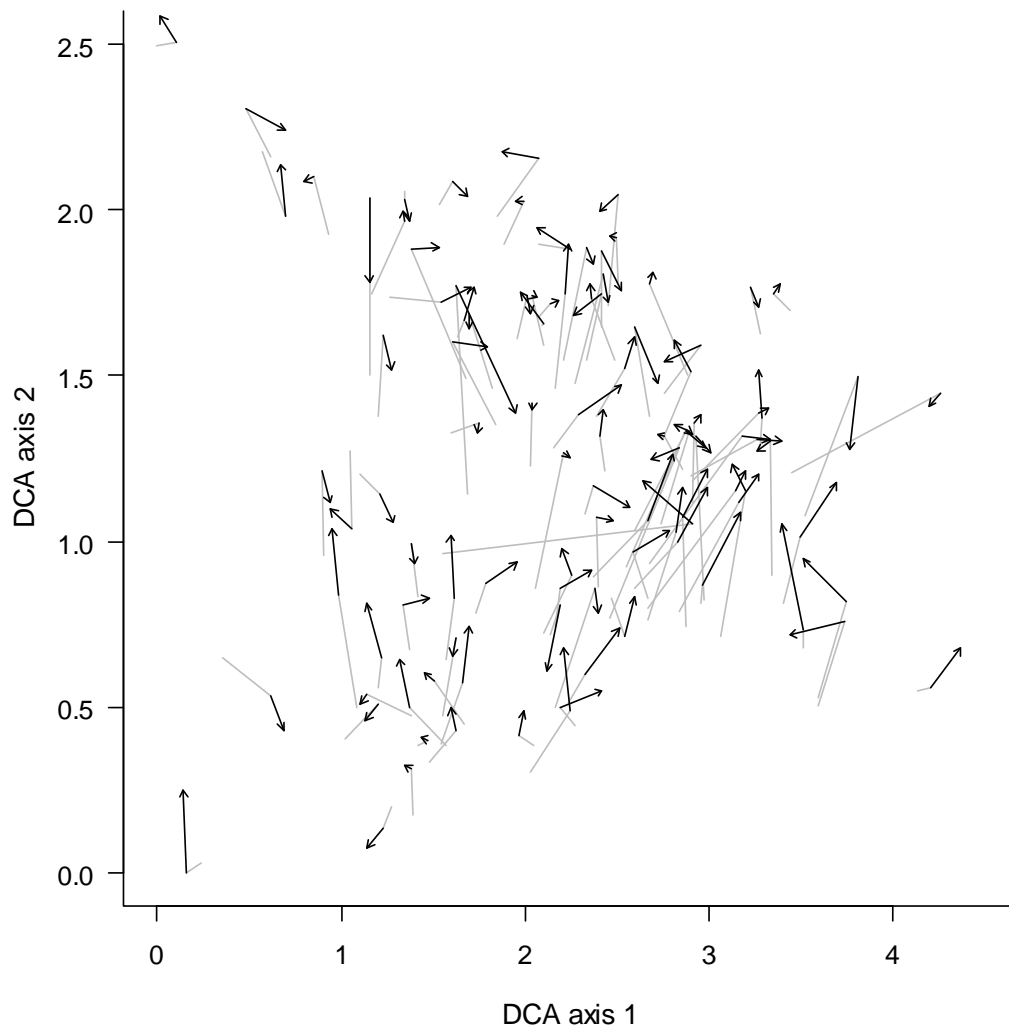
Figure 6: DCA scatterplot for 103 transects in short- and tall-tussock grassland communities showing changes in composition between each of the three measurements. Grey lines represent change in composition on one transect between the first and second measurements, black lines represent changes in composition between the second and third measurements. Each area of the graph is characterised by a certain species composition, so where a transect moves on this graph shows how it has changed in composition over time (see Figure 5).
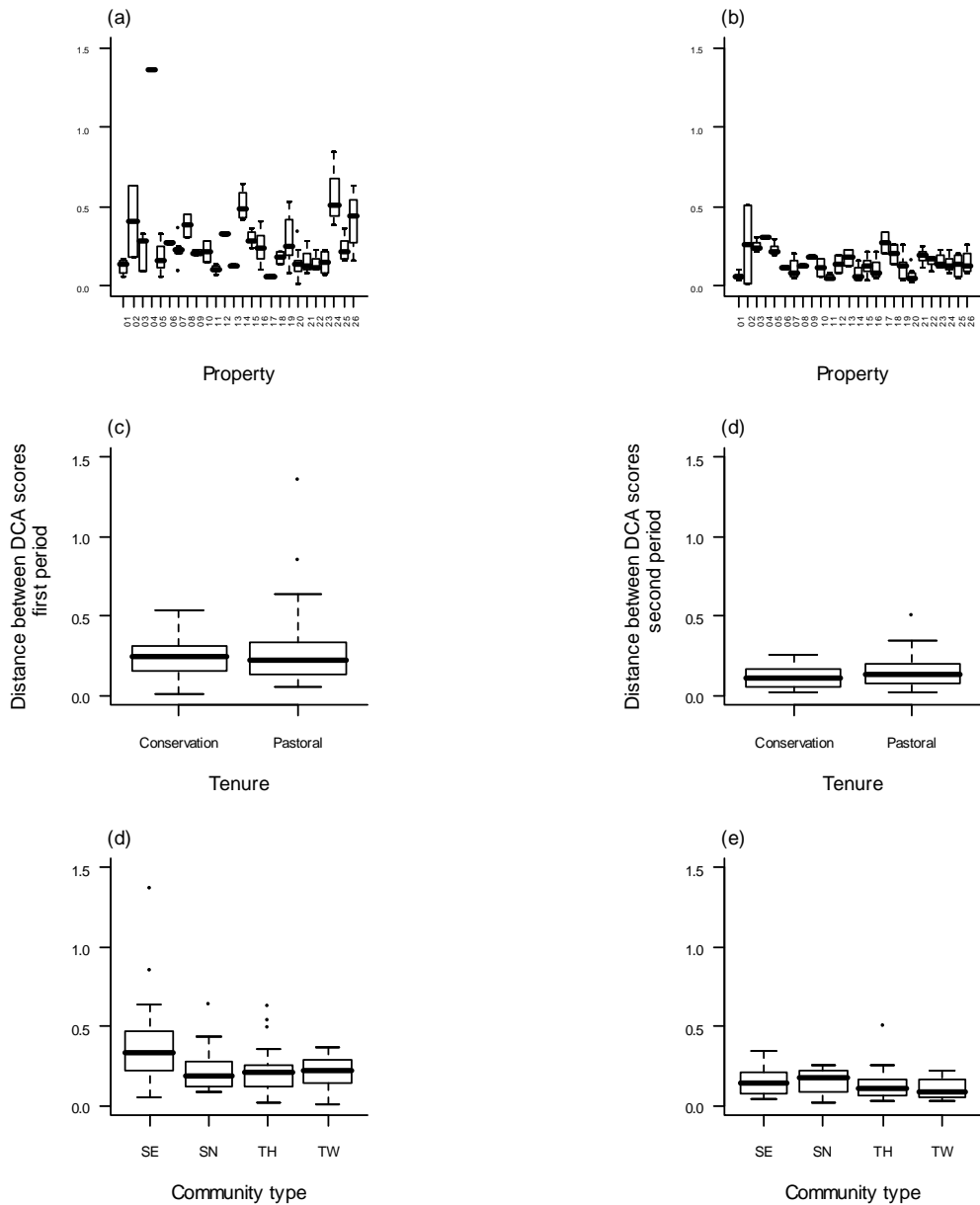
Figure 7: Relationship between the amount of change in species composition during the first period, and then for the second period by property (a, b), tenure (c, d) and community type (e, f). Community types: SE=Short-tussock grasslands dominated by exotic species, SN=Short-tussock grasslands dominated by native species, TH=Tall-tussock grasslands with herbaceous intertussock species, TW=Tall-tussock grasslands with woody intertussock species. See Table 7 for significant differences.
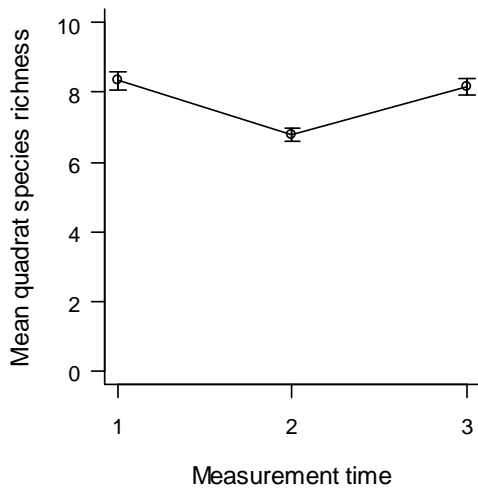
Figure 8: Mean quadrat species richness (± standard error) on 125 transects across the three measurement times. First measurement: 1982-1986, second measurement: 1993-1999, third measurement: 2005-2007. For the results of *t*-tests assessing the significance of changes in species richness between measurement times see Table 9.
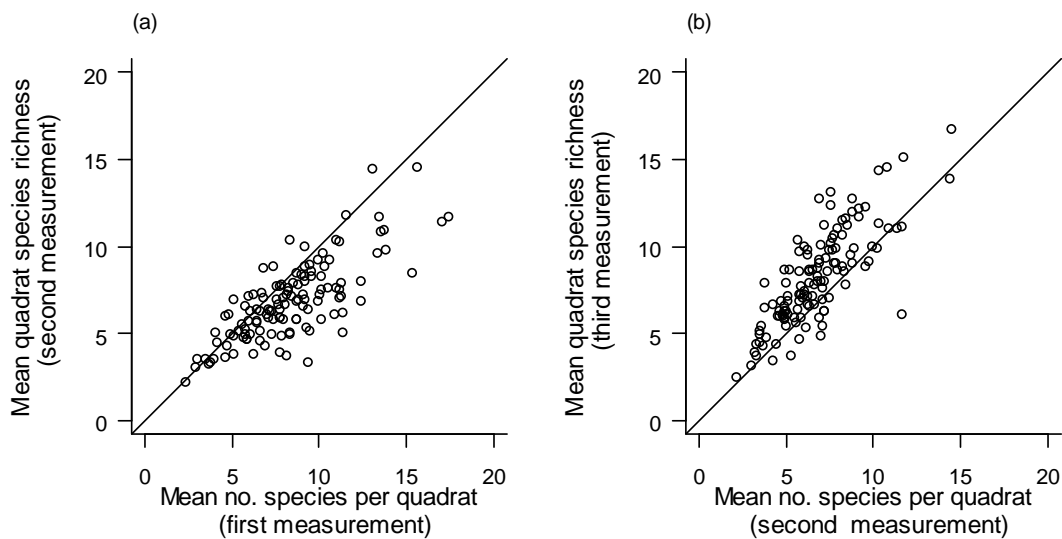
Figure 9: Mean quadrat species richness for 125 transects during the first period (a) and the second period (b). Points below the line are transects that have decreased in mean quadrat species richness between measurements, while those above the line have increased.
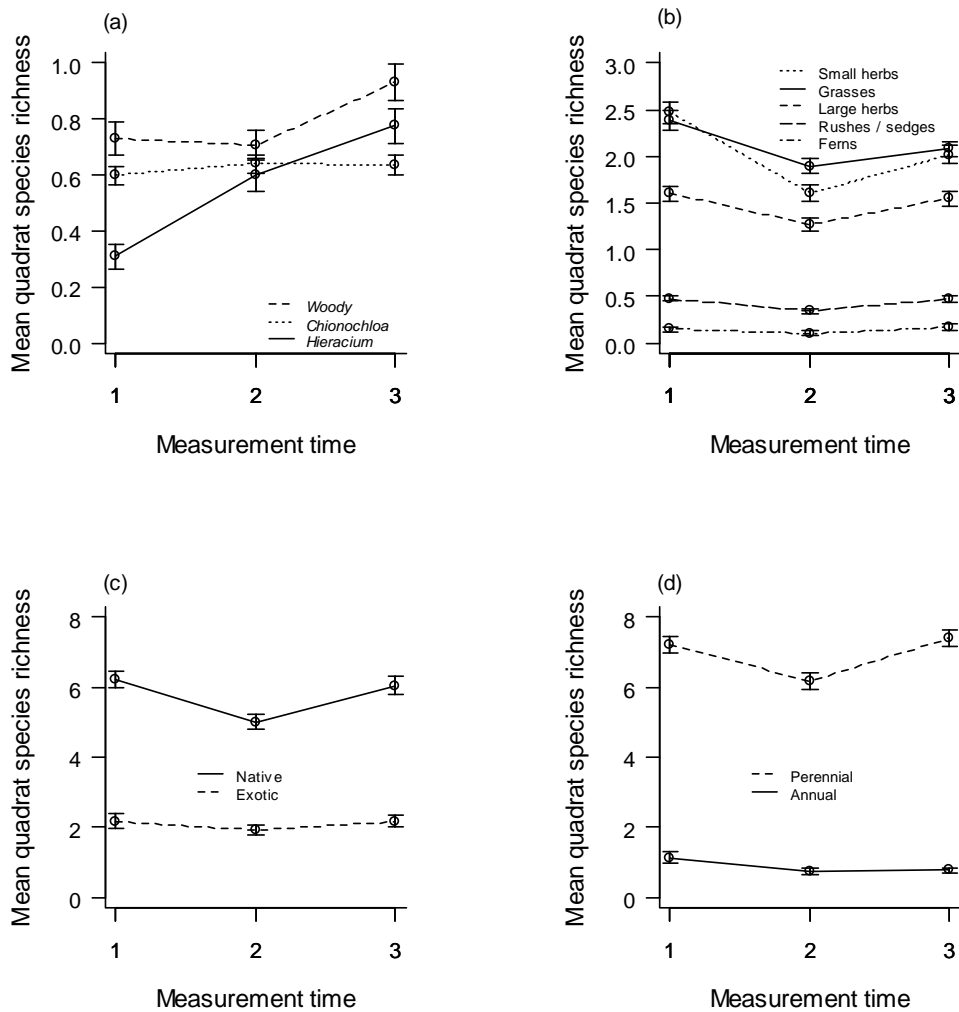
Figure 10: Mean quadrat species richness (± standard error) for each species group at each measurement in 0.25 m² quadrats for 125 transects. First measurement: 1982-1986, second measurement: 1993-1999, third measurement: 2005-2007. *Chionochloa* **species, woody species, and** *Hieracium* **species (a), small herbs, grass species excluding** *Chionochloa***, large herbs, rushes / sedges and ferns (b), species grouped by origin (native and exotic) (c), and by longevity (annual and perennial species) (d). Note that the scales are different. For the results of** *t***-tests assessing the significance of changes in species richness between measurement times see Table 9.**
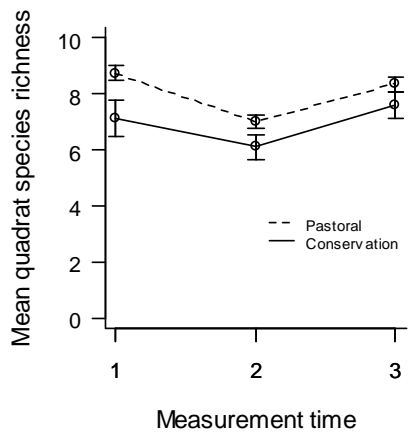
Figure 11: Mean quadrat species richness (± standard error) for each measurement on transects in conservation tenure and in pastoral tenure at the second measurement for 0.25 m² quadrats on 125 transects. For significant differences in changes in mean quadrat species richness see Table 10.
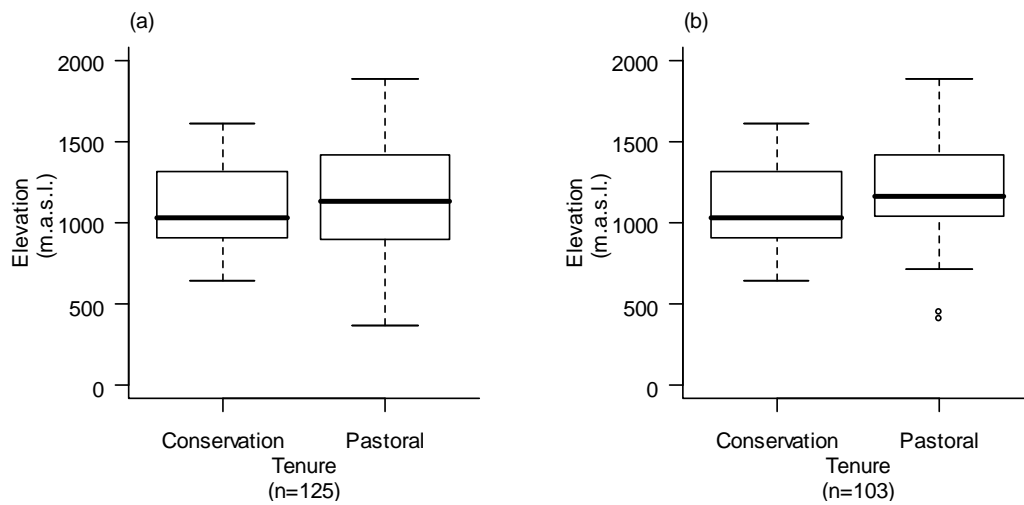
Figure 12: Relationship between tenure at the second measurement and elevation (metres above sea level) for all 125 transects (a) and the 103 transects in the short- and tall-tussock grasslands (b).
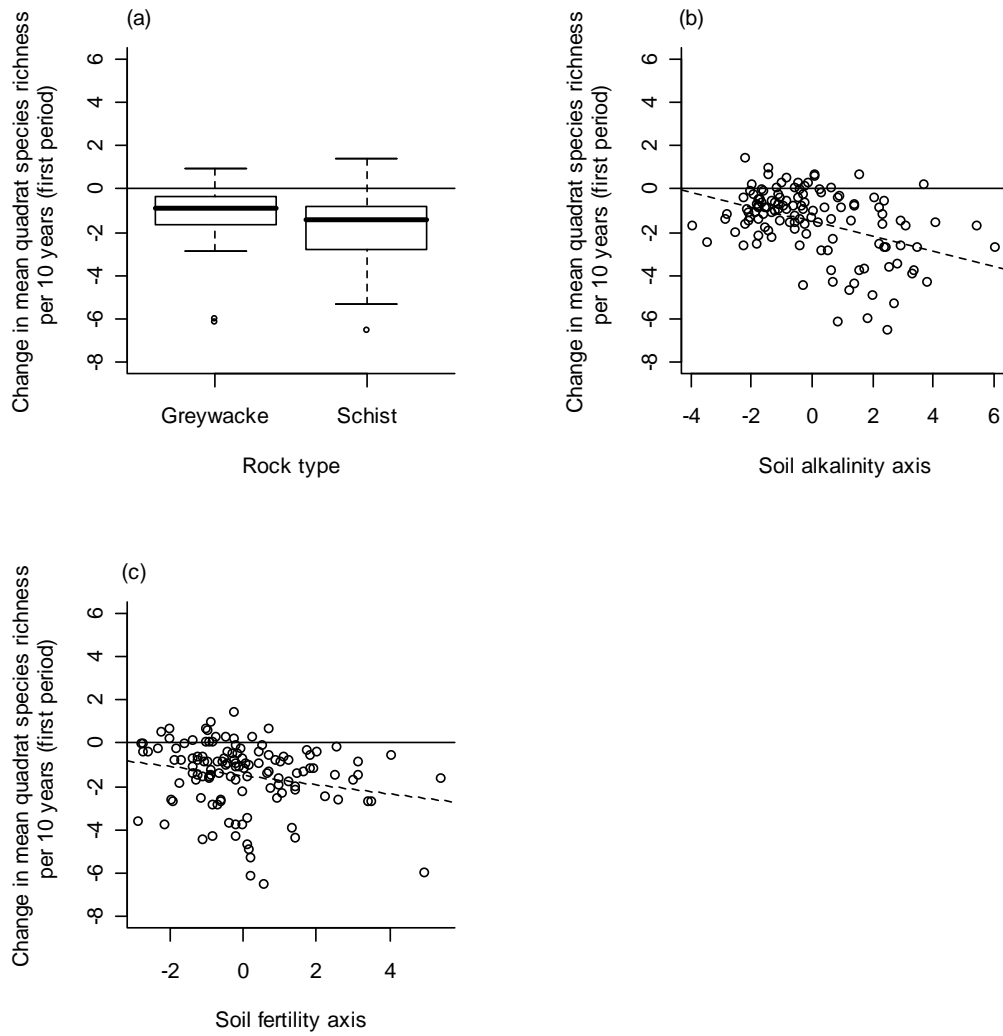
Figure 13: Significant predictors of change in mean quadrat species richness during the first period on 124 transects are rock type (a), soil alkalinity (line of best fit is from linear mixed-effects model including only soil alkalinity) (b), and soil fertility (line of best fit is from linear mixed-effects model including only soil fertility) (c).
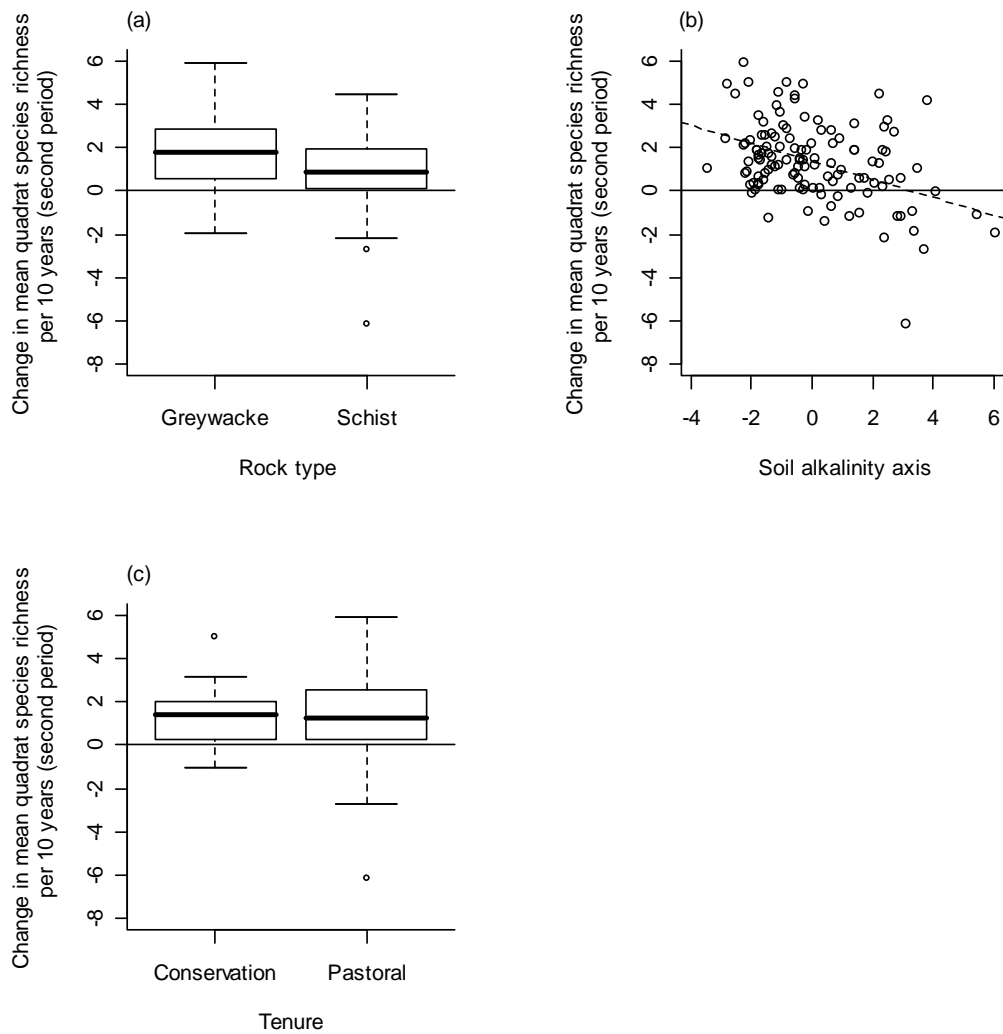
Figure 14: Significant predictors of change in mean quadrat species richness during the second period on 124 transects are rock type (a), soil alkalinity (line of best fit is from linear mixed-effects model including only soil alkalinity) (b), and tenure (at the second measurement) (c).

Table 1: Number of transects in each tenure category at each measurement. First measurement: 1982-1986, second measurement: 1993-1999, third measurement: 2005-2007.

Number of transects in tenure	First measurement	Second measurement	Third measurement
Conservation	16	31	41
Pastoral	109	94	84

Table 2: Results of the principal component analysis (PCA) for the measured soil chemistry variables. Values shown are the loadings of each variable on each of the first two axes.

Variable	PCA axis 1 Soil alkalinity	PCA axis 2 Soil fertility
Base saturation (%)	0.4843	0.1446
pH	0.4768	-0.0872
Calcium (me / 100 g)	0.3763	0.3621
Potassium (me / 100 g)	0.3437	0.3337
Bulk density (gm/ml)	0.3297	-0.4172
Magnesium (me / 100 g)	0.1738	0.3407
Phosphorus (μg / ml)	0.1373	0.1558
Sulphur (Ppm)	-0.0965	0.1147
Sodium (me / 100 g)	-0.2075	0.4007
Cation exchange capacity (me / 100 g)	-0.2612	0.4908
Cumulative percent variance explained	36.2	61.6

Table 3: Pearson correlation coefficient values for correlations between continuous variables. Mean monthly temperature and precipitation are based on 30-year averages.

Variable	Soil alkalinity (PCA axis 1)	Soil fertility (PCA axis 2)	Elevation (m.a.s.l.)	Mean monthly temperature (°C)	Mean monthly precipitation (mm)	Solar radiation (W/m^2)
Soil alkalinity	1.00					
Soil fertility	0.00	1.00				
Elevation	-0.66	-0.08	1.00			
Temperature	0.69	-0.02	-0.94	1.00		
Precipitation	-0.46	0.22	0.34	-0.40	1.00	
Solar radiation	0.41	-0.22	-0.25	0.22	-0.16	1.00

Table 4: Results from detrended correspondence analysis (DCA) for 194 species on 125 transects at three measurements in tussock grasslands. See text for definition of terms.

Axes	1	2	3	4
Eigenvalues	0.62	0.29	0.18	0.15
Lengths of gradient	5.9	3.11	3.38	3.41
Cumulative percentage variance of species data	8.7	12.6	15.1	17.3
Sum of all eigenvalues	7.192			

Table 5: Results from detrended correspondence analysis (DCA) for 194 species on 103 transects in short- and tall-tussock grassland communities at three measurements in tussock grasslands. See text for definition of terms.

Axes	1	2	3	4
Eigenvalues	0.45	0.24	0.15	0.12
Lengths of gradient	4.37	2.59	2.88	1.92
Species-environment correlations	0.93	0.78	0.56	0.50
Cumulative percentage variance of species data	8.1	12.4	15.0	17.3
Sum of all eigenvalues	5.55			

Table 6: Pearson correlation coefficients between environmental variables and the site scores for the first two DCA axes for the short- and tall-tussock grasslands.

Variable	DCA axis 1	DCA axis 2
Mean monthly temperature	0.81	0.23
Soil alkalinity (PCA axis 1)	0.77	-0.14
Elevation	-0.76	-0.31
Mean monthly precipitation	-0.46	0.39
Solar radiation	0.25	-0.17
Burnt between first and second measurements	0.17	0.03
Rock type	0.13	0.69
Soil fertility (PCA axis 2)	0.03	0.31
Tenure at second measurement	-0.02	0.44

Table 7: **Results of analysis of variance tests on the distance between points on the first and second DCA axes, for the short and tall tussock community groups (n = 103).**

Factor	Levels	F statistic of distance	
		First period	Second period
Property	12	7.88 ***	2.60 **
Tenure category	2	0.44 ns	2.74
Community type	4	4.89 **	2.09 ns

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = not significant

Table 8: Results of chi-square tests of independence for direction transect movement on the DCA graph for the short- and tall-tussock community groups (n=103).

Factor	Levels	X^2 statistic for direction	
		First period	Second period
Property	12	80.39 ns	95.10 *
Tenure category	2	0.50 ns	0.98 ns
Community type	4	19.97 *	11.03 ns

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = not significant

Table 9: Results of *t*-tests on the change in mean quadrat species richness per 10 years for 0.25 m^2 quadrats on 125 transects in tussock grasslands in Canterbury and Otago between each measurement.

Species group	First – second measurement		Second – third measurement	
	Change in mean quadrat species richness / 10 yrs Mean ± standard error	*t*-value (n = 125)	Change in mean quadrat species richness / 10 yrs Mean ± standard error	*t*-value (n = 125)
All species	-1.26 ± 0.14	-9.03 ***	1.60 ± 0.18	8.95 ***
Origin				
Native species	-1.04 ± 0.10	-10.27 ***	1.30 ± 0.14	9.18 ***
Exotic species	-0.23 ± 0.09	-2.66 ns	0.31 ± 0.08	3.67 *
Longevity				
Annual species	-0.35 ± 0.07	-4.90 ***	0.05 ± 0.07	0.79 ns
Perennial species	-0.92 ± 0.10	-8.76 ***	1.55 ± 0.15	10.54 ***
Growth form				
Hieracium species	0.23 ± 0.03	7.01 ***	0.20 ± 0.02	8.47 ***
Chionochloa species	0.03 ± 0.01	3.04 *	-0.002 ± 0.01	-0.20 ns
Woody species	-0.02 ± 0.02	-1.29 ns	0.25 ± 0.02	10.54 ***
Grass species (excl. *Chionochloa*)	-0.40 ± 0.05	-8.56 ***	0.21 ± 0.05	3.83 **
Large herb species (>2 cm tall)	-0.27 ± 0.04	-6.17 ***	0.32 ± 0.06	5.14 ***
Small herb species (<2 cm tall)	-0.68 ± 0.07	-10.21 ***	0.49 ± 0.07	7.17 ***
Fern species	-0.03 ± 0.01	-3.55 *	0.08 ± 0.02	3.99 **
Rush / sedge species	-0.11 ± 0.01	-8.14 ***	0.16 ± 0.02	6.46 ***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = not significant, after Bonferroni correction for multiple comparisons.

Table 10: Results of *t*-tests on the change in species richness per 10 years for 0.25 m^2 quadrats on 125 tussock grassland transects in conservation or pastoral tenure in Canterbury and Otago between each measurement. Tests were done using tenure at the second measurement. n = number of transects at the second measurement.

| Tenure | First period | | Second period | |
	Change in mean quadrat species richness / 10 yrs Mean ± standard error	*t*-value	Change in mean quadrat species richness / 10 yrs Mean ± standard error	*t*-value
Conservation (n = 31)	-0.87 ± 0.28	-3.13 **	1.47 ± 0.24	6.07 ***
Pastoral (n = 94)	-1.39 ± 0.16	-8.68 ***	1.65 ± 0.22	7.33 ***

* *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001, ns = not significant, after Bonferroni adjustment for multiple comparisons.

Table 11: Results of *t*-tests on the change in mean quadrat species richness per 10 years on transectss in conservation or pastoral tenure for 0.25 m^2 quadrats in Canterbury and Otago between each measurement.

| | First period | | Second period | |
	Change in mean quadrat species richness / 10 yrs Mean ± standard error	*t*-value	Change in mean quadrat species richness / 10 yrs Mean ± standard error	*t*-value
Conservation tenure				
Native species	-0.79 ± 0.23	-3.40 **	1.31 ± 0.23	5.66 ***
Exotic species	-0.08 ± 0.06	-1.26 ns	0.17 ± 0.06	2.94 *
Pastoral tenure				
Native species	-1.12 ± 0.11	-10.18 ***	1.29 ± 0.17	7.51 ***
Exotic species	-0.27 ± 0.11	-2.48 ns	0.36 ± 0.11	3.23 **

* *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001, ns = not significant, after Bonferroni adjustment for multiple comparisons.

Table 12: Results for mixed-effects model for change in mean quadrat species richness between the first and second measurements. The *F*-value is based on when the variable is added to the model last.

Variable	df	Effect category	n	Estimate in model ± standard error	F	Estimate alone ± standard error	F
Rock type	1	Greywacke	60	0 ± 0	11.74 **	0 ± 0	4.78 *
		Schist	64	-1.39 ± 0.41		-0.83 ± 0.38	
Soil axis 2	1			-0.25 ± 0.09	7.99 **	-0.23 ± 0.09	7.09 **
Soil axis 1	1			-0.25 ± 0.11	5.19 *	-0.35 ± 0.08	20.97 ***
Mean monthly temperature	1			-0.14 ± 0.26	0.28	-0.38 ± 0.08	20.57 ***
Elevation	1			<0.01 ± <0.01	0.28	0.002 ± <0.01	23.35 ***
Mean monthly precipitation	1			-0.01 ± 0.01	0.28	0.01 ± 0.01	1.83
Solar radiation	1			0.001 ± <0.01	0.10	<-0.01 ± <0.01	0.46
Change in mean quadrat *Chionochloa* species richness	2	Decreased	41	0 ± 0	0.81	0 ± 0	2.15
		Increased	52	-0.27 ± 0.28		-0.31 ± 0.29	
		Not present	31	0.15 ± 0.40		-0.78 ± 0.38	
Change in mean quadrat *Hieracium* species richness	2	Decreased	26	0 ± 0	0.62	0 ± 0	1.17
		Increased	81	0.18 ± 0.31		0.36 ± 0.34	
		Not present	17	0.51 ± 0.46		0.73 ± 0.49	
Burnt between first and second measurements	1	Burnt	11	0 ± 0	0.56	0 ± 0	1.22
		Not burnt	113	0.41 ± 0.55		0.70 ± 0.63	
Tenure	1	Conservation	31	0 ± 0	0.25	0 ± 0	1.23
		Pastoral	93	0.25 ± 0.49		-0.57 ± 0.51	

* *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001, ns = not significant, after Bonferroni adjustment for multiple comparisons.

Table 13: Results for mixed-effects model for change in mean quadrat species richness between the second and third measurements. The *F*-value is based on when the variable is added to the model last.

Variable	df	Effect category	n	Estimate in model ± standard error	F	Estimate alone ± standard error	F
Soil axis 1	1			-0.44 ± 0.14	9.39 **	-0.44 ± 0.09	22.56 ***
Tenure	1	Conservation	31	0 ± 0	8.63 **	0 ± 0	<0.001
		Pastoral	93	1.80 ± 0.61		0.02 ± 0.71	
Rock type	1	Greywacke	60	0 ± 0	5.91 *	0 ± 0	5.57 *
		Schist	64	-1.24 ± 0.51		-1.18 ± 0.50	
Soil axis 2	1			0.17 ± 0.11	2.51	0.24 ± 0.11	22.56 ***
Elevation	1			<-0.01 ± <0.01	0.99	0.001 ± 0.001	3.66
Mean monthly precipitation	1			0.02 ± 0.01	3.44	0.03 ± 0.01	16.32 ***
Change in mean quadrat *Chionochloa* species richness	2	Decreased	57	0 ± 0	1.13	0 ± 0	6.87 **
		Increased	36	0.31 ± 0.33		0.39 ± 0.36	
		Not present	31	-0.43 ± 0.46		-1.30 ± 0.42	
Mean monthly temperature	1			-0.11 ± 0.31	0.14	-0.26 ± 0.11	5.54 *
Solar radiation	1			<-0.01 ± <0.01	0.09	-0.01 ± <0.01	4.69 *
Change in mean quadrat *Hieracium* species richness	2	Decreased	16	0 ± 0	2.59	0 ± 0	2.34
		Increased	91	0.05 ± 0.46		0.53 ± 0.46	
		Not present	17	-1.08 ± 0.65		-0.49 ± 0.67	
Burnt between first and second measurements	1	Burnt	11	0 ± 0	0.86	0 ± 0	0.09
		Not burnt	113	0.62 ± 0.67		-0.24 ± 0.80	

* *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001, ns = not significant, after Bonferroni adjustment for multiple comparisons.

Table 14: Results of *t*-tests on the change in total transect species richness per 10 years between each measurement.

Species group	First period		Second period	
	Change in total transect species richness / 10 yrs Mean ± standard error	*t*-value (n = 125)	Change in total transect species richness / 10 yrs Mean ± standard error	*t*-value (n = 125)
All species	-1.65 ± 0.43	-3.81 **	1.37 ± 0.51	2.70
Origin				
Native species	-1.33 ± 0.32	-4.21 ***	1.20 ± 0.41	2.91 *
Exotic species	-0.33 ± 0.22	-1.51	0.13 ± 0.21	0.64
Longevity				
Annual species	-0.52 ± 0.18	-2.97 *	-0.29 ± 0.17	-1.66
Perennial species	-1.14 ± 0.33	-3.48 *	1.62 ± 0.42	3.82 **
Growth form				
Hieracium species	0.46 ± 0.06	7.29 ***	0.40 ± 0.09	4.42 ***
Chionochloa species	-0.004 ± 0.02	-0.24	-0.04 ± 0.03	-1.11
Woody species	0.17 ± 0.08	2.05	0.57 ± 0.11	5.04 ***
Grass species (excl. *Chionochloa*)	-0.57 ± 0.17	-3.39 **	-0.25 ± 0.19	-1.30
Large herb species (>2 cm tall)	-0.18 ± 0.18	-1.00	0.12 ± 0.19	0.62
Small herb species (<2 cm tall)	-1.45 ± 0.18	-7.90 ***	0.50 ± 0.27	1.82
Fern species	-0.02 ± 0.07	-0.32	0.13 ± 0.11	1.28
Rush / sedge species	-0.01 ± 0.05	-0.12	0.07 ± 0.06	1.02

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, ns = not significant, after Bonferroni adjustment for multiple comparisons.

Appendix I: Species codes and full botanical names for the 375 species that were recorded over all three measurement times on all 125 transects. Each species was classified into one of two "origin" classes (native=N, exotic=I), one of two longevity classes (annual=A, perennial=P), and one of eight growth form classes (*Hieracium* spp.=HIE, *Chionochloa* spp.=CHIsp, woody species=S, grasses (excluding *Chionochloa*)=G, small herbs (<2 cm tall)=H1, large herbs (>2 cm tall)=H2, ferns=F, rushes/sedges=R).

Species code	Botanical name	Origin	Longevity	Growth form
ABRcae	*Abrotanella caespitosa*	N	P	H1
ABRinc	*Abrotanella inconspicua*	N	P	H1
ACAagn	*Acaena agnipila*	I	P	H2
ACAbuc	*Acaena buchananii*	N	P	H2
ACAcae	*Acaena caesiiglauca*	N	P	H2
ACAfis	*Acaena fissistipula*	N	P	H1
ACAhor	*Aciphylla horrida*	N	P	H2
ACAine	*Acaena inermis*	N	P	H2
ACAnov	*Acaena novae-zelandiae*	N	P	H2
ACAsac	*Acaena saccaticupula*	N	P	H2
ACAtes	*Acaena tesca*	N	P	H1
ACHmil	*Achillea millefolium*	I	P	H2
ACIaur	*Aciphylla aurea*	N	P	H2
ACIcol	*Aciphylla colensoi*	N	P	H2
ACIhec	*Aciphylla hectori*	N	P	H2
ACIkirk	*Aciphylla kirkii*	N	P	H2
ACIlec	*Aciphylla lecomtei*	N	P	H2
ACIlom	*Aciphylla lomondii*	N	P	H2
ACIlya	*Aciphylla lyallii*	N	P	H2
ACImonr	*Aciphylla monroi*	N	P	H2
ACImont	*Aciphylla montana*	N	P	H2
ACIsim	*Aciphylla similis*	N	P	H2
AGRcap	*Agrostis capillaris*	I	P	G
AGRmue	*Agrostis muelleriana*	N	P	G
AGRmus	*Agrostis muscosa*	N	P	G
AGRpal	*Agrostis pallescens*	N	P	G
AGRper	*Agrostis personata*	N	P	G
AGRpet	*Agrostis petriei*	N	P	G
AIRcar	*Aira caryophyllea*	I	A	G
ANAarv	*Anagallis arvensis*	I	A	H1
ANAbel	*Anaphalioides bellidioides*	N	P	H1
ANEten	*Anemone tenuicaulis*	N	P	H2
ANIaro	*Anisotome aromatica*	N	P	H2
ANIfil	*Anisotome filifolia*	N	P	H2
ANIfle	*Anisotome flexuosa*	N	P	H2
ANIhaa	*Anisotome haastii*	N	P	H2
ANIimb	*Anisotome imbricata*	N	P	H1
ANIlan	*Anisotome lanuginosa*	N	P	H1
ANTodo	*Anthoxanthum odoratum*	I	P	G
APHarv	*Aphanes arvensis*	I	A	H1
AREser	*Arenaria serpyllifolia*	I	A	H1
ARRela	*Arrhenatherum elatius*	I	P	G
ASPflab	*Asplenium flabellifolium*	N	P	F
ASTniv	*Astelia nivicola*	N	P	H2
BLEpen	*Blechnum penna-marina*	N	P	F
BRAbel	*Brachyglottis bellidioides*	N	P	H2

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BRAhaa	*Brachyglottis haastii*	N	P	H2
BRAlon	*Brachyscome longiscapa*	N	P	H1
BRArad	*Brachyscome radicata*	N	P	H1
BRAsinp	*Brachyscome montana*	N	P	H1
BROdia	*Bromus diandrus*	I	A	G
BROhor	*Bromus hordeaceus*	I	A	G
BROtec	*Bromus tectorum*	I	A	G
BULang	*Bulbinella angustifolia*	N	P	H2
CARalp	*Carpha alpina*	N	P	R
CARcur	*Carmichaelia curta*	N	P	S
CAREsp	*Carex species*	N	P	G
CARMkir	*Carmichaelia kirkii*	N	P	S
CARmon	*Carmichaelia monroi*	N	P	S
CARMpet	*Carmichaelia petriei*	N	P	S
CARvex	*Carmichaelia vexillata*	N	P	S
CASful	*Cassinia fulvida*	N	P	S
CELalp	*Celmisia alpina*	N	P	H2
CELang	*Celmisia angustifolia*	N	P	H2
CELbon	*Celmisia bonplandii*	N	P	H2
CELbre	*Celmisia brevifolia*	N	P	H2
CELden	*Celmisia densiflora*	N	P	H2
CELdis	*Celmisia discolor*	N	P	H2
CELdur	*Celmisia du-rietzii*	N	P	H2
CELgla	*Celmisia glandulosa*	N	P	H1
CELgrac	*Celmisia gracilenta*	N	P	H2
CELhaa	*Celmisia haastii*	N	P	H2
CELhec	*Celmisia hectori*	N	P	H2
CELlar	*Celmisia laricifolia*	N	P	H1
CELlya	*Celmisia lyallii*	N	P	H2
CELpetr	*Celmisia petriei*	N	P	H2
CELsem	*Celmisia semicordata*	N	P	H2
CELses	*Celmisia sessiliflora*	N	P	H1
CELsin	*Celmisia sinclairii*	N	P	H2
CELspe	*Celmisia spectabilis*	N	P	H2
CELver	*Celmisia verbascifolia*	N	P	H2
CELves	*Celmisia vespertina*	N	P	H2
CELvis	*Celmisia viscosa*	N	P	H2
CELwal	*Celmisia walkeri*	N	P	H2
CENery	*Centaurium erythraea*	N	A	H2
CERfon	*Cerastium fontanum*	I	P	H2
CERglo	*Cerastium glomeratum*	I	A	H2
CHEfas	*Cheesemania fastigiata*	N	P	H2
CHEsie	*Cheilanthes humilis*	N	P	F
CHIden	*Chionohebe densifolia*	N	P	H1
CHIpul	*Chionohebe pulvinaris*	N	P	H1
CHIsp	*Chionochloa species*	N	P	CHIsp
CHItho	*Chionohebe thomsonii*	N	P	H1
CIRarv	*Cirsium arvense*	I	P	H2
CIRvul	*Cirsium vulgare*	I	A	H2
COLaci	*Colobanthus acicularis*	N	P	H1
COLaff	*Colobanthus affinis*	N	P	H1
COLape	*Colobanthus apetalus*	N	P	H1
COLbre	*Colobanthus brevisepalus*	N	P	H1
COLbuc	*Colobanthus buchananii*	N	P	H1

COLstr	*Colobanthus strictus*	N	P	H1
CONver	*Convolvulus verecundus*	N	P	H2
COPatr	*Coprosma atropurpurea*	N	P	S
COPche	*Coprosma cheesmanii*	N	P	S
COPnip	*Coprosma niphophila*	N	P	S
COPper	*Coprosma perpusilla*	N	P	S
COPpet	*Coprosma petriei*	N	P	S
CORcra	*Corallospartium crassicaule*	N	P	S
CORplu	*Coriaria plumosa*	N	P	H2
CRAsie	*Crassula sieberiana*	N	P	H2
CRAspp	*Craspedia* species	N	P	H2
CRAtet	*Crassula tetramera*	N	A	H2
CREcap	*Crepis capillaris*	I	A	H2
CYAdea	*Cyathodes dealbata*	I	P	S
CYNcri	*Cynosurus cristatus*	I	P	G
DACglo	*Dactylis glomerata*	I	P	G
DEScha	*Deschampsia chapmanii*	N	P	R
DESnov	*Deschampsia novae-zelandiae*	N	P	G
DEYave	*Deyeuxia avenoides*	N	A	G
DIAarm	*Dianthus armeria*	I	A	H2
DICcri	*Dichelachne crinita*	N	A	G
DICrep	*Dichondra repens*	N	P	H1
DIStou	*Discaria toumatou*	N	P	S
DOLlya	*Dolichoglottis lyallii*	N	P	H2
DOLsco	*Dolichoglottis scorzoneroides*	N	P	H2
DRAace	*Dracophyllum acerosum*	N	P	S
DRAlon	*Dracophyllum longifolium*	N	P	S
DRAmus	*Dracophyllum muscoides*	N	P	S
DRApol	*Dracophyllum politum*	N	P	S
DRApron	*Dracophyllum pronum*	N	P	S
DRAuni	*Dracophyllum uniflorum*	N	P	S
DROarc	*Drosera arcturi*	N	P	H1
ECHvul	*Echium vulgare*	I	A	H2
ELYrec	*Elymus rectisetus*	N	A	G
ELYsol	*Elymus solandri*	N	A	G
EPIsp	*Epilobium* species	N	A	H1
EROcic	*Erodium cicutarium*	I	A	H1
EROver	*Erophila verna*	I	A	H1
EUCrua	*Euchiton ruahinicum*	N	P	H2
EUPsp	*Euphrasia* species	N	P	H1
FESmad	*Festuca madida*	N	P	G
FESmat	*Festuca matthewsii*	N	P	G
FESmul	*Festuca multinodis*	N	P	G
FESnov	*Festuca novae-zelandiae*	N	P	G
FESrub	*Festuca rubra*	N	P	G
FESten	*Festuca tenuifolia*	I	P	G
FORsed	*Forstera sedifolia*	N	P	H2
GAIset	*Gaimardia setacea*	N	P	R
GALper	*Galium perpusillum*	N	P	H2
GAUcra	*Gaultheria crassa*	N	P	S
GAUdep	*Gaultheria depressa*	N	P	S
GAUmac	*Gaultheria macrostigma*	N	P	S
GAUnub	*Gaultheria nubicola*	N	P	S
GENama	*Gentiana amabilis*	N	P	H2

GENbell	*Gentiana bellidifolia*	N	P	H2
GENcor	*Gentiana corymbifera*	N	P	H2
GENdiv	*Gentiana divisa*	N	P	H2
GENmon	*Gentiana montana*	N	P	H2
GENser	*Gentiana serotina*	N	P	H2
GERmic	*Geranium microphyllum*	N	P	H1
GERses	*Geranium sessiliflorum*	N	P	H1
GEUlei	*Geum leiospermum*	N	P	H1
GEUpar	*Geum parviflorum*	N	P	H2
GINdec	*Gingidia decipiens*	N	P	H2
GNAaux	*Gnaphalium audax*	N	P	H2
GNAlat	*Gnaphalium laterale*	N	P	H1
GNAlut	*Gnaphalium luteo-album*	N	P	H2
GNAmac	*Gnaphalium mackayi*	N	P	H1
GONagg	*Gonocarpus aggregatus*	N	P	H2
GONmic	*Gonocarpus micranthus*	N	P	H2
GONmon	*Gonocarpus montanus*	N	P	H2
GRAgiv	*Grammitis givenii*	N	P	F
HEBbuc	*Hebe buchananii*	N	P	S
HEBhaa	*Hebe haastii*	N	P	S
HEBhec	*Hebe hectori*	N	P	S
HEBlyc	*Hebe lycopodioides*	N	P	S
HEBodo	*Hebe odora*	N	P	S
HEBtet	*Hebe tetrasticha*	N	P	S
HECcae	*Hectorella caespitosa*	N	P	H1
HELfil	*Helichrysum filicaule*	N	P	H2
HELplu	*Helichrysum plumeum*	N	P	S
HIEaur	*Hieracium aurantiacum*	I	P	HIE
HIEcae	*Hieracium caespitosum*	I	P	HIE
HIEequ	*Hierochloe equiseta*	N	P	G
HIElep	*Hieracium lepidulum*	I	P	HIE
HIEnov	*Hierochloe novae-zelandiae*	N	P	G
HIEpil	*Hieracium pilosella*	I	P	HIE
HIEpra	*Hieracium praealtum*	I	P	HIE
HIErec	*Hierochloe recurvata*	N	P	G
HOLlan	*Holcus lanatus*	I	P	G
HYDmon	*Hydrocotyle montana*	N	P	H1
HYDnov	*Hydrocotyle novae-zelandiae*	N	P	H1
HYMvil	*Hymenophyllum villosum*	N	P	F
HYPgra	*Hypericum gramineum*	I	A	H2
HYPmil	*Hypolepis millefolium*	N	P	F
HYPper	*Hypericum perforatum*	I	A	H2
HYPrad	*Hypochoeris radicata*	I	P	H1
ISOauk	*Isolepis aucklandica*	N	P	R
JUNant	*Juncus antarticus*	N	P	R
JUNpus	*Juncus pusillus*	I	P	R
KELchi	*Kelleria childii*	N	P	H1
KELdie	*Kelleria dieffenbachii*	N	P	H1
KELpad	*Kelleria padulosa*	N	P	H1
KELvil	*Kelleria villosa*	N	P	H1
KOEnov	*Koeleria novae-zelandiae*	N	P	G
KOEshe	*Koeleria cheesemanii*	N	A	G
KRInov	*Kirkianella novae-zelandiae*	N	P	H1
KUNeri	*Kunzea ericoides*	N	P	S

LACfil	*Lachnagrostis filiformis*	N	A	G
LAClya	*Lachnagrostis lyallii*	N	P	G
LAGcun	*Lagenifera cuneata*	N	P	H1
LAGpet	*Lagenifera petiolata*	N	P	H1
LEPalb	*Leptinella albida*	N	P	H1
LEPatr	*Leptinella atrata*	N	P	H1
LEPgoy	*Leptinella goyenii*	N	P	H1
LEPpec	*Leptinella pectinata*	N	P	H1
LEPpus	*Leptinella pusilla*	N	P	H1
LEPsco	*Leptospermum scoparium*	N	P	S
LEPser	*Leptinella serrulata*	N	P	H1
LEPsqu	*Leptinella squalida*	N	P	H1
LEUcol	*Leucopogon colensoi*	N	P	S
LEUfra	*Leucopogon fraseri*	N	P	S
LEUgra	*Leucogenes grandiceps*	N	P	H2
LINcat	*Linum catharticum*	I	A	H2
LOBlin	*Lobelia linnaeoides*	N	P	H1
LOLper	*Lolium perenne*	I	P	G
LOTped	*Lotus pedunculatus*	I	P	H2
LUZlep	*Luzula leptophylla*	N	P	R
LUZpum	*Luzula pumila*	N	P	R
LUZruf	*Luzula rufa*	N	P	R
LUZulo	*Luzula ulophylla*	N	P	R
LYCaus	*Lycopodium australianum*	N	P	H2
LYCfas	*Lycopodium fastigiatum*	N	P	H2
LYCsca	*Lycopodium scariosum*	N	P	H2
MARgra	*Marsippospermum gracile*	N	P	R
MARvul	*Marrubium vulgare*	I	P	H2
MELalp	*Melicytus alpinus*	N	P	S
MENcun	*Mentha cunninghamii*	N	P	H2
MICsca	*Microseris scapigera*	N	P	H2
MICuni	*Microtis unifolia*	N	P	H2
MONfon	*Montia fontana*	N	P	H1
MRYnum	*Myrsine nummularia*	N	P	S
MUEaxi	*Muehlenbeckia axillaris*	N	P	S
MUEcom	*Muehlenbeckia complexa*	N	P	S
MYOdis	*Myosotis discolor*	I	A	H2
MYOdru	*Myosotis pygmaea var drucei*	N	P	H1
MYOpul	*Myosotis pulvinaris*	N	P	H1
MYOpyg	*Myosotis pygmaea*	N	P	H1
MYOstr	*Myosotis stricta*	I	A	H1
NAVsqu	*Navarettia squarrosa*	I	A	H2
NEOaus	*Neopaxia australasica*	N	P	H1
NERbal	*Nertera balfouriana*	N	P	H1
NERset	*Nertera setulosa*	N	P	H1
OLEodo	*Olearia odorata*	N	P	S
OPHcor	*Ophioglossum coriaceum*	N	P	H1
OREpec	*Oreobolus pectinatus*	N	P	R
OREsp	*Oreomyrrhis* species	N	P	H2
OREsub	*Oreostylidium subulatum*	N	P	H1
OROmin	*Orobanche minor*	I	P	H2
OURcae	*Ourisia caespitosa*	N	P	H1
OURgla	*Ourisia glandulosa*	N	P	H1
OURses	*Ourisia sessilifolia*	N	P	H1

OURsim	*Ourisia simpsonii*	N	P	H2
OXAexi	*Oxalis exilis*	N	P	H1
OXAlac	*Oxalis lactea*	N	P	H1
OZOlep	*Ozothamnus leptophyllus*	N	P	S
PACsp	*Pachycladon* species	N	P	H2
PENpum	*Pentachondra pumila*	N	P	H1
PHOcoo	*Phormium cookianum*	N	P	H2
PHYsp	*Phyllachne* species	N	P	H1
PIMore	*Pimelea oreophila*	N	P	S
PIMpse	*Pimelea pseudo-lyallii*	N	P	S
PIMtra	*Pimelea traversii*	N	P	S
PLAsp	*Plantago* species	N	P	H1
POAann	*Poa annua*	I	P	G
POAbre	*Poa breviglumis*	N	P	G
POAcit	*Poa cita*	N	P	G
POAcol	*Poa colensoi*	N	P	G
POAint	*Poa intrusa*	N	P	G
POAkir	*Poa kirkii*	N	P	G
POAlin	*Poa lindsayi*	N	A	G
POAman	*Poa maniototo*	N	P	G
POApra	*Poa pratensis*	I	P	G
POApyg	*Poa pygmaea*	N	P	G
POAton	*Poa tonsa*	N	P	G
PODniv	*Podocarpus nivalis*	N	P	S
POLves	*Polystichum vestitum*	N	P	F
PRAang	*Pratia angulata*	N	P	H1
PRAcol	*Prasophyllum colensoi*	N	P	H2
PRAmac	*Pratia macrodon*	N	P	H1
PRUvul	*Prunella vulgaris*	I	P	H2
PSYnov	*Psychrophila novae-zelandiae*	N	P	H1
PSYobt	*Psychrophila obtusa*	N	P	H1
PTEcyc	*Pterostylis cycnocephala*	N	P	H1
PTEesc	*Pteridium esculentum*	N	P	F
PTEmut	*Pterostylis mutica*	N	P	H1
PTEven	*Pterostylis venosa*	N	P	H2
RANeny	*Ranunculus enysii*	N	P	H1
RANfol	*Ranunculus foliosus*	N	P	H1
RANgra	*Ranunculus gracilipes*	N	P	H1
RANmac	*Ranunculus maculatus*	N	P	H1
RANmul	*Ranunculus multiscapus*	N	P	H1
RANroy	*Ranunculus royi*	N	P	H1
RAOaus	*Raoulia australis*	N	P	H1
RAObea	*Raoulia beauverdii*	N	P	H1
RAOexi	*Raoulia eximia*	N	P	H1
RAOgra	*Raoulia grandiflora*	N	P	H1
RAOhec	*Raoulia hectorii*	N	P	H1
RAOhoo	*Raoulia hookeri*	N	P	H1
RAOpar	*Raoulia parkii*	N	P	H1
RAOsub	*Raoulia subsericea*	N	P	H1
RAOten	*Raoulia tenuicaulis*	N	P	H1
ROSgra	*Rostkovia magellanica*	N	P	R
ROSrub	*Rosa rubiginosa*	I	P	S
RUMace	*Rumex acetosella*	I	P	H1
RUMobt	*Rumex obtusifolius*	I	P	H2

| RYTsp	*Rytidosperma* species	N	P	G
SCHcoc	*Schizeilema cockaynei*	N	P	H1
SCHcya	*Schizeilema haastii var cyanopeta*	N	P	H2
SCHexi	*Schizeilema exiguum*	N	P	H1
SCHhyd	*Schizeilema hydrocotyloides*	N	P	H1
SCHpau	*Schoenus pauciflorus*	N	P	R
SCLbro	*Scleranthus brockiei*	N	P	H1
SCLuni	*Scleranthus uniflorus*	N	P	H1
SEDacr	*Sedum acre*	I	P	H1
SENsp	*Senecio* species	N	P	H2
SILcon	*Silene conica*	I	A	H2
SILgal	*Silene gallica*	I	A	H2
SPErub	*Spergularia rubra*	I	A	H1
STAmin	*Stackhousia minima*	N	P	H1
STEgrac	*Stellaria gracilenta*	N	P	H1
STEpar	*Stellaria parviflora*	N	P	H2
TARmag	*Taraxacum magellanicum*	N	P	H2
TARoff	*Taraxacum officinale*	I	P	H2
THElon	*Thelymitra longifolia*	N	P	H2
THYvul	*Thymus vulgaris*	I	P	S
TRIarv	*Trifolium arvense*	I	A	H2
TRIdub	*Trifolium dubium*	I	A	H1
TRIglo	*Trifolium glomeratum*	I	A	H2
TRIhyb	*Trifolium hybridum*	I	P	H2
TRIpra	*Trifolium pratense*	I	P	H2
TRIrep	*Trifolium repens*	I	P	H2
TRIspi	*Trisetum spicatum*	N	P	G
UNCsp	*Uncinia* species	N	P	R
URTure	*Urtica urens*	N	A	H2
UTRmon	*Utricularia monanthos*	N	A	H1
VERarv	*Veronica arvensis*	I	A	H2
VERser	*Veronica serpyllifolia*	I	A	H2
VERtha	*Verbascum thapsus*	I	A	H2
VERvir	*Verbascum virgatum*	I	A	H2
VICsat	*Vicia sativa*	I	P	H2
VIOcun	*Viola cunninghamii*	N	P	H2
VITaus	*Vittadinia australis*	N	P	H2
VULbro	*Vulpia bromoides*	I	A	G
WAHalb	*Wahlenbergia albomarginata*	N	P	H1
WAHgra	*Wahlenbergia gracilis*	N	P	H1

Appendix II: Examples of each cluster group at each measurement time.
1) Alpine vegetation dominated by low-growing and mat-forming species

First measurement
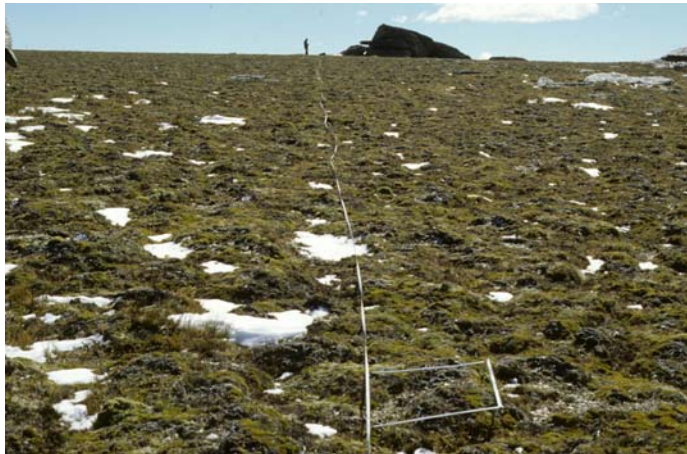
Second measurement
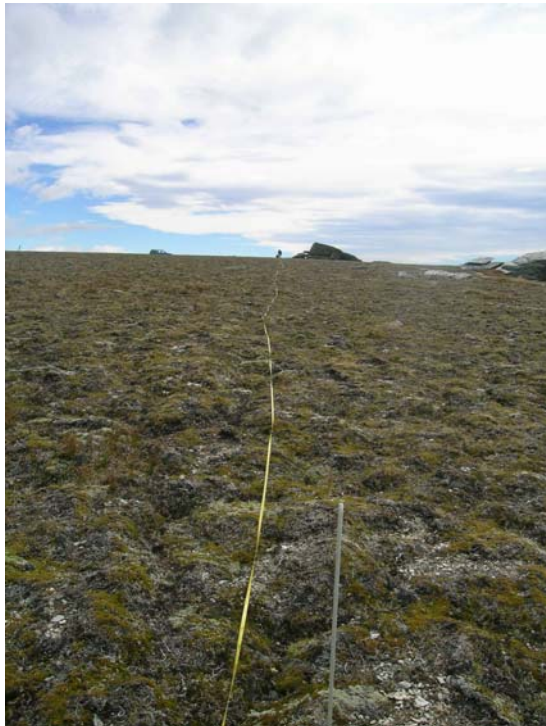
Third measurement

2) Short-tussock grasslands dominated by native species

First measurement

Second measurement

Third measurement

3) Tall-tussock grasslands with herbaceous inter-tussock species

First measurement

Second measurement

Third measurement

4) Tall-tussock grasslands with woody intertussock species

First measurement

Second measurement

Third measurement

5) Short-tussock grasslands dominated by exotic species

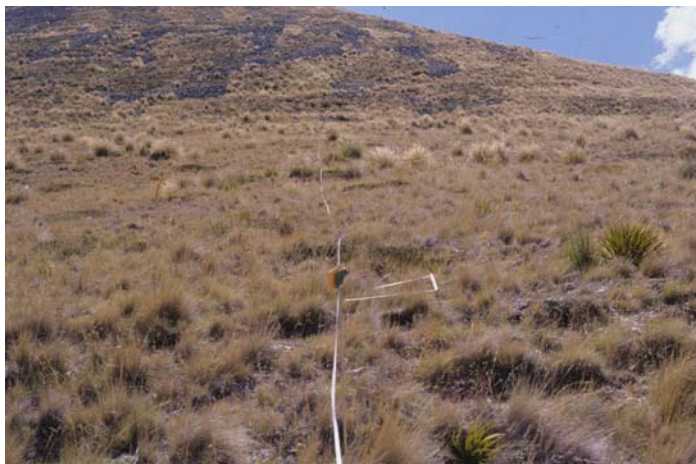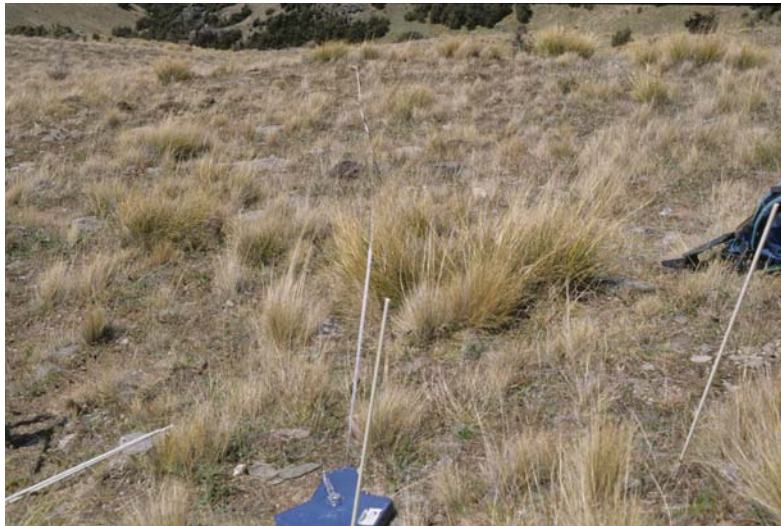First measurement

Second measurement
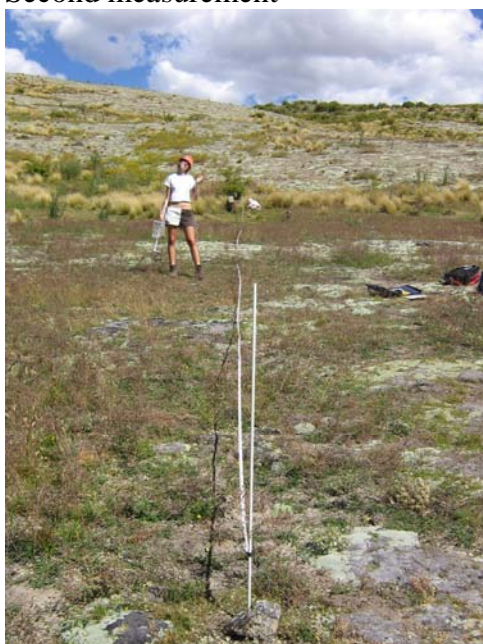

Third measurement

6) Weedy, highly-modified grasslands

First measurement

Second measurement

Third measurement

Appendix III: Transect information for transects under Department of Conservation tenure. Information for transects under pastoral tenure is not included to avoid the publication of information that identifies individual pastoral lease properties.

Site	Property	Tenure at first measurement	Tenure at second measurement	Tenure at third measurement	Easting	Northing	Status	Year officially transferred to DoC	Year of first measurement	Year of second measurement	Year of third measurement
FRAT001	Fraser Basin	PASTORAL	PASTORAL	DOC	2210300	5531500	DoC land Kopuwai Conservation Area	2002	1984	1998	2005
FRAT002	Fraser Basin	PASTORAL	PASTORAL	DOC	2207600	5535800	DoC Land - Lower Fraser Basin Special Lease	2002	1984	1998	2005
FRAT003	Fraser Basin	PASTORAL	PASTORAL	DOC	2207900	5538900	DoC Land - Lower Fraser Basin Special Lease	2002	1984	1998	2005
FRAT004	Fraser Basin	PASTORAL	PASTORAL	DOC	2207000	5540000	DoC Land - Lower Fraser Basin Special Lease	2002	1984	1998	2005
FRAT005	Fraser Basin	PASTORAL	PASTORAL	DOC	2205000	5539500	DoC Land - Lower Fraser Basin Special Lease	2002	1984	1998	2005
FRAT006	Fraser Basin	PASTORAL	PASTORAL	DOC	2203600	5538800	DoC Land - Lower Fraser Basin Special Lease	2002	1984	1998	2005
FRAT007	Fraser Basin	PASTORAL	PASTORAL	DOC	2206900	5536900	DoC Land - Lower Fraser Basin Special Lease	2002	1984	1998	2005
FRAT008	Fraser Basin	PASTORAL	PASTORAL	DOC	2212400	5539000	DoC land Kopuwai Conservation Area	2002	1984	1994	2005
FRAT009	Fraser Basin	PASTORAL	PASTORAL	DOC	2211200	5532800	DoC land Kopuwai Conservation Area	2002	1984	1998	2005
FRAT010	Fraser Basin	PASTORAL	PASTORAL	DOC	2210500	5534100	DoC land Kopuwai Conservation Area	2002	1984	1998	2005
KIRT020	Kirkliston	PASTORAL	DOC	DOC	2313400	5625400	DoC Stewardship Land	1987	1982	1995	2006
KIRT021	Kirkliston	PASTORAL	DOC	DOC	2314397.7	5624657.8	DoC Stewardship Land	1987	1982	1995	2006
KIRT024	Kirkliston	PASTORAL	DOC	DOC	2316399.3	5631056.3	DoC Stewardship Land	1987	1982	1995	2006

Site	Property	Tenure1	Tenure2	Tenure3	easting	northing	Status	Year officially transferred to DoC	First measurement	Second measurement	Third measurement
KIRT025	Kirkliston	PASTORAL	DOC	DOC	2316088.3	5630917.1	DoC Stewardship Land	1987	1982	1995	2006
KIRT026	Kirkliston	PASTORAL	DOC	DOC	2315873.3	5632036.9	DoC Stewardship Land	1987	1982	1995	2006
KIRT027	Kirkliston	PASTORAL	DOC	DOC	2315722.2	5631654.5	DoC Stewardship Land	1987	1982	1995	2006
OHAT010	Ohau Range	DOC	DOC	DOC	2251842.3	5654800	DoC Land	1981	1983	1997	2006
OHAT015	Ohau Range	DOC	DOC	DOC	2252056	5653561.9	DoC Land	1981	1983	1997	2006
OHAT019	Ohau Range	DOC	DOC	DOC	2251502.8	5652612.9	DoC Land	1981	1983	1997	2006
OHAT021	Ohau Range	DOC	DOC	DOC	2250208.3	5652141.8	DoC Land	1981	1983	1997	2006
OHAT024	Ohau Range	DOC	DOC	DOC	2250865.6	5651917.4	DoC Land	1981	1983	1997	2006
OHAT025	Ohau Range	DOC	DOC	DOC	2250421.7	5650978.2	DoC Land	1981	1983	1997	2006
OHAT042	Ohau Range	DOC	DOC	DOC	2255420.2	5651044.9	DoC Land	1981	1983	1993	2006
OHAT043	Ohau Range	DOC	DOC	DOC	2255124.2	5652116.5	DoC Land	1981	1983	1993	2006
OHAT044	Ohau Range	DOC	DOC	DOC	2255165.5	5656761.4	DoC Stewardship Land	1981	1983	1993	2006
OHAT045	Ohau Range	DOC	DOC	DOC	2255000.8	5657509	DoC Stewardship Land	1981	1983	1993	2006
PORT002	Porters	PASTORAL	DOC	DOC	2403473.2	5767309.4	DoC Land	1996	1984	1996	2006
PORT007	Porters	PASTORAL	DOC	DOC	2403543.5	5770115.9	DoC Land	1996	1984	1996	2006
PORT015	Porters	PASTORAL	DOC	DOC	2400443.5	5768718.8	DoC Stewardship Land	1987	1984	1996	2006
PORT016	Porters	PASTORAL	DOC	DOC	2400701.9	5768505.2	DoC Stewardship Land	1987	1984	1996	2006
STUT001	Mt Studholme	DOC	DOC	DOC	2344842.9	5614737.9	DoC Stewardship Land	1983	1983	1995	2006
STUT002	Mt Studholme	DOC	DOC	DOC	2344665.1	5615342.6	DoC Stewardship Land	1983	1983	1995	2006
STUT004	Mt Studholme	DOC	DOC	DOC	2344582	5614350.2	DoC Stewardship Land	1983	1983	1995	2006
STUT005	Mt Studholme	DOC	DOC	DOC	2344566.6	5614521	DoC Stewardship Land	1983	1983	1995	2006
STUT006	Mt Studholme	DOC	DOC	DOC	2344613.3	5614273.1	DoC Stewardship Land	1983	1983	1995	2006
STUT009	Mt Studholme	DOC	DOC	DOC	2344800	5615200	DoC Stewardship Land	1983	1983	1995	2006