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RESEARCH

The shifting floristic complexion of Molesworth

Sean W. Husheer[1] and Simon H. Moore[2]*

[1]New Zealand Forest Surveys, Hastings Aerodrome, Hawkes Bay 4120
[2]Department of Conservation, Private Bag 5, Nelson 7042
*Author for correspondence (Email: shmoore@doc.govt.nz)

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Abstract: Drought-resistant woody communities were once widespread in the intermontane basins and slopes of Molesworth Recreation Reserve, northeastern South Island, New Zealand. These forests, woodlands, and shrublands had established by 6000 years BP, and were largely converted to tussock grassland by fire before 1800 AD. Sheep and rabbit herbivory, and regular burning had altered the vegetation by 1940. From the 1940s, beef cattle grazing was adopted on Molesworth along with repeated aerial over-sowing of exotic pasture grasses and suppression of fires. A series of permanent plots were subjectively located (*n* = 22), randomly located (*n* = 80) and paired along fence lines (*n* = 66) between 1989 and 2008. Plots were re-measured in 2016 to determine vegetation change on Molesworth. We used these data to investigate the effects of cattle grazing and aerial oversowing of exotic pasture grasses on changes in vegetation. Native species richness, cover, and biomass increased between 1989 and 2016. Native herbaceous species cover and biomass increased more at higher elevation and at sites fenced to exclude cattle. Woody biomass, predominantly low-statured native species, increased most on oversown, low elevation slopes in the northern part of Molesworth. The number of exotic species in plots increased at a similar rate to native species, but the biomass of exotic herbaceous species increased at more than twice the rate of native herbaceous species. Data from plots measured in 1952 (*n* = 24), 1960 (*n* = 10), 1987 (*n* = 591), and 2012 (*n* = 9) were used to show that cover of native species has been increasing for the past six decades, as have woody species, both native and exotic. Restoration of native plant communities on Molesworth requires control of grazing and browsing pressures, ongoing fire suppression and active management of invasive plants.

Keywords: cattle grazing, exotic weed invasion, height frequency intercept, Molesworth Recreation Reserve, *Pilosella officinarum*

Introduction

Most eastern South Island tussock grasslands were previously drought-resistant forest and short-statured woodlands, which were transformed by repeated fires prior to European colonisation c. ad 1400–1600 (McGlone 2001; Rogers et al. 2007; McWethy et al. 2010; McGlone & Wood 2019). Vegetation composition would have been spatially heterogeneous. Change may have been locally dynamic and unstable where disturbance from bird herbivory and erosion was pronounced (Lee et al. 2010). Following the initiation of farming in the 1850s, these fire-induced eastern grasslands were increasingly modified by invasive herbaceous and woody weeds, and exotic pasture grasses (Zotov 1938; Grove et al. 2002). Grazing by stock and associated management burning of tussock grasslands from the 1850s reduced the structural dominance of tall tussocks and shrubs and reduced the cover of native species (Mather 1982; Walker et al. 2009a). Some areas were overgrazed by sheep to the extent that farming became uneconomic within several decades (Petrie 1883; Cockayne 1919). Since the 1990s, several hundred thousand hectares of South Island high-elevation tussock grassland have come under the administration of the Department of Conservation (DOC). Low elevation grasslands and alluvial floodplains associated with terraces and wetlands are usually highly modified and are mostly unprotected nationally (< 2%; Mark 1994; Brower 2007; Weeks et al. 2013). They have commonly been given freehold status and are now further threatened by intensification of farming (Williams et al. 2007; Cieraad et al. 2015).

Some farming and conservation activities can be mutually beneficial (O'Connor 1980; Tanentzap et al. 2015). For instance, many exotic animal and plant species are both conservation and farming pests, so their successful control benefits both conservation and pastoral farming. Removal of grazing can allow fast-growing exotic graminoids to exclude native species (Lord 1990, 1999; Walker et al. 2009a; Young et al. 2016). There are also potential conflicts. Exotic grasses favoured for cattle production can displace slower-growing native plant species. Native grasses can also be palatable to cattle, rendering them susceptible to over-grazing. Wetland and riparian plants are vulnerable to cattle trampling and eutrophication.

Ongoing burning without nutrient replacement can lead to soil degradation, which in turn can limit plant growth (Calder et al. 1992; McIntosh et al. 1996; Ross et al. 1997). If fires

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are controlled, tussock grasslands can become increasingly dominated by both exotic and native shrub species (Rogers 1994; Rogers & Leathwick 1994). Restoring native tussock grassland and shrubland requires careful management, and a thorough understanding of how plants respond to suppression of fires, grazing, trampling, and short-term (< decade) or permanent removal of cattle. Ideally, where cattle are present, management needs to maintain cattle grazing at levels which suppress fast growing exotic species, while avoiding damage to vulnerable habitats through grazing and trampling. Molesworth Recreation Reserve, southern Marlborough (c. 180 500 ha; hereafter referred to as Molesworth) retains extensive areas of montane to alpine native plant communities typical of inland South Island basins east of the main dividing mountains of the Southern Alps (Kā Tiritiri o te Moana). Communities associated with alluvial terraces, well-drained terminal and lateral moraines, and ephemeral wetlands, are highly depleted and under-protected outside of Molesworth (Walker & Lee 2000; Rogers & Walker 2002). Molesworth has 112 of the 250 threatened plant species found in DOC's Nelson-Marlborough Region (Jones & Hutzler 2002; de Lange et al. 2018). Most of these species are graminoids, herbs and sub-shrubs (< 50 cm high) which have at least some tolerance of shading from taller tussocks and shrubs, extremes in climate and long periods of water deficit. They are often vulnerable to grazing, trampling, exotic plant invasion and fires.

Molesworth comprises a series of steep-sided greywacke ranges (1400–2200 m a.s.l.) with flat valley floors (< 20 slope; 200–2000 m wide; 500–1400 m a.s.l.) formed from geological faulting, alluvial deposition and, in parts of the west, glacial moraine deposits. Frost days are common (c. 225 frost days annually; NIWA 2016) which would limit the establishment of many species. Annual rainfall increases from east to west (c. 600–2000 mm). Prior to the advent of anthropogenic fires, beech species (Nothofagaceae) were the most common forest type in the west, with drought-tolerant *Podocarpus laetus* and *Hoheria lyallii* forest reaching 1600 m on valley slopes in the east. Valley floor vegetation would have been diverse drought- and frost-tolerant grassland and shrubland species including *Coprosma*, *Discaria*, *Halocarpus*, *Veronica*, *Melicytus*, *Olearia*, and *Ozothamnus* shrub species (Walker & Lee 2002; Rogers et al. 2005; Walker et al. 2006).

The early management history of Molesworth has been documented by Johnson (1967), McCaskill (1969), and Moore (1976). Grazing and burning, along with impacts from rabbits, depleted the vegetation on Molesworth making sheep farming uneconomic by the 1930s. Drier eastern terraces were particularly depleted. Bare ground was common. Grazing- and drought-tolerant herbaceous plants such as *Raoulia* and *Rumex* dominated ground cover. From the late 1940s burning ceased, intensive rabbit control was introduced, sheep were removed and aerial over-sowing of pasture plants such as *Agrostis*, *Dactylis*, *Phleum*, *Lolium*, and *Trifolium* was undertaken to increase food availability for stock. Exotics such as *Pilosella*, *Hieracium*, and *Hypochaeris* contaminated seed sources, and were widely dispersed during oversowing. In the 1950s aerial topdressing of fertiliser and over-sowing of seed in some areas resulted in increases of fast-growing exotic grasses, and increased stock carrying capacity. Farm managers increased cattle numbers from < 2000 in the 1940s to c. 10 000 by the 1960s. Results from surveys reported by Dickinson et al. (1992) and Courtney and Arand (1994), prompted fencing of 11 000 ha of Molesworth between 1989 and 1995 to exclude cattle (6.0% of Molesworth). These areas tend to be higher elevation, are less modified and dominated by native shrubs, and are less valued for cattle grazing. Over 43 000 ha has been oversown (24% of Molesworth). The administration of Molesworth changed in 2005 from a special lease to a DOC administered Recreation Reserve, with Landcorp Farming Ltd provided a lease for grazing purposes. Molesworth is subject to a management plan which seeks to balance cattle grazing with protection of threatened plant populations and habitats (DOC 2013).

In the past two decades, cattle numbers have been reduced by c. 40% to c. 6000 to reduce farming risks during drought, increase long-term farm profitability and allow vegetation recovery. With successful management of grazing, there would be expected increases in the species richness, cover and biomass of native plants, especially tall tussocks and shrubs (Walker et al. 2014). Increases in native woody species at low elevation might advantage slow-growing, stress-tolerant native species at the expense of fast-growing exotic grasses and herbaceous species (King & Wilson 2006; Laliberté et al. 2012). Therefore, increasing the cover and biomass of native shrubs at Molesworth could facilitate increases in stress-tolerant native herbs, grasses and sedges, and reductions in exotic species. We used estimates of cover of individual species to determine if plant species richness and composition had changed from 1952 to 2016 at Molesworth, and if changes were related to the effects of oversowing and cattle grazing. We also used permanent plot data to test if the number, biomass and proportion of native species increased. We expected native species and both native and exotic woody species to increase in biomass and cover in line with changes in the grazing regime and reductions in fires over this period. Changes in plant biomass were estimated from plots repeatedly measured from 1989 to 2016. These data were used to test if reductions and complete removal of cattle grazing and trampling has led to a recovery of native tussock grasslands and native woody species richness and biomass during this time.

Methods

Molesworth vegetation monitoring

Formal vegetation monitoring on Molesworth began in the 1940s, in association with the adoption of management influenced by research (McCaskill 1969; Broad 2013; Table 1). The frequency of plot measurement increased following the establishment of DOC in 1987 (Courtney & Arand 1994; NB Peet, SHM, unpubl. data). Permanently marked vegetation monitoring plots were progressively established from 1989, using a mixture of subjectively located plots (1989 n = 20; 1995 n = 1; 2016 n = 1), randomly selected plots (2007 n = 80) and paired fenced and unfenced plots (2008 n = 66). All plots were re-measured between January and March 2016. Protocols are described in detail by Husheer (2018). In all three series of plots, vegetation was assessed using the height frequency intercept (HFI) method described by Dickinson et al. (1992), which is a modification of Scott's (1965) method. The HFI plots established in 1989 were re-measured in 1995, 2001, and 2006. Cover of individual species was also estimated in fixed-area quadrats established in 2007 and 2008. This is a widely used approach for monitoring grasslands (relevé or recce description, Mueller-Dombois & Ellenberg 1974; Hurst & Allen 2007). For the 2007 survey, twenty 600 m transects were randomly established on a northern bearing. Four 20 × 20 m plots were placed on each transect at 200 m intervals. All vascular plants

Table 1. Summary of all surveys used for analysis. Data were obtained from Table 1 of Moore (1976). Data for Wraight (1960), Courtney and Arand (1994) and DOC (2015) were obtained from National Vegetation Survey (NVS) databank. Data from Dickinson et al. (1992) and Husheer (2016) were obtained from field records. All relevé data used cover scores (1–6) described in the RECCE plot method (Hurst & Allen 2007).

Survey reference	Measurement method	Establishment approach	Years measured	N plots	Data used	Response variables and analysis procedure
Moore (1976)	Relevés. Cover of vascular plants were recorded in variable area unmarked plots without height tiers on a 1–6 scale	Haphazard in north-eastern Molesworth short tussock grasslands	1952	21	Cover scores from published data	Species composition and number as response variables. Proportion of native and woody species. DCA and GLMM with Gaussian error distribution for com-position, binomial for proportions, generalised Poisson for counts.
Wraight (1960)	Frequency intercept. Presence of vascular plants recorded in 100 15.2 cm diameter (182 cm^2) intercepts in marked plots without height tiers	Haphazard in western Molesworth short tussock grasslands	1960, 1972	10	Cover scores (1–6) were calculated from frequency of occurrence in intercepts	As above
Courtney and Arand (1994)	Relevés. Presence of vascular plants recorded in unmarked variable area plots without height tiers	Haphazard throughout Molesworth	1987	591	Cover scores from data (1–6)	As above
Dickinson et al. (1992)	Height frequency intercept (HFI). Presence of vascular plants recorded in 100 intercepts in marked plots with 5 cm height tiers	Haphazard in western Molesworth tall and short tus-sock grasslands	1989, 1995, 2001, 2006, 2016	22	Cover scores (1–6) were calculated from intercepts	As above, plus proportion of woody and native species in intercepts, and HFI summed for an index of biomass. Binomial GLMM for proportions and negative binomial for HFI biomass.
Husheer (2016)	HFI and Relevés. Presence of vascular plants recorded in fifty 20 cm^2 intercept and cover estimated in 20 × 20 m plots	Four plots on 20 randomly located transects	2007, 2016	80	Cover scores from relevé data (1–6), HFI for biomass	As for Dickinson (1992) plus proportion of woody and native species in HFI plots. Binomial GLMM for proportions.
Husheer (2016)	HFI and Relevés. Same measurement protocol as used in 2007 random plot survey. Described by Husheer (2016)	Paired plots along cattle exclusion fences	2008, 2016	66	Cover scores from relevé data (1–6)	As for Husheer (2016)
Bellingham et al. (2015)	Relevés. Cover of vascular plants estimated in 20 ×20 m plots	Systematic on an 8 km grid	2010	3	Cover scores from relevé data (1–6)	As for Moore (1976)
Bellingham et al. (2015)	Relevés. Same measurement protocol as used in 2010 survey. Described in DOC (2019)	Systematic on an 8 km grid	2013–2015	9	Cover scores from relevé data (1–6)	As for Moore (1976)

were identified by species and their cover assessed within six height tiers (< 0.1 m, 0.1–0.3 m, 0.3–1 m, 1–2 m, 2–5 m, > 5 m) on a 1–6 log-cover scale. The Global Positioning System (GPS) location (±1 m) was recorded for each plot.

A further 66 paired fenced and unfenced plots were established in 2008 along either side of cattle exclusion fences. These fences were constructed between 1989 and 2008 across valley bottoms. Plot locations were selected for representative vegetation. In the plots established as part of the 1989 series, 100 height frequency (HF) intercepts were measured along a 50 m long transect line. In the 2007 and 2008 surveys, 50 HF intercepts were measured along five parallel 5 m long lines located within a 5 m × 5 m sub-plot. Intercepts in all surveys consisted of 4.47 cm × 4.47 cm sized vertical columns spaced at 0.5 m intervals. These columns were divided up into 5 cm height tiers and the presence of live vascular plant species (excluding flowering and seeding parts) occurring in each height tier was recorded. Thus, each 100 cm high column was divided into twenty 100 cm^3 cubes.

Records were obtained from Moore (1976) for 21 relevés recorded in 1952. In 2016, the National Vegetation Survey databank was searched for vegetation plot data from Molesworth (Wiser et al. 2001). Data were obtained from ten plots established in the Wairau Valley in 1960 (Wraight 1960) and re-measured in 1972. Frequency of occurrence data from the 1960 and 1972 Wairau surveys (100 intercepts in each plot), and 1989–2016 HFI surveys (Wraight 1963, n = 10 plots; Dickinson et al. 1992, 100 intercepts in each plot) were converted into the 1–6 cover scores for comparison with cover data (Hurst & Allen 2007; plants occurring in 1 intercept = 1, 2–5 intercepts = 2, 6–25 = 3, 26–50 = 4, 51–75 = 5, > 75 intercepts = 6). In 1987, a Protected Natural Areas Programme survey of the general Molesworth region measured 873 plots, of which 591 were on Molesworth. For Wraight's (1960) plots, 100 circular intercepts (c.15.2 cm diameter) were spaced at two link intervals (c. 40.1 cm) along a transect two chain lengths long (c. 40.2 m). The presence of all vascular plant species rooted within the intercept was recorded. Staff of New Zealand Forest Surveys Ltd measured three 20 × 20 m plots in 2010 (Beets 2012). DOC's national monitoring system established nine 20 × 20 m plots from 2013–2015 (DOC 2019). Both surveys used an 8 km nation-wide grid. All data are available from the National Vegetation Survey data bank (Wiser et al. 2001).

Data analysis

Response variables

Generalised linear mixed-effects regression models (GLMM) were used to estimate changes in the proportion and numbers of native and exotic vascular plant species, vascular species composition, and cover and biomass of the most commonly occurring species using the R package glmmTMB version 1.1.1 (Brooks et al. 2017; R Development Core Team 2023; Table 1). Cover data on a 1–6 scale, derived from all surveys, were used to show changes in the number of native and exotic species in plots, as well as proportions of herbaceous and woody species. Composition scores for each species, plot and survey were calculated using detrended correspondence analysis (DCA) from cover scores of common plant species (these were species occurring in at least 32 of 80 randomly located plots measured in 2016; Oksanen et al. 2018). Detrended correspondence analysis scores were represented in graphics with a spectrum of colours. Height frequency intercept data were used to index biomass by summing intercepts for each plot (Scott 1965). The proportions of woody and native species recorded in HFI plots were used as response variables in separate GLMMs. The co-occurrence of common species was examined with a Pearson correlation matrix. Changes in plot mean cover scores and HFI scores between 2007 and 2016 were tested with a series of paired t-tests, and random effects coefficients for each species from a GLMM (Appendix S1).

Predictor variables and model diagnostics

All GLMMs used the same predictor variables: location (easting, northing and elevation in m), landform, cattle exclusion, and records of aerial oversowing (Table 2). Aerial application of artificial fertilisers often occurred with aerial oversowing of exotic grasses, but there are no records of fertiliser application. Plot elevation was extracted from a digital elevation model (Hijmans 2016; LRIS 2022). Landform was classified into either terrace or slope. Firstly, the locations of streams were predicted from elevation data, and then river terraces were identified as pixels less than 400 m from a stream and with less than 20° slope (Holmgren 1994; GRASS 2018). Oversowing maps from Moore (1976) and DOC (2013) were digitised and geo-referenced. For each plot location, grazing, landform, and oversowing classifications were extracted from raster files. All numeric predictor variables were scaled to a mean of zero and a standard deviation of one before analysis so that the importance of co-coefficients could be directly compared in all models. Terrace, oversowing, and fencing were factors in models. All models used first order interaction terms among predictors. Site identity was included as a random effect term to reduce over-dispersion of residuals and to specify when plots were established in pairs across fence lines. For models comparing common species cover scores and HFI between 2007 and 2008, a random effect term of species with slope varying by year was also included. Residual diagnostics were undertaken using the R package DHARMa (Hartig 2022). The GLMM models for species composition used a Gaussian error term; models for proportions of native and woody species used binomial or quasi-binomial error terms; biomass and cover models used generalised Poisson terms. Candidate models were selected based on Akaike's information criterion (Bozdogan 1987). Goodness of fit was assessed using Nakagawa's (2017) R^2. A stepwise procedure using the R 4.3.2 package buildmer 2.9 was applied to confirm that the exclusion of any predictor did not make significant improvements to any model (Voeten 2021). Inclusion of a zero inflation term and a spatial correlation matrix were trialled for all models, but did not improve model fit and were not included in any model.

Results

Increasing number, cover and biomass of native and exotic herbaceous and native woody plants

There has been an increase in the number of both native and exotic herbaceous species, and the number of native woody species present in plots since the 1950s (Fig. 1, coefficient tables 4–12 in supplementary material). The proportion of woody species present in plots on Molesworth has increased more than three-fold during this time, slightly more so on slopes fenced from cattle (1952 = 0.05, 1989 = 0.11, 2016 = 0.18 vs. proportion on unfenced terraces with oversowing 1952 = 0.04, 1989 = 0.09, 2016 = 0.16). Native woody species such as *Acrothamnus colensoi* and *Dracophyllum rosmarinifolium*

Table 2. Summary of coefficients from GLMMs for the proportion of native and woody species present in plots, proportion of native and woody plant biomass (HFI), mean native and woody species cover, and plant species composition (DCA scores). Full coefficient tables are included as supplementary material. Large positive influences of an effect (↑↑), positive influence (↑), negative influence (↓) and little or no effect (↔) are shown. Native and woody (native and exotic) species richness, cover, and biomass increased with time (↑). Between 2006 and 2016, native herbaceous species cover and biomass increased more at higher elevation, particularly in the south and west, and at oversown sites fenced to exclude cattle (→). Woody species richness and biomass tended to decrease with elevation. Between 2006 and 2016, woody biomass increased most on northern, low elevation slopes. Species composition was summarised by DCA axis 1 and 2 scores. DCA axis 1 scores increased and axis 2 scores decreased with elevation (→). Oversowing had greater effects in the opposite direction in ordination space (decreasing DCA axis 1 scores and increasing axis 2 scores ←).

Coefficients	Native species richness (1952–2016 cover data)	Woody (exotic + native) species richness (1952–2016 cover data)	Native biomass (2007–2016)	Woody (exotic + native) biomass (2007–2016)	Native and woody (exotic + native) cover (1952–2016)	Species composition (1952–2016)
Time	↑↑	↑↑	↑↑	↑↑	↑	↑
Easting	↓	↔	→	↔	↔	↓
Northing	↓	↔	↔	↑	↔	↓
Elevation	→	↓	→	↓	↑	→
Terrace	↔	↔	↔	↓	↑	↓
Oversown	→	↔	→	↑	↔	←
Grazed	→	↔	↔	↔	↔	→

increased most (Tables 1, 2, and 3 in supplementary material). With the exception of *Rosa rubiginosa*, there is little evidence from plot data of widespread increases in the cover of exotic woody species from 1952 to 2016. Conspicuous woody trees and shrubs, such as native matagouri (*Discaria toumatou*) and mānuka (*Leptospermum scoparium*), and exotic Scotch broom (*Cytisus scoparius*) were present in all surveys from 2007 onwards but were not widespread enough to occur on ≥ 32 of the 80 randomly located plots in 2016. Wildling pines are conspicuously present on Molesworth, but were recorded in one plot only, reflecting their localised occurrence and efforts to contain their spread.

The HFI results were consistent with cover data from 1952 to 2016. Total woody plant biomass in the 80 randomly located plots was mostly composed of low-statured native species, and this increased between 2007 and 2016 (Fig. 2). Exotic herbaceous species in the daisy family (Asteraceae: *Hieracium*, *Hypochaeris*, *Pilosella*) generally showed little change from 2007 to 2016, with only *Hieracium pollichiae* and *Pilosella praealta* continuing to increase in occurrence, cover, and biomass. Exotic and native woody biomass tended to be higher in the north and at low elevation, and also in areas oversown and not selected for cattle exclusion on Molesworth. Pairwise correlations of the change in HFI scores among the 22 species occurring in ≥ 20 of the 80 random HFI plots in 2016, showed little evidence of competitive interactions. Mean Pearson's correlation coefficients were generally positive, providing little evidence that increased biomass of one species was associated with decreases in another (minimum = –0.05, mean = 0.01, maximum = 0.05). Only two native grasses and one native herb had mean negative correlations with other common species of less than –0.2 (*Anthosachne solandri*, *Chionochloa flavescens*, and *Wahlenbergia albomarginata*). Native woody species (*Acrothamnus colensoi*, *Gaultheria depressa*, *Leucopogon fraseri*) and the exotic *Rosa rubiginosa* had positive correlations with other species, suggesting that facilitative effects may have been more important than competitive displacement.

Complex changes in species composition

While there have been clear increases in the cover and biomass in functional groups of exotic and native herbaceous and native woody plants at Molesworth, changes at the individual species level were far less clear. The GLMM models of DCA scores for cover data on the 802 plots measured between 1952 and 2016 show changes in species composition on Molesworth, but much less than species pooled into functional groups (DCA 1 change in plot scores = 0.1%,

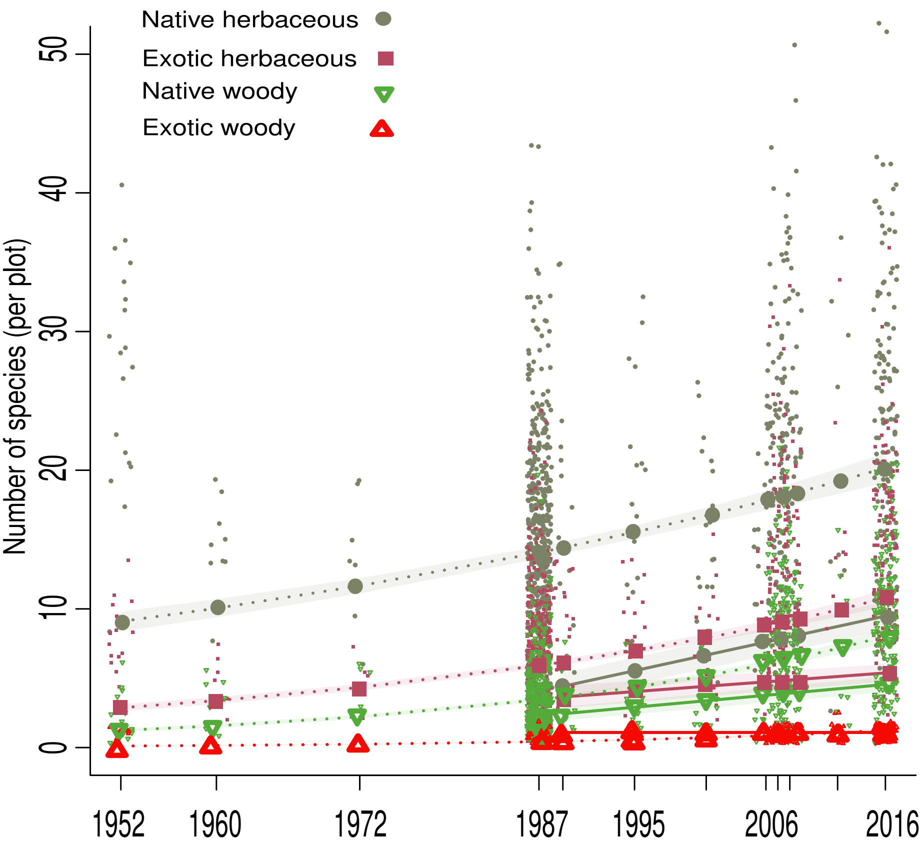

Figure 1. Change in numbers of native herbaceous, exotic herbaceous, native woody, and exotic woody species from 802 plots measured between 1952 and 2016. Points indicate numbers of vascular plants recorded in individual plots. Colours are assigned from a spectrum using mean DCA 1 and DCA 2 species scores. The intensity of green increases while red decreases with increasing DCA axis 1 scores, which is associated with a gradient of increases in the occurrence of native species. The intensity of blue decreases with increasing DCA axis 2 scores, which is associated with a gradient of increases in woody species. Lines are fitted for relevés (····) and HFI plots (—) from two individual GLMM models.

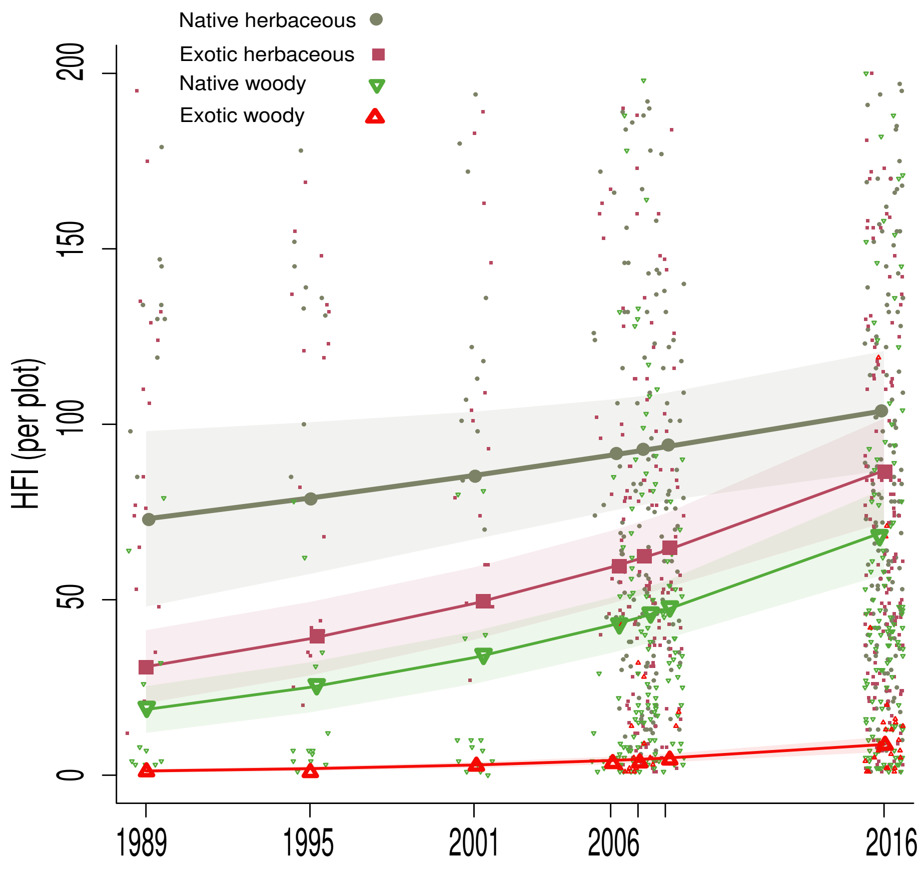

Figure 2. Change in biomass of native herbaceous, exotic herbaceous, native woody and exotic woody species from 168 HFI plots measured between 1989 and 2016. Lines are predicted fits from a GLMM model. Colour codes are calculated from mean DCA 1 and DCA 2 species scores for each form. The intensity of green increases while red decreases with increasing DCA axis 1 scores, which is associated with a gradient of increases in the occurrence of native species. The intensity of blue decreases with increasing DCA axis 2 scores, which is associated with a gradient of increases in woody species. HFI biomass above 200 is not plotted, so forms in some plots are not displayed.

range among surveys = 5.3%, DCA 2 plot score change = 1.7%, range = 4.8%). Most plots had a limited range of DCA scores, which changed little between 1952 and 2016 (1952 mean DCA 1 plot score = 2.1, 2016 mean DCA 1 plot score = 2.2, 1952 mean DCA 2 plot score = 2, 2016 mean DCA 2 plot score = 2.7, Fig. 3). DCA lower 25% and upper 75% quantiles of plot scores demonstrate similar composition of common species in 1952 (DCA 1 25%–75% quantile = 1.8–2.5, DCA 2 = 1.8–2.2), and in 2016 (DCA 1 25%–75% quantile = 1.9–2.5, DCA 2 = 2.5–2.9, Fig. 4). This was partly due to inconsistent increases in the cover of grasses, shrubs and exotic herb species throughout Molesworth, and widespread increased native herb occurrence and biomass. Changes among species in cover and biomass were complex, due to interactions of the effects of exclusion of cattle, landform, location, elevation, and oversowing. This makes interpretation of changes in species composition and changes in individual species difficult. Increasing DCA axis 1 scores were associated with a lower proportion of the cover of exotics. Only three of the twelve lowest DCA 1 scoring species were native (< 2.4). One of the 20 highest DCA 1 scoring species was exotic, *Hieracium pollichiae*, which increased in cover between 1952 and 2016. Elevation had an important effect on the ordination. Four commonly occurring exotic plants associated with grazing in valley bottoms had low DCA axis 1 scores (*Agrostis capillaris*, *Anthoxanthum odoratum*, *Rosa rubiginosa*, *Trifolium repens*). Small increases in mean DCA scores with time (≈2%) masked larger changes in individual species, and groups of species at low altitude. DCA scores increased between 1952 and 2016 at low elevation plots (predicted DCA 1 at 460 m a.s.l. in 1952 = 0.4 and DCA 2 = 2.5, 2016 DCA 1 = 1.2 and DCA 2 = 3, Fig. 5). Hieraciinae exotics had high DCA axis 1 and 2 scores and increased in cover in plots from 1952. *Pilosella officinarum* was not detected in plots until 1972, *Pilosella praealta* until 1989, and *Hieracium pollichiae* and *Pilosella caespitosa* were not detected until 2007. Trends for tussocks and graminoids were more ambiguous. Some grass and tussock species increased in cover and biomass in permanent plots between 2007 and 2016 and had accordingly high DCA scores (such as *Festuca novae-zelandiae*, *Koeleria novozelandica*, and *Poa colensoi*), while others did not. Woody species increased in cover in plots between 1952 and 2016, had high DCA axis 2 scores, and included native species such as *Acrothamnus colensoi*, *Dracophyllum rosmarinifolium*, *Ozothamnus vauvilliersii*, and *Pimelea oreophila*, and the exotic briar rose (*Rosa rubiginosa*).

Discussion

The current pattern of vegetation on Molesworth reflects a legacy of over a century of herbivory and exotic plant colonisation, with increasing frequency of fires over several centuries. Reductions in the cover and biomass of native species, and the establishment and subsequent expansion of exotic forbs had occurred prior to the initiation of permanent plot establishment in 1989. The transformation from pre-human ecosystems dominated by native woody species to mixed exotic and native grasslands and shrublands has been profound. Terraces, valley floors, toeslopes, and rolling hill country associated with pastoral farming have been subject to the greatest transformations. The recent trend of increasing native woody cover and biomass is evidence of recovery from the 1950s when intensive farm management practices including

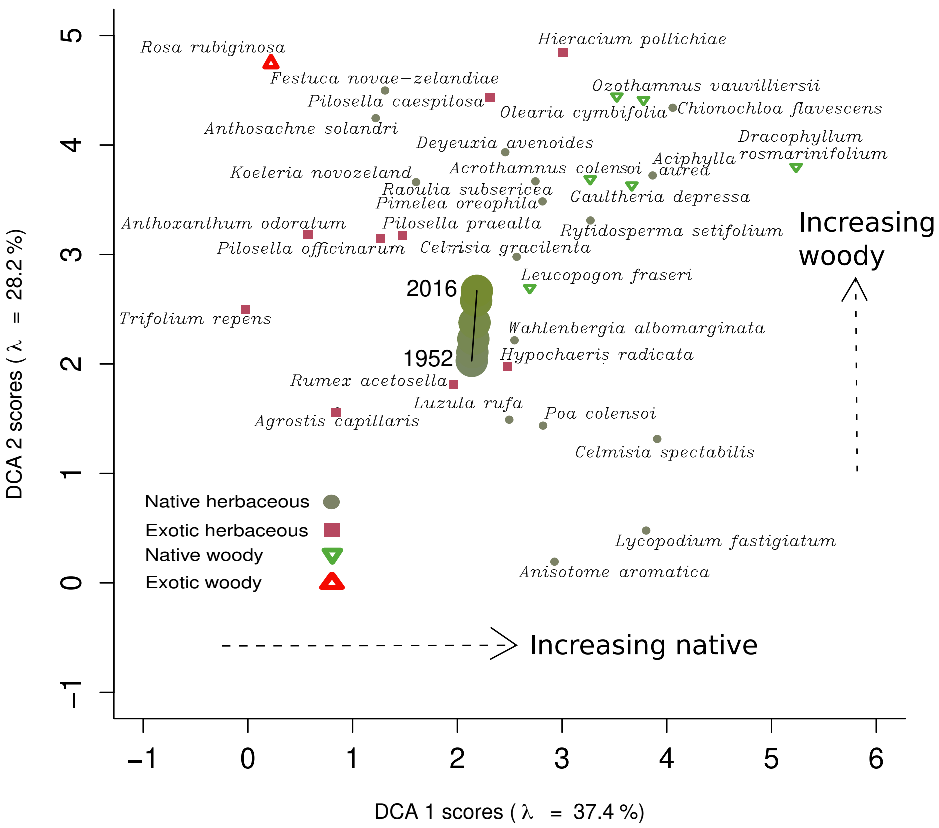

Figure 3. Decorana axis 1 and 2 scores for 32 commonly occurring species. The predicted mean plot scores from a mixed effects model are shown in overlapping coloured circles at the centre of the plot. The intensity of green increases while red decreases with increasing DCA axis 1 scores, which is associated with a gradient of increases in the occurrence of native species. The intensity of blue decreases with increasing DCA axis 2 scores, which is associated with a gradient of increases in woody species.

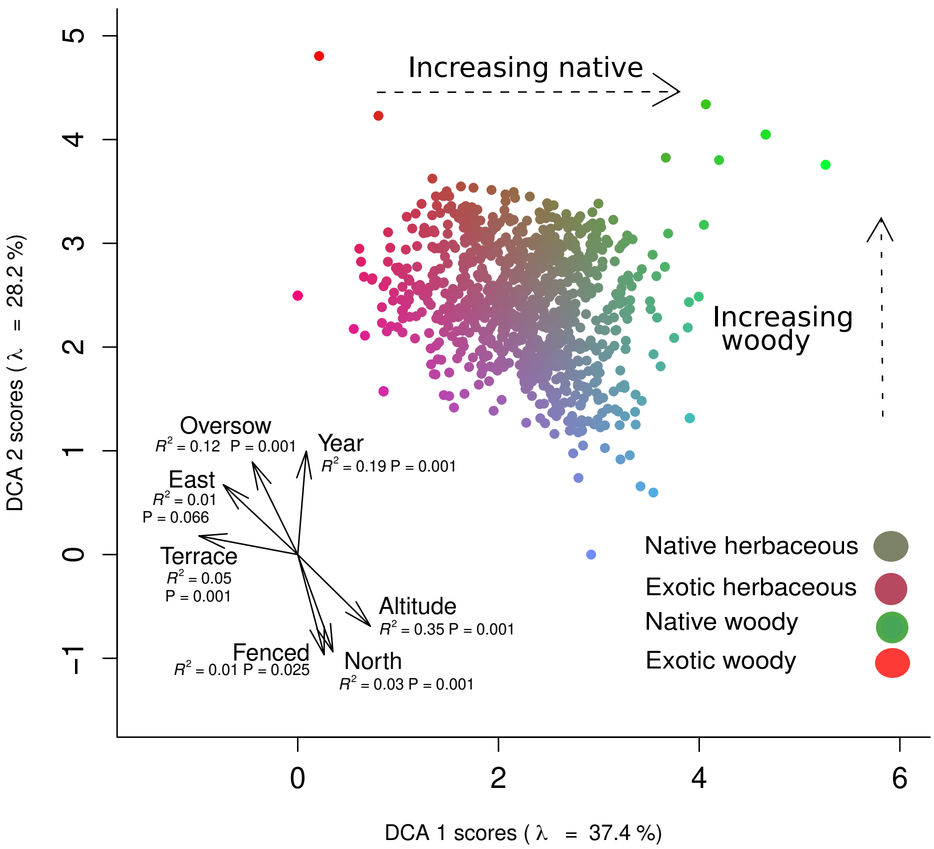

Figure 4. Decorana plot scores from 1952–2016, with eigenvalue scores explained by each axis (λ) and fitted correlation coefficients for predictors from 802 plots established between 1952 and 2015 (168 plots were remeasured in 2016). Coefficients, R^2, and P values are generated from the Enviro fit function in vegan (Oksanen et al. 2018). Data are from estimated cover (< 0.1 m height tier) of vascular species which occurred in ≥32 of 80 randomly located plots in the 2016 survey. In the main plot the intensity of green increases while red decreases with increasing DCA axis 1 scores, which is associated with a gradient of increases in the occurrence of native species. The intensity of blue decreases with increasing DCA axis 2 scores, which is associated with a gradient of increases in woody species. The legend displays these designated colours of DCA mean scores for native herbaceous, exotic herbaceous, native woody and exotic woody species.

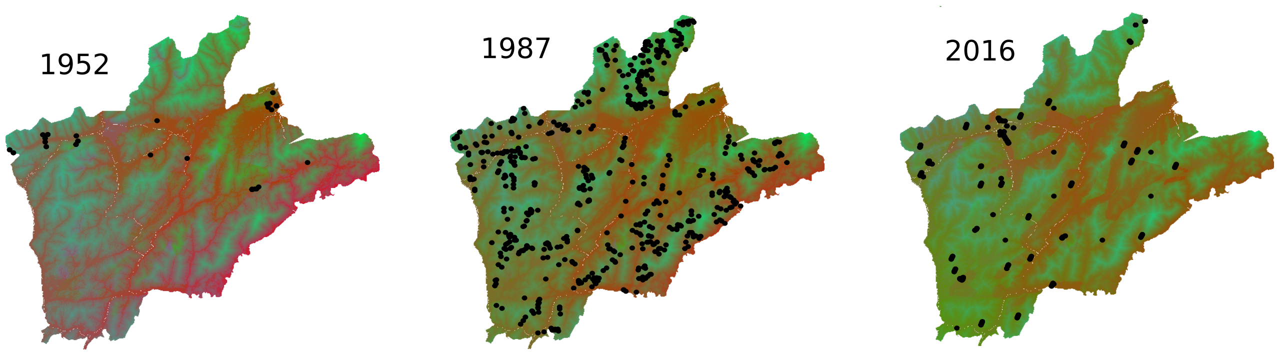

Figure 5. Map of predicted changes in the composition of common species (occurring in >32 plots in 2016) on Molesworth, from a mixed effects model using data from 802 plots established between 1952 and 2015 (168 plots were remeasured in 2016). Points show a) plots from 1952 and 1960 surveys, b) 1986–1987 PNA survey, and c) 2016 survey. The map colour indicates the predicted changes. The intensity of green increases while red decreases with increasing DCA axis 1 scores, which is associated with a gradient of increases in the occurrence of native species. The intensity of blue decreases with increasing DCA axis 2 scores, which is associated with a gradient of increases in woody species. Low-elevation terraced and oversown species composition increased in DCA 1 and 2 scores over time (increased green, decreased red and blue), from a dominance of lower scoring species in 1952 towards increased importance of higher scoring native species and native and exotic woody species in 2016.

annual burning, coupled with high rabbit numbers, had left large parts of Molesworth's vegetation in a highly depleted state (Moore 1976). From the 1950s, increasing cattle numbers in combination with aerial application of fertiliser and exotic grasses, has driven the compositional change of vegetation communities. While removing sheep and suppressing rabbits and fires has allowed development of a tussock and shrub dominated canopy, the period of oversowing from the 1950s to 1980s saw an expansion in the distribution of exotic herbs and grasses. Contamination with seed from exotic members of the daisy family (Asteraceae, e.g. dandelion (*Hypochaeris*), hawkweeds sub-tribe Hieraciinae: *Hieracium* and *Pilosella* species) meant that the spread of these species has occurred from near absence in 1952 to presence in most plots by 2016. The distributional limits of the most common of these species, mouse-eared hawkweed (*Pilosella officinarum*) has probably been reached on Molesworth. Biomass and cover of hawkweed could increase further where disturbance provides opportunities, particularly on sparsely vegetated areas on dry, low-elevation terraces in eastern Molesworth (Miller et al. 2015). Hawkweeds have been linked with the displacement of native species through allelopathy and by reducing nitrogen availability (Scott et al. 2001). Invasion of hawkweeds on Molesworth is more likely to be symptomatic of depleted vegetation and soil disturbance, rather than the direct displacement of native species (Radford et al. 2010; Day & Buckley 2013). We found no evidence that the increasing abundance of hawkweed on Molesworth is directly related to reductions in the cover or biomass of native plants or to ongoing grazing (Walker et al. 2005, 2016).

At a plot scale, native herbaceous species richness more than doubled between 1952 and 2016 on Molesworth. Increases in native and exotic herbaceous species richness, cover and biomass were greatest in the past two decades, when woody plant species richness and biomass, particularly low-statured native species, also increased substantially. Vegetation growth over much of Molesworth is constrained by seasonal climatic extremes and the availability of water. Natural changes in plant communities in low productivity habitats are slow (Hawkes & Sullivan 2001), which can place vulnerable slow-growing native herbs at greater risk from displacement from exotic grasses. Increases in native woody species may decrease the availability of nutrients and light, minimising the ability of light-demanding exotic grasses to competitively exclude slow-growing, stress-tolerant native species (King & Wilson 2006; Laliberté et al. 2012). Therefore, increasing cover and biomass of native shrubs on Molesworth may have facilitated stress tolerant native herbs, grasses and sedges, which have increased in species richness. Biomass of exotic herbaceous and native woody species has increased at a faster rate than native herbaceous species between 1989 and 2016. This mirrors other parts of the South Island drylands which have also slowly transformed towards woody shrublands, coetaneous with the invasion of exotic herbaceous plants (Walker et al. 2008, 2009a, 2009b, 2016; Young et al. 2016; Hua & Ohlemüller 2018). Our results do not support predictions that increasing shrubland biomass and cover competitively excludes native herbaceous species (Rogers et al. 2005; Ropars et al. 2018). Instead, increases in the cover, biomass and diversity of native tussocks and low-statured woody species appear to be fostering a corresponding increase in native herbs and graminoids.

Responses to reductions and removal of grazing at Molesworth were complex. Our results did not identify a specific combination of grazing activity, oversowing, landform, and location where recovery of woody and native plants was consistently higher. Native woody species cover was not significantly different between fenced and unfenced plots, but there was a weak trend in grazed plots for decreases in native herbaceous plant cover and biomass. There was little evidence of differences in cover and biomass between fenced and unfenced sites for individual species. Responses to the exclusion of cattle were highly variable, with grazing likely having high localised impacts, while other sites appear largely unaffected. Reduced grazing impacts and suppression of fires over the past six decades has probably contributed to the overall increase in the cover and biomass of tall and short native tussocks. Previous studies also show these inconsistencies, with recovery of native communities following cessation of regular burning and removal of sheep and cattle grazing (e.g. Malcolm 1925), decline (e.g. Sewell 1952; Barker 1953), or little change (e.g. Moffat 1957; Scott et al. 1988; Rose & Platt 1992; Rose et al. 1995, 2004; Duncan et al. 1997; Walker et al. 2003). Recovery of native species numbers and biomass was slowest on terraces. There may be good reasons for this. Cattle grazing is likely to have been more intense on terraces rather than slopes prior to the establishment of permanent plots. These sites may have been irreversibly modified. Drought and frosts on terraces in Molesworth are common, which can further reduce rates of recovery. Where native seed sources are limited, even restricted grazing by cattle may prevent previously displaced, naturally uncommon native species from flourishing and spreading. The relationships between weed invasion, fire suppression and grazing are also complex (Lord et al. 2022; Padullés Cubino et al. 2018). The degree to which pollination, successful seed-set and dispersal mechanisms have been impacted over the range of sites and species is unknown. As the timespan and number of New Zealand monitoring studies increases, clearer spatial and temporal trends may become apparent.

Management implications and future work

The most depleted vegetation communities on Molesworth are those on low-elevation, low-gradient landforms. These areas have been subject to the highest level of modification over the past 150 years. Restoring these communities is imperative to protect the full range of natural diversity on Molesworth. Future management actions for Molesworth favouring continued increases in the biomass, diversity and cover of native woody species should be encouraged. We predict that over time, increased biomass of low-stature woody species and tall tussocks will lead to continued increases in the proportion of native herb and grass species at Molesworth. Increased woody biomass and native species richness has been observed elsewhere in South Island dryland ecosystems where grazing and burning have been prevented or reduced (Mark et al. 2011; Walker et al. 2014). As well as enhancing native biodiversity, increasing the abundance of native tussock and non-invasive woody species may help to suppress light-demanding weeds such as mouse-eared hawkweed (*Pilosella*; Steer & Norton 2013). There would also be a positive contribution to the national trend of modified grasslands to sequester carbon (Scott et al. 2000; Carswell et al. 2015).

The decadal re-measurement of permanent plots will guide future decision-making for land management on Molesworth. It will supplement data from other South Island dryland plot networks to provide trend information for some of New Zealand's most vulnerable and undervalued ecosystems. Additional targeted monitoring to specifically explore finer-scale effects on wetland ecosystems would help to better understand the direct impacts of cattle grazing and trampling.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Mean cover data and coefficient tables from generalised linear mixed models

Appendix S2. Assessment of the reliability of vegetation monitoring on Molesworth

The New Zealand Journal of Ecology provides supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed but any issues relating to this information (other than missing files) should be addressed to the authors.