

## Supplementary Material to “The shifting floristic complexion of Molesworth”

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

All generalised linear mixed models (GLMM) used the same fixed and random effects. Numeric fixed effects of  $\beta_1$  to  $\beta_4$  of year of measurement, northing, easting and plot elevation derived from a digital elevation model, were scaled and analysed with first order (two-way) interactions. Factors of terrace, grazing and oversown were not scaled. To allow for potential bias from correlation from repeated measurements, plot identity  $i$  was used as a random effect, which for all models reduced over-dispersion of residuals for each measurement  $j$ . Alternate candidate models included zero inflation terms, exponential spatial covariance matrices and a series of alternative error terms. For count, detrended correspondence analysis (DCA) and summed height frequency intercept (HFI) data, Gaussian, Poisson, generalised Poisson, and quasi-binomial error families were compared. For proportions, binomial and generalised binomial error families were compared using Akaike information criterion (AIC) for selection. Inclusion of zero inflation, covariance structures or alternate error terms did not improve model fit sufficiently to warrant their inclusion (as determined by AIC scores).

$$Y_{ij} = \beta_0 + u_{0i} + (\beta_1 : \times : \beta_7) + so_{ij} + \epsilon_{ij} \quad (1)$$

Error terms for variance of residuals were specified in each model with error families of Gaussian, Poisson or binomial to minimise variance and heterogeneity of residuals.

- $u_0 \sim Normal(0, \sigma_{u0})$
- $\epsilon \sim Normal, Poisson, binomial(0, \sigma)$

Species	Cover change (%)±	Cover coefficient	t value	P	HFI change (%)±	HFI coefficient	t value	P	Family
Native herbaceous plants									
<i>Aciphylla aurea</i>	-1±3	-0.2	0.116	0.908	32±28	-162.2	0.345	0.73	Apiaceae
<i>Anisotome aromatica</i>	3±2	0.5	0.461	0.645	207±112	5.3	0.226	0.821	Apiaceae
<i>Celmisia gracilenta</i>	1±3	-0.9	0.292	0.777	206±103	162.5	1.163	0.246	Asteraceae
<i>Celmisia spectabilis</i>	7±2	-0.3	0.865	0.388	262±119	-173.8	0.267	0.79	Asteraceae
<i>Raoulia subsericea</i>	1±2	-0.9	0	1	246±115	20	0.038	0.97	Asteraceae
<i>Wahlenbergia albomarginata</i>	1±2	-1.1	0.315	0.753	439±146	49.7	0.947	0.345	Campanulaceae
Exotic herbaceous plants									
<i>Hiernicum pollichiae</i>	12±3	-2.7	2.054	0.041	16±4	-158.6	2.882	0.004	Asteraceae
<i>Hypochaeris radicata</i>	3±2	-0.6	0.763	0.446	351±122	16.2	1.714	0.088	Asteraceae
<i>Pilosella caespitosa</i>	12±3	-0.3	1.39	0.166	270±123	-11.4	0.811	0.418	Asteraceae
<i>Pilosella officinarum</i>	25±4	1.2	1.937	0.054	192±77	317.2	1.059	0.291	Asteraceae
<i>Pilosella praecaltia</i>	9±3	-1.9	1.233	0.218	62±30	4.9	3.472	0.001	Asteraceae
<i>Rumex acetosella</i>	2±2	-0.8	0.669	0.504	749±194	346.2	2.513	0.013	Polygonaceae
<i>Trifolium repens</i>	-6±3	-7.4	1.393	0.165	124±64	-185.9	1.097	0.274	Fabaceae
Native grasses, tussocks, sedges and rushes									
<i>Anthosachne solandri</i>	16±3	3.1	2.657	0.008	118±76	-62.8	0.563	0.574	Poaceae
<i>Chionochloa flarescens</i>	6±3	-1.2	0.706	0.481	199±116	-104.8	0.967	0.335	Poaceae
<i>Deyeuxia acenoides</i>	2±3	-0.1	0.342	0.733	232±115	5.5	0.422	0.673	Poaceae
<i>Festuca novae-zelandiae</i>	24±4	1.7	2.16	0.032	28±31	-358.2	2.038	0.042	Poaceae
<i>Koeleria novozelandica</i>	9±3	2.5	1.686	0.093	23±7	-164.4	2.47	0.014	Poaceae
<i>Luzula rufa</i>	-1±3	-1.1	0.149	0.882	509±155	-61.9	0.853	0.394	Juncaceae
<i>Poa colensoi</i>	22±4	1	2.723	0.007	457±150	206.3	0.014	0.989	Poaceae
<i>Ryhdosperma setifolium</i>	8±3	-1.2	0.627	0.531	79±46	218.4	1.541	0.124	Poaceae
Exotic grasses, sedges and rushes									
<i>Agrostis capillaris</i>	20±5	-1.3	1.889	0.06	195±83	257.7	0.879	0.38	Poaceae
<i>Anthoxanthum odoratum</i>	21±4	3.6	2.695	0.007	128±58	152.9	0.851	0.396	Poaceae
Native woody plants									
<i>Acrothamnus colensoi</i>	16±3	1.5	1.846	0.066	101±43	82.1	0.776	0.439	Ericaceae
<i>Dracophyllum rosmarinifolium</i>	11±3	-1.3	1.038	0.3	14±7	4.4	0.358	0.721	Ericaceae
<i>Gaultheria depressa</i>	4±3	0.4	0.491	0.624	286±132	1.4	0.616	0.538	Ericaceae
<i>Leucopogon fraseri</i>	4±3	1.4	0.631	0.528	194±106	10.3	0.841	0.401	Ericaceae
<i>Olearia cymbifolia</i>	5±2	3.3	0.827	0.409	66±59	-144.9	0.474	0.636	Asteraceae
<i>Ozothamnus vacuilliersii</i>	3±3	-0.4	0.372	0.71	28±23	-125.1	1.292	0.197	Asteraceae
<i>Pimelea oreophila</i>	4±2	-0.3	0.699	0.485	168±102	-14.1	2.552	0.011	Thymelaeaceae
Exotic woody plants									
<i>Rosa rubiginosa</i>	13±3	4.8	1.734	0.084	93±72	-148.1	0.73	0.466	Rosaceae

Table 1: Change in mean cover scores and summed HF intercepts (%± S.E.M.) of common species in 146 plots established randomly (n=80) in 2007 and paired along fencelines (n=66) in 2008, and remeasured in 2016 throughout Molesworth. Common species occurred in >32 of 80 randomly located plots measured in 2016. Coefficients of slope (converted to change between 2008 and 2016, %) were extracted from a random effects model summarised in Supplementary Tables 6 and 7.

Species	m1952±s1952	m1960±s1960	m1972±s1972	m1987±s1987	m1989±s1989	m1995±s1995	m2001±s2001	m2006±s2006	m2007±s2007	m2008±s2008	2010–2015±	m2016±s2016	family
Native herbaceous plants													
<i>Aciphylla aurea</i>	0.11±0.07	0.0	0.6±0.4	0.06±0.01	0.0	0.0	0.1±0.1	0.05±0.05	0.46±0.06	0.39±0.06	0.33±0.17	0.42±0.04	Apiaceae
<i>Anisotome gramatica</i>	0.0	0.7±0.4	0.1±0.1	0.41±0.02	1.05±0.29	1.15±0.3	1.25±0.32	1.45±0.31	0.44±0.06	0.56±0.06	0.33±0.17	0.52±0.04	Apiaceae
<i>Celmisia gracilenta</i>	0.74±0.18	1.6±0.4	0.9±0.48	0.31±0.02	0.0	0.05±0.05	0.35±0.21	0.5±0.2	0.79±0.05	0.8±0.05	0.56±0.18	0.81±0.03	Asteraceae
<i>Celmisia spectabilis</i>	0.11±0.07	1.4±0.52	0.9±0.41	0.54±0.03	0.05±0.05	0.0	0.0	0.05±0.05	0.8±0.01	0.7±0.09	0.56±0.29	0.84±0.08	Asteraceae
<i>Rauvolfia subsericea</i>	0.74±0.18	0.0	0.3±0.3	0.01±0.01	0.63±0.23	1.0±0.27	0.95±0.29	1.1±0.29	0.54±0.06	0.74±0.06	0.67±0.33	0.63±0.04	Asteraceae
<i>Wahlenbergia altomarginata</i>	1.68±0.15	2.2±0.51	1.6±0.4	0.53±0.02	1.05±0.31	1.35±0.37	1.0±0.29	0.9±0.29	0.92±0.03	0.71±0.06	0.89±0.11	0.84±0.03	Campanulaceae
Exotic herbaceous plants													
<i>Hieracium pollicifera</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.35±0.06	0.05±0.03	0.0	0.32±0.04	Asteraceae
<i>Hypochaeris radicata</i>	1.37±0.17	1.8±0.66	1.4±0.54	0.61±0.02	1.53±0.28	0.95±0.25	0.8±0.26	0.5±0.21	0.81±0.04	0.82±0.05	0.78±0.15	0.85±0.03	Asteraceae
<i>Pilosella caespitosa</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.01±0.08	0.77±0.06	1.01±0.11	1.01±0.05	Asteraceae
<i>Pilosella officinarum</i>	0.0	0.0	0.4±0.31	0.75±0.04	2.21±0.33	2.6±0.39	2.9±0.46	3.4±0.45	2.22±0.21	2.24±0.17	2.56±0.5	2.62±0.15	Asteraceae
<i>Pilosella pratensis</i>	0.0	0.0	0.0	0.0	0.79±0.26	0.85±0.24	1.3±0.34	1.55±0.35	0.3±0.06	0.56±0.08	0.0	0.5±0.05	Asteraceae
<i>Rumex acetosella</i>	1.63±0.16	2.7±0.47	2.0±0.56	0.73±0.02	2.37±0.31	2.05±0.3	1.75±0.3	2.0±0.29	0.91±0.03	0.95±0.03	1.33±0.24	0.95±0.02	Polygonaceae
<i>Trifolium repens</i>	1.0±0.24	0.1±0.1	0.2±0.2	0.39±0.03	1.58±0.41	1.25±0.35	0.85±0.29	0.95±0.29	0.68±0.1	0.61±0.09	1.0±0.5	0.52±0.05	Fabaceae
Native grasses, tussocks, sedges and rushes													
<i>Anthosachne solandri</i>	1.37±0.11	0.0	0.0	0.02±0.01	0.63±0.27	0.3±0.21	0.35±0.21	0.15±0.08	0.41±0.06	0.32±0.06	0.67±0.17	0.53±0.04	Poaceae
<i>Chionochoa flavescens</i>	2.2±0.63	0.4±0.27	0.4±0.27	0.03±0.01	0.11±0.11	0.15±0.15	0.15±0.15	0.2±0.2	0.61±0.09	0.14±0.04	0.78±0.36	0.46±0.06	Poaceae
<i>Dryoxia aeneoides</i>	0.58±0.21	0.4±0.16	0.0	0.01±0.0	0.16±0.12	0.35±0.18	0.2±0.16	0.25±0.18	0.44±0.06	0.64±0.06	0.56±0.18	0.55±0.04	Poaceae
<i>Festuca novae-zelandiae</i>	3.84±0.14	0.0	1.1±0.38	0.03±0.01	0.0	0.0	0.0	0.0	0.98±0.09	0.8±0.12	0.67±0.29	1.14±0.08	Poaceae
<i>Koeleria novozelandica</i>	0.68±0.13	0.0	0.0	0.09±0.01	0.0	0.0	0.0	0.0	0.38±0.05	0.05±0.03	0.0	0.32±0.04	Poaceae
<i>Luzula rufa</i>	0.68±0.13	0.0	1.3±0.45	0.52±0.02	1.79±0.3	1.75±0.3	1.5±0.29	1.35±0.28	0.78±0.05	0.86±0.04	0.44±0.18	0.81±0.03	Juncaceae
<i>Poa colensoi</i>	1.89±0.3	3.9±0.23	3.0±0.3	0.86±0.04	2.47±0.41	2.35±0.39	2.75±0.36	2.25±0.4	1.19±0.07	1.0±0.6	1.33±0.24	1.31±0.06	Poaceae
<i>Rytidosperma setifolium</i>	0.26±0.1	3.6±0.58	3.7±0.47	0.19±0.02	1.0±0.32	0.8±0.3	0.9±0.31	0.75±0.28	1.11±0.11	0.92±0.1	0.67±0.33	1.1±0.08	Poaceae
Exotic grasses, sedges and rushes													
<i>Agrostis capillaris</i>	0.37±0.14	0.3±0.3	1.7±0.52	0.3±0.03	3.63±0.36	3.1±0.45	3.5±0.34	3.5±0.35	0.62±0.07	1.11±0.1	1.56±0.65	1.01±0.06	Poaceae
<i>Anthoxanthum odoratum</i>	0.16±0.09	0.0	0.3±0.3	0.3±0.03	0.89±0.3	0.9±0.33	0.7±0.3	0.55±0.26	0.66±0.07	0.76±0.06	2.44±0.6	0.9±0.06	Poaceae
Native woody plants													
<i>Acrothamnus colensoi</i>	0.16±0.09	0.0	0.6±0.4	0.15±0.02	0.21±0.16	0.35±0.18	0.4±0.22	0.55±0.26	1.01±0.08	1.0±0.1	1.0±0.37	1.18±0.07	Ericaceae
<i>Dracophyllum rosmarinifolium</i>	0.11±0.07	0.0	0.0	0.11±0.02	0.0	0.0	0.0	0.0	0.76±0.12	0.3±0.06	0.0	0.67±0.08	Ericaceae
<i>Gaultheria depressa</i>	0.0	1.0±0.45	1.1±0.48	0.01±0.0	0.53±0.25	0.45±0.22	0.5±0.24	0.45±0.25	0.48±0.07	0.68±0.09	0.33±0.24	0.61±0.06	Ericaceae
<i>Leucopogon fraseri</i>	0.53±0.16	1.4±0.58	1.1±0.57	0.36±0.02	1.42±0.38	1.35±0.36	1.45±0.37	1.55±0.34	0.78±0.06	0.94±0.08	0.89±0.31	0.9±0.06	Ericaceae
<i>Olearia cymbifolia</i>	0.0	0.0	0.0	0.03±0.01	0.0	0.0	0.0	0.0	0.42±0.06	0.14±0.04	0.44±0.18	0.34±0.04	Asteraceae
<i>Ozobothamus vacillansii</i>	0.37±0.14	0.0	0.0	0.0	0.0	0.0	0.05±0.05	0.1±0.07	0.46±0.07	0.45±0.08	0.0	0.49±0.05	Asteraceae
<i>Pinus ooreophila</i>	0.0	0.0	0.0	0.08±0.01	0.53±0.22	0.35±0.2	0.6±0.22	0.55±0.21	0.74±0.05	0.33±0.06	0.22±0.15	0.6±0.04	Thymelaeaceae
Exotic woody plants													
<i>Rosa rubiginosa</i>	0.37±0.11	0.0	0.0	0.04±0.01	0.0	0.0	0.0	0.0	0.54±0.07	0.12±0.05	1.44±0.41	0.49±0.07	Rosaceae

Table 2: Mean cover scores ( $\pm$  S.E.M.) of common species from 802 plots measured between 1952 to 2016. Plots measured in 1952, 1960 and 1972 were subjectively located in north and western Molesworth. The 1987 survey plots were haphazardly located throughout. Plots measured between 1989–2007 were in northern Molesworth. Plots measured in 2007, 2010–2015 and 2016 were randomly and systematically located throughout Molesworth. Common species occurred in >32 of 80 randomly located plots measured in 2016. Raw data used to calculate these means was also used in Decorana ordinations, and GLMM models of changes in the proportions of woody and exotic species

Species	HFI±change	Cover 2007±	Cover 2016±	DCA 1	DCA2	Family
Native herbaceous plants						
<i>Aciphylla aurea</i>	±	±	±			
	1.11±0.48	0.46±0.06	0.51±0.06	0.55	0.04	Apiaceae
<i>Anisotome aromatica</i>	0.31±0.32	0.44±0.06	0.44±0.06	0.6	2.06	Apiaceae
<i>Celmisia gracilentia</i>	0.50±0.22	0.79±0.05	0.78±0.05	1.6	1.64	Asteraceae
<i>Celmisia spectabilis</i>	0.28±0.54	0.8±0.1	0.89±0.11	0.41	1.56	Asteraceae
<i>Raoulia subsericea</i>	0.01±0.08	0.54±0.06	0.56±0.06	1.3	1.87	Asteraceae
<i>Wahlenbergia albomarginata</i>	1.21±0.33	0.92±0.03	0.92±0.03	1.64	1.29	Campanulaceae
Exotic herbaceous plants						
	±	±	±			
<i>Hieracium polliciaae</i>	1.24±0.47	0.35±0.06	0.54±0.06	1.83	0.34	Asteraceae
<i>Hypochaeris radicata</i>	0.60±0.24	0.81±0.04	0.85±0.04	1.63	1	Asteraceae
<i>Pilosella caespitosa</i>	-2.15±1.06	1.01±0.08	1.07±0.08	2.06	1.41	Asteraceae
<i>Pilosella officinarum</i>	0.61±0.60	2.22±0.21	2.59±0.21	2.65	1.24	Asteraceae
<i>Pilosella praecalta</i>	0.70±0.20	0.3±0.06	0.45±0.06	1.99	2.32	Asteraceae
<i>Rumex acetosella</i>	0.72±0.39	0.91±0.03	0.99±0.03	1.83	1.48	Polygonaceae
<i>Trifolium repens</i>	-4.09±2.14	0.68±0.1	0.51±0.07	3.8	1.72	Fabaceae
Native grasses, tussocks, sedges and rushes						
	±	±	±			
<i>Anthosachne solandri</i>	2.36±0.76	0.41±0.06	0.66±0.06	2.75	0.57	Poaceae
<i>Chionochloa flavescens</i>	10.50±3.08	0.61±0.09	0.76±0.1	0.62	-0.23	Poaceae
<i>Deyeuxia avenoides</i>	0.16±0.28	0.44±0.06	0.51±0.06	1.98	0.15	Poaceae
<i>Festuca novae-zelandiae</i>	1.89±1.59	0.98±0.09	1.35±0.1	2.21	0.81	Poaceae
<i>Koeleria novozelandica</i>	1.38±0.40	0.38±0.05	0.44±0.06	2.53	0.87	Poaceae
<i>Luzula rufa</i>	0.00±0.34	0.78±0.05	0.76±0.05	1.25	1.58	Juncaceae
<i>Poa colensoi</i>	2.28±1.18	1.19±0.07	1.32±0.07	1.5	2.1	Poaceae
<i>Rytidosperma setifolium</i>	0.95±1.51	1.11±0.11	1.18±0.11	1.44	2.4	Poaceae
Exotic grasses, sedges and rushes						
	±	±	±			
<i>Agrostis capillaris</i>	2.11±1.40	0.62±0.07	0.85±0.09	2.28	1.75	Poaceae
<i>Anthoxanthum odoratum</i>	0.26±2.20	0.66±0.07	0.89±0.08	2.9	0.26	Poaceae
Native woody plants						
	±	±	±			
<i>Acrothamnus colensoi</i>	5.03±1.21	1.01±0.08	1.18±0.1	1.5	0.67	Ericaceae
<i>Dracophyllum rosmarinifolium</i>	7.30±2.01	0.76±0.12	0.86±0.14	-0.23	0.04	Ericaceae
<i>Gaultheria depressa</i>	0.62±0.49	0.48±0.07	0.56±0.08	0.31	2.22	Ericaceae
<i>Leucopogon fraseri</i>	1.15±0.37	0.78±0.06	0.76±0.06	1.81	1.48	Ericaceae
<i>Olearia cymbifolia</i>	1.68±0.53	0.42±0.06	0.5±0.07	0.76	-0.04	Asteraceae
<i>Ozothamnus vaucilliersii</i>	0.76±0.42	0.46±0.07	0.49±0.07	1.18	0.72	Asteraceae
<i>Pimelea oreophila</i>	0.45±0.24	0.74±0.05	0.76±0.05	1.76	1.18	Thymelaeaceae
Exotic woody plants						
	±	±	±			
<i>Rosa rubiginosa</i>	3.25±1.37	0.54±0.07	0.76±0.1	3.74	0.75	Rosaceae

Table 3: Changes in common species HFI's from 2007 to 2016 from 80 random plots established on 20 lines in 2007. Mean ground cover scores (20 m × 20 m, <0.1 m high) and DCA species scores derived from cover data are from the same 80 plots. Common species occurred in >32 of 80 plots in 2016.

	Estimate $\pm$ Std Error	Z value	P value
Woody	-2.51 $\pm$ 0.10	-25.35	0.001
Intercept	1.95 $\pm$ 0.04	55.43	0.001
Woody x Native	1.24 $\pm$ 0.10	12.82	0.001
Native	0.80 $\pm$ 0.03	28.32	0.001
Altitude x Native	0.40 $\pm$ 0.03	15.51	0.001
Oversown x Fenced	0.35 $\pm$ 0.15	2.25	0.024
Altitude	-0.34 $\pm$ 0.04	-9.96	0.001
Fenced	-0.33 $\pm$ 0.09	-3.67	0.001
Year	0.29 $\pm$ 0.03	10.39	0.001
Year x Woody	0.23 $\pm$ 0.03	9.15	0.001
Oversown	0.19 $\pm$ 0.07	2.72	0.007
Fenced x Native	0.18 $\pm$ 0.05	3.76	0.001
Oversown x Native	-0.16 $\pm$ 0.04	-3.59	0.001
Northing x Native	-0.15 $\pm$ 0.02	-6.10	0.001
Terrace x Woody	-0.15 $\pm$ 0.05	-2.69	0.007
Oversown x Woody	-0.13 $\pm$ 0.06	-2.26	0.024
Northing (m)	0.13 $\pm$ 0.03	4.07	0.001
Northing x Fenced	0.12 $\pm$ 0.07	1.79	0.073
Year x Native	-0.12 $\pm$ 0.02	-6.18	0.001
Easting x Fenced	-0.12 $\pm$ 0.07	-1.52	0.128
Year x easting	-0.11 $\pm$ 0.02	-5.08	0.001
Terrace x Fenced	0.10 $\pm$ 0.10	1.03	0.304
Altitude x Oversown	0.08 $\pm$ 0.06	1.35	0.177
Year x Easting	-0.08 $\pm$ 0.02	-4.32	0.001
Easting x Native	-0.07 $\pm$ 0.02	-3.12	0.002
Northing x Woody	-0.07 $\pm$ 0.03	-2.33	0.020
Easting x y	-0.06 $\pm$ 0.02	-2.79	0.005
Year x altitude	0.06 $\pm$ 0.03	2.42	0.016
Year x Terrace	-0.06 $\pm$ 0.04	-1.62	0.105
Terrace	0.05 $\pm$ 0.06	0.94	0.347
Year x Fenced	-0.05 $\pm$ 0.04	-1.16	0.244
Altitude x Woody	-0.05 $\pm$ 0.03	-1.51	0.130
Easting x Oversown	0.04 $\pm$ 0.06	0.73	0.468
Altitude x Terrace	0.04 $\pm$ 0.04	1.17	0.242
Easting x Terrace	0.04 $\pm$ 0.04	0.94	0.349
Northing x Terrace	-0.03 $\pm$ 0.04	-0.79	0.429
Altitude x Fenced	0.03 $\pm$ 0.05	0.59	0.557
Easting x Woody	-0.03 $\pm$ 0.03	-1.05	0.293
Easting x altitude	0.03 $\pm$ 0.02	1.59	0.111
Northing x altitude	-0.03 $\pm$ 0.02	-1.66	0.096
Year x Oversown	0.03 $\pm$ 0.04	0.68	0.495
Northing x Oversown	0.02 $\pm$ 0.06	0.36	0.715
Terrace x Oversown	0.02 $\pm$ 0.10	0.20	0.840

Fenced x Woody	-0.02 ± 0.06	-0.29	0.771
Easting (m)	0.01 ± 0.03	0.47	0.642
Terrace x Native	0.00 ± 0.04	0.03	0.978

Table 4: Coefficients from a GLMM ( $\pm$ S.E.) for numbers of vascular plant species from relevés measured between 1952 and 2016. Marginal  $R^2 = 0.709$ , Conditional  $R^2 = 0.815$ . Coefficients of location and time are scaled and are presented in order of effect size. A Poisson error term is specified in the model.

	Estimate $\pm$ Std Error	Z value	P value
Woody	-19.34 $\pm$ 1501.93	-0.01	0.990
Woody x Native	18.59 $\pm$ 1501.93	0.01	0.990
Intercept	1.61 $\pm$ 0.12	13.95	0.001
Oversown	0.54 $\pm$ 0.38	1.42	0.156
Native	0.52 $\pm$ 0.09	6.06	0.001
Easting x Oversown	-0.50 $\pm$ 0.36	-1.39	0.163
Altitude	-0.44 $\pm$ 0.09	-4.94	0.001
Northing (m)	0.42 $\pm$ 0.10	4.29	0.001
Altitude x Oversown	0.40 $\pm$ 0.10	3.99	0.001
Oversown x Fenced	0.37 $\pm$ 0.38	0.97	0.334
Easting x Fenced	-0.36 $\pm$ 0.13	-2.86	0.004
Fenced x Woody	-0.34 $\pm$ 0.14	-2.55	0.011
Altitude x Native	0.30 $\pm$ 0.05	5.78	0.001
Oversown x Native	-0.29 $\pm$ 0.11	-2.57	0.010
Northing x Native	-0.28 $\pm$ 0.05	-5.34	0.001
Easting x Woody	-0.26 $\pm$ 0.07	-3.50	0.001
Easting x y	0.26 $\pm$ 0.07	3.62	0.001
Fenced	-0.20 $\pm$ 0.19	-1.08	0.278
Altitude x Terrace	0.19 $\pm$ 0.10	1.81	0.070
Easting x Native	-0.16 $\pm$ 0.05	-2.91	0.004
Altitude x Woody	-0.15 $\pm$ 0.07	-2.21	0.027
Northing x Terrace	-0.13 $\pm$ 0.11	-1.18	0.237
Terrace x Woody	-0.12 $\pm$ 0.13	-0.93	0.351
Terrace x Fenced	-0.12 $\pm$ 0.19	-0.60	0.551
Oversown x Woody	0.10 $\pm$ 0.16	0.60	0.547
Easting (m)	0.09 $\pm$ 0.08	1.16	0.247
Northing x Oversown	-0.08 $\pm$ 0.35	-0.23	0.821
Year	0.07 $\pm$ 0.04	1.57	0.117
Northing x altitude	0.07 $\pm$ 0.04	1.63	0.102
Year x Native	0.06 $\pm$ 0.04	1.53	0.125
Easting x Terrace	-0.06 $\pm$ 0.10	-0.57	0.570
Terrace x Oversown	0.05 $\pm$ 0.24	0.21	0.832
Terrace x Native	-0.05 $\pm$ 0.09	-0.55	0.586
Year x Terrace	-0.05 $\pm$ 0.04	-1.21	0.226
Altitude x Fenced	0.05 $\pm$ 0.12	0.42	0.673
Year x Oversown	-0.05 $\pm$ 0.05	-0.96	0.334
Northing x Fenced	0.04 $\pm$ 0.12	0.30	0.763
Fenced x Native	0.04 $\pm$ 0.11	0.32	0.750
Easting x altitude	0.03 $\pm$ 0.07	0.42	0.673
Year x Easting	0.02 $\pm$ 0.02	0.86	0.391
Northing x Woody	-0.01 $\pm$ 0.07	-0.23	0.819

Terrace	-0.01 ± 0.15	-0.05	0.962
Year x altitude	-0.01 ± 0.02	-0.23	0.817
Year x Fenced	-0.01 ± 0.05	-0.10	0.918
Year x Woody	-0.00 ± 0.05	-0.05	0.959
Year x easting	0.00 ± 0.02	0.06	0.955

Table 5: Coefficients from a GLMM ( $\pm$ S.E.) for numbers of vascular plant species from HFI plots measured between 2006 and 2016. Marginal  $R^2 = 0.604$ , Conditional  $R^2 = 0.697$ . Coefficients of location and time are scaled and are presented in order of effect size. A Poisson error term is specified in the model.



	Estimate $\pm$ Std Error	Z value	P value
Intercept	-0.41 $\pm$ 0.10	-4.16	0.001
Altitude x Terrace	0.19 $\pm$ 0.07	2.52	0.012
Terrace x Oversown	0.18 $\pm$ 0.18	1.02	0.309
Northing x Oversown	-0.14 $\pm$ 0.18	-0.76	0.447
Terrace x Fenced	-0.12 $\pm$ 0.15	-0.80	0.422
Oversown	-0.11 $\pm$ 0.21	-0.54	0.587
Oversown x Fenced	0.11 $\pm$ 0.20	0.54	0.587
Easting (m)	0.07 $\pm$ 0.05	1.55	0.122
Easting x y	0.07 $\pm$ 0.05	1.39	0.164
Year	0.06 $\pm$ 0.02	3.44	0.001
Terrace	-0.06 $\pm$ 0.10	-0.63	0.527
Easting x Fenced	-0.03 $\pm$ 0.11	-0.31	0.755
Easting x Terrace	-0.03 $\pm$ 0.07	-0.46	0.643
Fenced	0.03 $\pm$ 0.11	0.26	0.795
Easting x Oversown	0.03 $\pm$ 0.15	0.18	0.856
Altitude	-0.03 $\pm$ 0.05	-0.52	0.603
Easting x altitude	-0.03 $\pm$ 0.05	-0.54	0.589
Northing x Terrace	-0.02 $\pm$ 0.09	-0.25	0.803
Year x Oversown	-0.02 $\pm$ 0.02	-0.94	0.350
Altitude x Oversown	0.02 $\pm$ 0.09	0.20	0.840
Year x altitude	-0.01 $\pm$ 0.01	-1.15	0.252
Year x easting	-0.01 $\pm$ 0.01	-0.94	0.348
Northing x Fenced	-0.01 $\pm$ 0.10	-0.12	0.907
Altitude x Fenced	-0.01 $\pm$ 0.09	-0.11	0.915
Northing (m)	0.01 $\pm$ 0.05	0.09	0.925
Year x Terrace	-0.01 $\pm$ 0.02	-0.21	0.833
Year x Fenced	0.01 $\pm$ 0.02	0.22	0.829
Year x Easting	-0.00 $\pm$ 0.01	-0.38	0.705
Northing x altitude	0.00 $\pm$ 0.04	0.11	0.914

Table 6: Coefficients from a GLMM ( $\pm$  S.E.) for recce cover scores of common species in 146 plots established randomly ( $n=80$ ) in 2007 and paired along fencelines ( $n=66$ ) in 2008, and remeasured in 2016 throughout Molesworth. Common species occurred in  $>32$  of 80 randomly located plots measured in 2016.  $R^2 = NA$ . Coefficients of location and time are scaled and are presented in order of effect size. A Poisson error term is specified in the model. Altitude, eastings and northings are scaled from m a.s.l.

	Estimate $\pm$ Std Error	Z value	P value
Easting x Oversown	145.67 $\pm$ 102.20	1.43	0.15
Easting (m)	-114.93 $\pm$ 63.50	-1.81	0.07
Terrace x Oversown	101.00 $\pm$ 90.39	1.12	0.26
Easting x y	87.53 $\pm$ 31.84	2.75	0.01
Northing x Terrace	81.41 $\pm$ 59.86	1.36	0.17
Easting x Terrace	74.52 $\pm$ 57.27	1.30	0.19
Altitude x Terrace	67.05 $\pm$ 26.43	2.54	0.01
Northing (m)	-57.98 $\pm$ 57.84	-1.00	0.32
Altitude x Oversown	40.66 $\pm$ 38.36	1.06	0.29
Oversown	29.20 $\pm$ 583.69	0.05	0.96
Altitude	-28.05 $\pm$ 27.18	-1.03	0.30
Intercept	27.08 $\pm$ 55.37	0.49	0.62
Terrace	-23.25 $\pm$ 53.97	-0.43	0.67
Northing x altitude	20.60 $\pm$ 12.11	1.70	0.09
Oversown x Fenced	-11.70 $\pm$ 20.98	-0.56	0.58
Year x Oversown	-7.89 $\pm$ 5.50	-1.44	0.15
Northing x Fenced	-7.61 $\pm$ 7.42	-1.03	0.30
Northing x Oversown	7.52 $\pm$ 393.66	0.02	0.98
Year	6.68 $\pm$ 3.96	1.69	0.09
Easting x Fenced	5.09 $\pm$ 6.32	0.81	0.42
Easting x altitude	3.47 $\pm$ 7.42	0.47	0.64
Terrace x Fenced	2.66 $\pm$ 17.53	0.15	0.88
Year x easting	-2.34 $\pm$ 2.26	-1.03	0.30
Year x Terrace	-1.29 $\pm$ 3.50	-0.37	0.71
Year x Easting	1.11 $\pm$ 1.47	0.76	0.45
Year x altitude	-0.97 $\pm$ 1.37	-0.70	0.48
Year x Fenced	-0.81 $\pm$ 1.92	-0.42	0.67
Altitude x Fenced	0.70 $\pm$ 7.56	0.09	0.93
Fenced	-0.33 $\pm$ 18.72	-0.02	0.99

Table 7: Coefficients from a GLMM ( $\pm$  S.E.) for summed HF intercepts of common species in 146 plots established randomly ( $n=80$ ) in 2007 and paired along fencelines ( $n=66$ ) in 2008, and remeasured in 2016 throughout Molesworth. Common species occurred in  $>32$  of 80 randomly located plots measured in 2016.  $R^2 = 1$ . Coefficients of location and time are scaled and are presented in order of effect size. A Poisson error term is specified in the model. Altitude, eastings and northings are scaled from m a.s.l.

	Estimate $\pm$ Std Error	Z value	P value
Intercept	4.21 $\pm$ 0.16	26.01	0.001
Woody	-2.53 $\pm$ 0.21	-11.89	0.001
Oversown	1.91 $\pm$ 0.72	2.67	0.008
Native x Woody	1.89 $\pm$ 0.21	8.93	0.001
Easting x Oversown	-1.00 $\pm$ 0.52	-1.92	0.054
Oversown x Native	-0.97 $\pm$ 0.20	-4.83	0.001
Northing x Oversown	0.94 $\pm$ 0.56	1.68	0.093
Altitude x Native	0.71 $\pm$ 0.08	9.09	0.001
Altitude	-0.69 $\pm$ 0.11	-6.28	0.001
Northing (m)	0.62 $\pm$ 0.13	4.76	0.001
Terrace x Woody	-0.54 $\pm$ 0.17	-3.08	0.002
Altitude x Oversown	0.48 $\pm$ 0.15	3.25	0.001
Northing x Native	-0.47 $\pm$ 0.10	-4.89	0.001
Oversown x Fenced	0.41 $\pm$ 0.52	0.80	0.423
Native	0.34 $\pm$ 0.14	2.50	0.013
Fenced x Native	0.34 $\pm$ 0.13	2.57	0.010
Oversown x Woody	0.33 $\pm$ 0.19	1.71	0.088
Fenced x Woody	-0.29 $\pm$ 0.15	-1.89	0.059
Year	0.28 $\pm$ 0.10	2.89	0.004
Year x Oversown	-0.27 $\pm$ 0.13	-2.11	0.035
Northing x Woody	-0.27 $\pm$ 0.09	-2.86	0.004
Year x Woody	0.26 $\pm$ 0.07	3.76	0.001
Terrace x Fenced	-0.26 $\pm$ 0.29	-0.90	0.370
Altitude x Terrace	0.23 $\pm$ 0.14	1.72	0.086
Terrace	0.22 $\pm$ 0.19	1.18	0.240
Easting x Fenced	-0.20 $\pm$ 0.17	-1.17	0.243
Year x Native	-0.18 $\pm$ 0.06	-3.02	0.002
Year x easting	-0.17 $\pm$ 0.06	-3.00	0.003
Altitude x Fenced	-0.16 $\pm$ 0.14	-1.14	0.256
Altitude x Woody	-0.15 $\pm$ 0.09	-1.75	0.080
Easting x Woody	-0.14 $\pm$ 0.08	-1.78	0.075
Year x Terrace	-0.11 $\pm$ 0.11	-0.99	0.321
Easting (m)	-0.10 $\pm$ 0.13	-0.78	0.435
Northing x altitude	0.09 $\pm$ 0.05	1.71	0.088
Northing x Fenced	0.09 $\pm$ 0.17	0.53	0.599
Northing x Terrace	-0.08 $\pm$ 0.16	-0.52	0.601
Year x Easting	0.08 $\pm$ 0.04	1.96	0.051
Terrace x Native	-0.07 $\pm$ 0.17	-0.45	0.656
Year x altitude	0.05 $\pm$ 0.04	1.18	0.239
Easting x Terrace	-0.04 $\pm$ 0.15	-0.30	0.761
Terrace x Oversown	-0.04 $\pm$ 0.36	-0.12	0.903
Easting x Native	-0.04 $\pm$ 0.08	-0.49	0.624
Year x Fenced	0.03 $\pm$ 0.07	0.46	0.644

Fenced	-0.03 ± 0.26	-0.10	0.922
Easting x altitude	0.02 ± 0.08	0.20	0.840
Easting x y	0.01 ± 0.08	0.13	0.900

Table 8: Coefficients from a GLMM ( $\pm$  S.E.) for total HFI (an index of biomass) from analysis of plots measured between 1989 and 2016. Marginal  $R^2 = 0.434$ , Conditional  $R^2 = 0.53$ . Coefficients of location and time are scaled and are presented in order of effect size. A negative-binomial error term is specified in the model.

	Estimate $\pm$ Std Error	Z value	P value
Easting x Oversown	-2.91 $\pm$ 1.28	-2.28	0.023
Oversown	1.77 $\pm$ 1.79	0.99	0.322
Northing x Oversown	0.99 $\pm$ 1.37	0.72	0.470
Intercept	0.93 $\pm$ 0.35	2.65	0.008
Altitude	0.86 $\pm$ 0.24	3.60	0.001
Terrace x Oversown	0.78 $\pm$ 0.92	0.86	0.392
Altitude x Oversown	0.68 $\pm$ 0.37	1.83	0.067
Northing (m)	-0.57 $\pm$ 0.28	-1.99	0.046
Fenced x Oversown	0.45 $\pm$ 1.29	0.35	0.727
Altitude x Fenced	-0.43 $\pm$ 0.36	-1.19	0.236
Northing x Fenced	0.34 $\pm$ 0.41	0.83	0.408
Terrace x Fenced	-0.30 $\pm$ 0.73	-0.41	0.680
Year x Terrace	-0.24 $\pm$ 0.04	-6.32	0.001
Easting x altitude	0.23 $\pm$ 0.20	1.17	0.241
Terrace	-0.23 $\pm$ 0.40	-0.58	0.563
Easting (m)	-0.21 $\pm$ 0.30	-0.71	0.480
Year x easting	-0.20 $\pm$ 0.02	-10.42	0.001
Fenced	0.18 $\pm$ 0.63	0.28	0.776
Year x Oversown	0.15 $\pm$ 0.05	2.92	0.003
Easting x Terrace	-0.14 $\pm$ 0.38	-0.36	0.720
Year	0.12 $\pm$ 0.03	3.54	0.001
Altitude x Terrace	0.11 $\pm$ 0.34	0.32	0.748
Year x Easting	0.09 $\pm$ 0.01	6.72	0.001
Year x altitude	0.09 $\pm$ 0.01	5.92	0.001
Easting x y	0.07 $\pm$ 0.20	0.37	0.714
Easting x Fenced	0.04 $\pm$ 0.44	0.10	0.920
Year x Fenced	0.04 $\pm$ 0.02	1.97	0.049
Northing x altitude	-0.02 $\pm$ 0.13	-0.16	0.873
Northing x Terrace	0.00 $\pm$ 0.39	0.01	0.992

Table 9: Coefficients from a binomial GLMM ( $\pm$  S.E.) of the proportion of native plants from HFI plots measured between 1989 and 2016. Marginal  $R^2 = 0.486$ , Conditional  $R^2 = 0.996$ . Coefficients of location and time are scaled and are presented in order of effect size. A binomial error term is specified in the model.

	Estimate $\pm$ Std Error	Z value	P value
Oversown	4.08 $\pm$ 2.34	1.75	0.081
Easting x Oversown	-3.77 $\pm$ 1.68	-2.25	0.024
Fenced x Oversown	-3.19 $\pm$ 1.71	-1.86	0.062
Northing x Oversown	2.97 $\pm$ 1.79	1.66	0.097
Intercept	-1.93 $\pm$ 0.46	-4.22	0.001
Fenced	1.53 $\pm$ 0.82	1.86	0.062
Terrace x Fenced	-1.44 $\pm$ 0.96	-1.50	0.132
Altitude x Fenced	-0.89 $\pm$ 0.47	-1.88	0.060
Northing (m)	-0.84 $\pm$ 0.37	-2.27	0.023
Terrace x Oversown	0.84 $\pm$ 1.20	0.70	0.483
Altitude x Terrace	0.76 $\pm$ 0.45	1.68	0.093
Terrace	-0.70 $\pm$ 0.52	-1.35	0.177
Easting x Fenced	0.49 $\pm$ 0.58	0.84	0.398
Northing x Fenced	0.45 $\pm$ 0.54	0.84	0.402
Altitude x Oversown	0.38 $\pm$ 0.47	0.80	0.423
Northing x Terrace	-0.22 $\pm$ 0.51	-0.43	0.666
Year	0.19 $\pm$ 0.04	4.99	0.001
Year x Fenced	-0.12 $\pm$ 0.04	-3.04	0.002
Northing x altitude	-0.11 $\pm$ 0.17	-0.66	0.509
Easting (m)	0.08 $\pm$ 0.39	0.21	0.832
Year x Oversown	0.08 $\pm$ 0.05	1.62	0.106
Easting x altitude	-0.08 $\pm$ 0.26	-0.31	0.756
Easting x y	0.06 $\pm$ 0.26	0.23	0.820
Altitude	-0.06 $\pm$ 0.31	-0.18	0.854
Year x altitude	-0.05 $\pm$ 0.02	-2.34	0.019
Year x Easting	0.04 $\pm$ 0.02	1.68	0.093
Easting x Terrace	-0.03 $\pm$ 0.50	-0.06	0.949
Year x easting	0.03 $\pm$ 0.02	1.14	0.253
Year x Terrace	0.02 $\pm$ 0.05	0.47	0.639

Table 10: Coefficients from a binomial GLMM ( $\pm$  S.E.) of the proportion of woody plants from HFI plots measured between 1989 and 2016. Marginal  $R^2 = 0.305$ , Conditional  $R^2 = 0.997$ . Coefficients of location and time are scaled and are presented in order of effect size.

A binomial error term is specified in the model.

	Estimate $\pm$ Std Error	Z value	P value
Intercept	2.27 $\pm$ 0.04	52.85	0.001
Altitude	0.28 $\pm$ 0.04	6.86	0.001
Oversown	-0.26 $\pm$ 0.10	-2.62	0.009
Oversown x Fenced	0.19 $\pm$ 0.25	0.76	0.446
Easting x y	0.12 $\pm$ 0.03	3.38	0.001
Easting x Fenced	-0.11 $\pm$ 0.11	-0.95	0.342
Terrace	-0.09 $\pm$ 0.07	-1.30	0.193
Year x Oversown	-0.08 $\pm$ 0.04	-1.93	0.054
Northing (m)	-0.08 $\pm$ 0.04	-2.00	0.045
Northing x Fenced	0.07 $\pm$ 0.10	0.68	0.494
Northing x Oversown	-0.07 $\pm$ 0.09	-0.72	0.473
Year x Terrace	0.07 $\pm$ 0.04	1.57	0.117
Terrace x Oversown	0.06 $\pm$ 0.15	0.38	0.705
Altitude x Terrace	0.05 $\pm$ 0.06	0.88	0.380
Easting x altitude	0.05 $\pm$ 0.03	1.72	0.085
Terrace x Fenced	0.04 $\pm$ 0.15	0.27	0.790
Easting (m)	0.04 $\pm$ 0.04	1.08	0.278
Altitude x Fenced	0.04 $\pm$ 0.08	0.47	0.639
Fenced	-0.04 $\pm$ 0.12	-0.30	0.760
Easting x Oversown	-0.04 $\pm$ 0.09	-0.40	0.688
Year x easting	-0.03 $\pm$ 0.03	-1.35	0.176
Year x altitude	-0.03 $\pm$ 0.03	-1.05	0.292
Altitude x Oversown	0.03 $\pm$ 0.09	0.31	0.758
Northing x altitude	0.02 $\pm$ 0.03	0.63	0.529
Year x Easting	0.01 $\pm$ 0.02	0.72	0.474
Easting x Terrace	0.01 $\pm$ 0.06	0.20	0.845
Year x Fenced	0.01 $\pm$ 0.04	0.12	0.901
Northing x Terrace	0.01 $\pm$ 0.07	0.08	0.937
Year	0.00 $\pm$ 0.03	0.08	0.938

Table 11: Coefficients from a GLMM ( $\pm$ S.E.) for DCA axis 1 scores from analysis of relevés measured between 1952 and 2016. Marginal  $R^2=0.283$ , Conditional  $R^2=0.959$ . Coefficients are scaled and are presented in order of effect size. A Gaussian error term is included in the model.

	Estimate $\pm$ Std Error	Z value	P value
Intercept	2.44 $\pm$ 0.04	69.13	0.001
Oversown x Fenced	0.35 $\pm$ 0.20	1.73	0.084
Altitude	-0.29 $\pm$ 0.03	-8.50	0.001
Fenced	-0.28 $\pm$ 0.10	-2.83	0.005
Terrace x Fenced	0.19 $\pm$ 0.12	1.54	0.122
Year	0.17 $\pm$ 0.03	6.86	0.001
Altitude x Fenced	0.16 $\pm$ 0.07	2.42	0.015
Oversown	0.13 $\pm$ 0.08	1.62	0.105
Easting x Oversown	0.13 $\pm$ 0.07	1.70	0.089
Year x Terrace	-0.13 $\pm$ 0.04	-3.47	0.001
Terrace	-0.12 $\pm$ 0.06	-2.09	0.036
Northing (m)	0.11 $\pm$ 0.03	3.60	0.001
Easting x Fenced	-0.09 $\pm$ 0.09	-0.97	0.331
Northing x Fenced	-0.09 $\pm$ 0.08	-1.05	0.295
Easting x Terrace	0.08 $\pm$ 0.05	1.70	0.089
Altitude x Oversown	0.07 $\pm$ 0.07	1.02	0.307
Terrace x Oversown	0.07 $\pm$ 0.12	0.62	0.537
Northing x Terrace	-0.07 $\pm$ 0.05	-1.35	0.178
Easting x altitude	0.06 $\pm$ 0.02	2.39	0.017
Year x Fenced	0.05 $\pm$ 0.04	1.32	0.187
Year x altitude	-0.04 $\pm$ 0.03	-1.80	0.072
Year x Oversown	-0.04 $\pm$ 0.04	-0.99	0.320
Northing x altitude	-0.03 $\pm$ 0.02	-1.42	0.154
Northing x Oversown	-0.03 $\pm$ 0.08	-0.33	0.743
Easting (m)	-0.02 $\pm$ 0.03	-0.83	0.407
Year x easting	-0.02 $\pm$ 0.02	-1.02	0.309
Year x Easting	-0.02 $\pm$ 0.02	-1.04	0.298
Altitude x Terrace	0.02 $\pm$ 0.05	0.32	0.746
Easting x y	-0.00 $\pm$ 0.03	-0.11	0.909

Table 12: Coefficients from a GLMM ( $\pm$ S.E.) for DCA axis 2 scores from analysis of relevés measured between 1952 and 2016. Marginal  $R^2 = 0.306$ , Conditional  $R^2 = 0.946$ . Coefficients of location and time are scaled and are presented in order of effect size. A Gaussian error term is included in the model.



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

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. A variety of methods have been employed for indexing shrub- and grassland biomass in New Zealand, usually without validation with measurements of biomass at a species level. There are some extensive networks including the Land Use and Carbon Analysis System (LUCAS) plot system (Beets and Brandon, 2011; Beets, 2012; Beets and Holt, 2012; Ministry for the Environment, 2013), the Department of Conservation (DOC)'s national five-yearly return measurement of plots (Bellingham et al., 2014), and the former New Zealand Forest Service's grassland plot system (Wraight, 1960, 1962, 1963, 1966; Holloway et al., 1963; Tanentzap et al., 2009). We also used uncalibrated and unsubstantiated methods to estimate biomass and cover of grassland and shrub vegetation on Molesworth. To improve the credibility of future tussock grassland and shrubland plot surveys, calibration exercises using direct measurement of biomass should be undertaken.

Vegetation monitoring on Molesworth has a seven-decade history. Such long-term plot-based vegetation monitoring studies will always have potential to suffer from changes in protocols, drift in implementation of unchanged protocols, variation in measurements from different field staff — or even changes from the same field staff as they age. There have been changes in methodology of plot measurement, nomenclature, access and funding, which has allowed the establishment of a more rigorous plot system. Access was originally restricted to use of horse tracks, making widespread establishment of randomly located

plots impractical. Plots established by Moore (1976) were restricted to northern Molesworth. Plots established by Wraight (1963) made use of a road between Hamner and St Arnaud. From the 1950s to 1970s road construction improved access and allowed widespread establishment of plots in the late 1980s. During analysis, several approaches have been undertaken to overcome these potential problems, which can be broken down into five broad issues; variation in plot locations, changes in field staff, changes in protocols, and errors made during species identification or processing of data.

### **1. Location and re-measurement of plots**

Plots subjectively located by Moore (1976) and Dickinson et al. (1992), and systematically located plots included in DOC's national monitoring programme, tended to sample modified tussock grasslands. Plots established by Wraight (1963) and Courtney and Arand (1994) were generally in areas with higher presence of native shrub and grassland species, rather than modified short-statured grasslands. Plots established in 2007 were at 200-m intervals along randomly located lines. Plots established in 2008 were subjectively located along fencelines. Changing plot locations has potential to bias results. We allowed for this, by explicitly modelling spatial location with each plot having x,y,z values (easting, northing and elevation in meters). More importantly we also allowed for this during interpretation and emphasis. Results for changes in functional groups were clear and consistent. Randomly located permanent plots provide the least bias, and when they are consistent with the wider plot network, results are most convincing. Results for changes in species composition were more ambiguous. These later results may even have been compounded by changes in plot locations over time.

Some plots were located close to one another (paired plots along fencelines were often < 100 m apart), while others on a national grid were >8 km apart. This meant there was a possibility of spatial auto-correlation among some surveys. We attempted to identify this

during analysis, and found little evidence. We added spatial covariance structures to candidate models. This did not improve model fit in any case. We calculated Moran's statistic for auto-correlation and found little evidence of a systematic problem.

The 80 plots established on 20 random transect lines in 2007 have provided the most useful data for determining change in Molesworth vegetation. Future monitoring should utilise these plots as a priority. DOC's tier 1 monitoring system has established  $20 \times 20$  plots in Molesworth on an 8 km grid, and not utilised the random transect system. One tier 1 plot was established  $\approx 220$  m from a 2007 random transect plot, when most if not all of the tier 1 plots could have been established at random plot sites. Such new plot systems waste the benefits of previous investments. Although plots on transects have potential to suffer from auto-correlation issues, they have several advantages over a grid system: 1) Randomly located transect lines with plots at 200 m spacings provide a more representative sample of steep areas, than do a planar grid system. 2) A grid system costs at least twice as much to establish the same number of plots, because it maximises the distance between plots. Time spent on travel is time not spent collecting data. 3) Fine scale plots-on-line sampling used on Molesworth has provided data suitable for spatial modelling. In some instances use of complex spatial analysis is beneficial. Although a transect-based system will inherently have less spatial independence between plots (e.g. Moran's index of spatial auto-correlation can show evidence of correlation among plots spaced closely), that can be allowed for quite easily with modern statistical approaches. It is more economic to use more complex analyses than walk or fly several km through mountainous terrain. Low rates of change and productivity means that plots on Molesworth should not be re-measured more frequently than every decade.

## **2. Variation among field staff**

Because of increased effort in counting all plants in plots in most recent surveys, and changes in the application of methodology, we are open to criticism that increases in species richness in relevés could be partly explained by changes in methods. The changes in methodology are probably less important than the normal variation that might be expected in field surveys. Studies comparing the ability of field workers to detect all species occurring in a plot, show that it is common for over 10–20% of species to be missed (Walker et al., 2016; Lavorel et al., 2008; Cook et al., 2010; Fitzpatrick et al., 2009; Brandon et al., 2003), or miss-identified. This rate increases with increasing plot size (Archaux et al., 2006, 2007). Estimates of cover tend to be much more consistent among workers (Sykes et al., 1983; Bergstedt et al., 2009), but see (Carlsson et al., 2005). Results from the Molesworth audit of two plots confirm that variability in cover estimates between operators is low (Figure 1), with differences between operators generally being less than one cover class. Quadrat plots in general are poor at assessing plant abundance either through estimates of cover, or counts of individual plants (Kennedy and Addison, 1987; McCune, 1997). Therefore, a point occurrence method (e.g. Levy and Madden, 1933; Scott, 1965; Wraight, 1960) is preferred as an index of abundance, cover or biomass (Jonasson, 1988). Nevertheless, audit results confirm that estimates of cover for the most common species are likely to be useful (Chiarucci et al., 1999; Gotfryd and Hansell, 1985; Kennedy and Addison, 1987). Likewise, repeatedly measured intercepts (e.g. HFI) are more reliable. For this reason an emphasis has been placed on using HFI data and only common species occurring in recce plots. Increasing species richness from HFI established in 2006, are consistent with estimates of cover from relevés. They also showed increases in the number of native herbaceous species from 1989 to 2016, in comparison to the increase in biomass

of woody native and exotic herbaceous species, particularly at plots in areas excluded from cattle. This provides reassurance during interpretation of results.

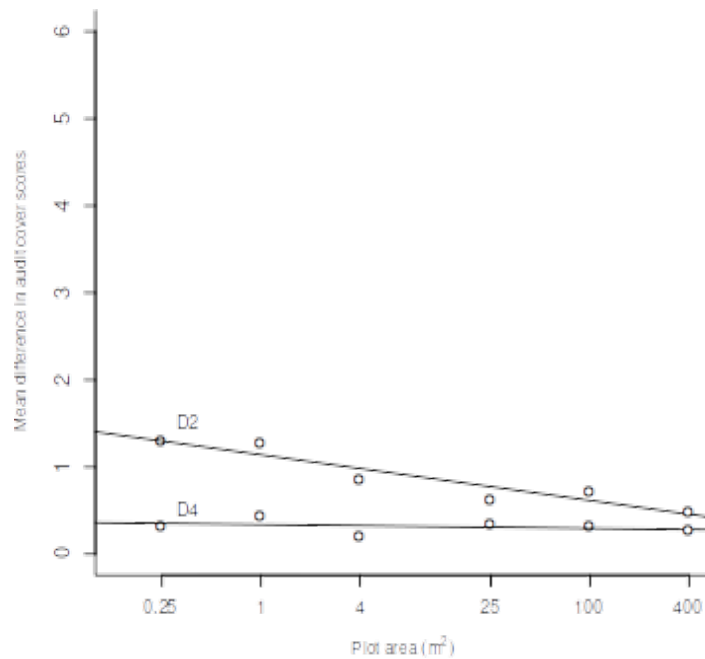


Figure 1: Relationship between audit cover scores and measurement scores for two plots measured on same day in 2016.

For Molesworth, two plots were independently and repeatedly measured on the same day by two groups of similarly experienced and highly qualified workers (Dr Sean Husheer and Dr Graeme Jane in one team, and Emiliana Guerra and Dr Alžbeta Cejková in another). There were no differences in identification of any species by either team, showing taxonomic standards were high in the 2016 survey. There was reasonable consistency in the overall number of species found by both teams, but both teams missed >20% of species. For plot D-2, one team found 35 species (including nine not found by the other team) and the other team 37 species (eleven not found by the other team). One team found 41 species in D-4 (including ten not found by the other team) and the other team 42 species. Despite

considerable search effort, field workers are destined to overlook inconspicuous plants occurring in plots. This does not vary with sub-plot size. A review of 52 repeatedly measured plots shows that pseudo-turnover (the percentage of species overlooked by one observer but not another) was 10–30% (Morrison, 2015). Unfortunately, data for uncommon and inconspicuous species will be inherently unreliable. To address this issue, we grouped species into functional groups and focused on the 32 most common species found in 2016 plots.

### **3. Comparability of protocols**

Point intercepts from Wright (1963),  $n=10$  plots; Dickinson et al., 1992; 100 intercepts in each plot) were converted to cover scores so that point intercept data could be compared to cover estimates from recce data (Hurst and Allen, 2007b; plants occurring in 1 intercept = 1, 2–5 intercepts = 2; 6–25 = 3, 26–50 = 4, 51–75 = 5, >75 intercepts = 6). To validate this approach, we compared plots measured in 2007 where both recce cover estimates and HFI was measured, and converted to cover score estimates. This showed that most estimates of cover scores derived from intercept data was within one cover class of actual cover estimates (Figure 2). This is similar to variation in cover estimates between different field staff.

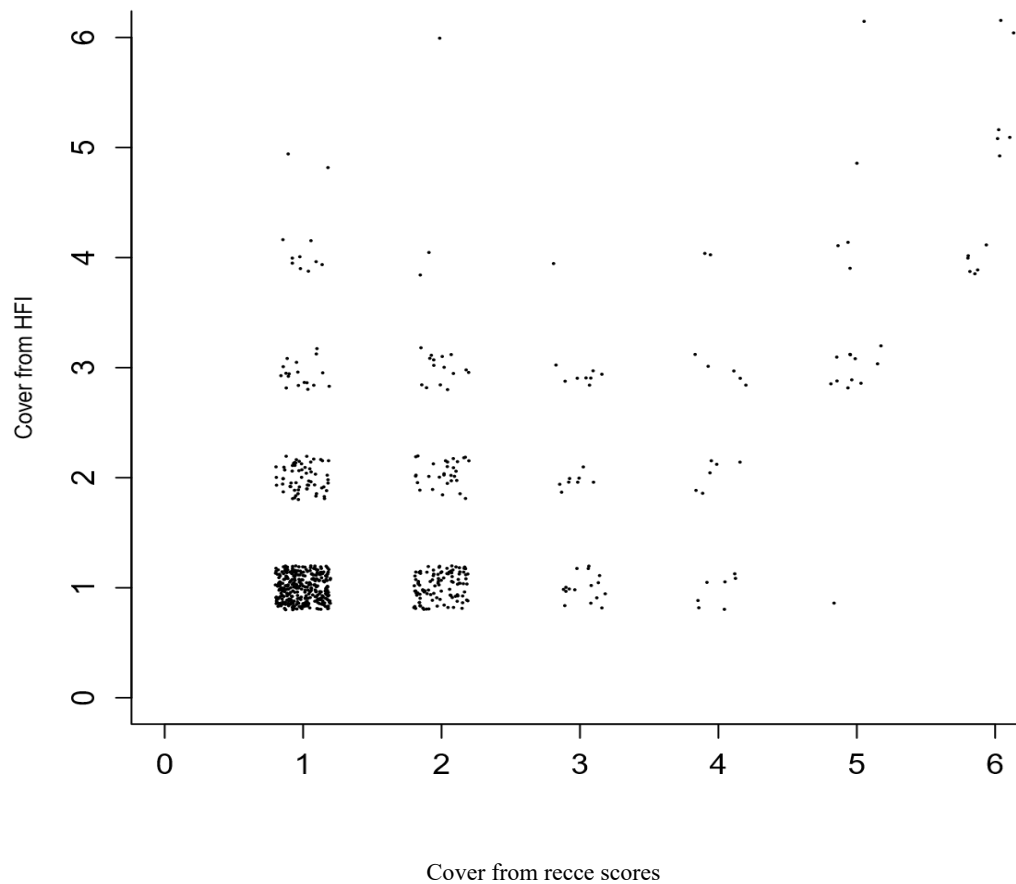


Figure 2: Relationship between species cover scores and cover estimated from HFI from randomly located plots measured in 2007.

#### 4. Data quality assurance

When explanatory variables are correlated inferential statistics can become biased. We selected variables for analysis that had correlation coefficients  $<0.5$  to overcome this potential problem (Table 13, Prairie and Bird, 1989). Initial analysis investigated the value of included publicly available geospatial data on predicted rainfall, nutrient availability and geology. These predictions often are correlated to one another as spatial location is consistently used as a predictor. In future surveys it would be valuable to directly measure soil characteristics, instead of having to rely on modelled predictions. Bioassay (Lee and Fenner, 1989; Husheer et al., 2006) along with chemical assay of key nutrients and micro-

nutrients could prove to be useful during future analysis. Errors can be induced during data processing. The data entry process for the 2016 survey proved to be very reliable. Data entry was audited by placing 33 fake data entry errors into the  $\approx 24,000$  rows of data entered for the 2016 survey. All data was then checked twice line by line. The first check detected 27 of the 33 errors, and only 32 real data entry errors. This suggests that under ten data entry errors remain. Two transcription errors were detected during automated data checking processing undertaken as part of statistical analysis. During data checking some errors were detected in data from surveys from 1989 to 2008. Data errors detected during the data entry process were corrected in raw data files. Errors detected during analysis were not corrected in raw data as many required guesses as to what field workers may have observed. Instead, these errors are listed in a series of data correction files used for rectifications during analysis.

	Fencing to exclude cattle	Easting	Northing	Altitude	Terraced	Oversown
Fenced	1.00	-0.30	0.18	0.02	0.25	-0.14
East	-0.30	1.00	0.24	-0.05	-0.21	0.12
North	0.18	0.24	1.00	0.38	0.19	-0.21
Altitude	0.02	-0.05	0.38	1.00	-0.31	-0.29
Terrace	0.25	-0.21	0.19	-0.31	1.00	0.01
Oversown	-0.14	0.12	-0.21	-0.29	0.01	1.00

Table 13: Paired correlation coefficients of predictor variables.

## 5. Plant identification and changes in nomenclature in Molesworth tussock grasslands

Many species on Molesworth are challenging, but with experience and plenty of checking of specimens they can be consistently identified. Some genera have inconsistent forms among individuals making classification into species sometimes frustrating. These were genera such as *Chionochoa* that are usually really easy to work with elsewhere, but on some occasions on Molesworth are of intermediate or unusual form. Tussock grasslands



are dominated by tussock and graminoid forms from members of the grass (Poaceae), sedge (Cyperaceae) and rush (Juncaceae) families, which can be challenging to consistently identify in the field. We refer to the following species as tussocks because of their tightly bunched stems and rolled leaves >10 cm long: *Chionochloa flavescens* (broad leaved snow tussock), *C. macra* (slim snow tussock), *C. pallens* (mid-ribbed snow tussock), *C. rubra* (red tussock), *Festuca matthewsii* (upland hard tussock), *F. novae-zelandiae* (hard tussock), *Poa cita* (silver tussock), *P. colensoi* (blue tussock), *Rytidosperma setifolium* (bristle tussock). *Chionochloa* species are generally tall tussocks with >50 cm long leaves, while *Festuca*, *Poa* and *Rytidosperma* tussocks are shorter. We refer to *C. australis* (carpet grass) and *C. oreophila* (snow hollow grass) as graminoids.

We attempted to reduce errors in species identification and field staff bias through repeated self-audit and collection of voucher specimens for independent verification. Nomenclature in previous surveys was updated to most recent nomenclature published online at [www.nzpcn.org.nz](http://www.nzpcn.org.nz).

***Hieracium* and *Pilosella* species – hawkweeds** NZFS's two European field botanists had to group their classification of hawkweeds (sub-tribe *Hieraciinae*) to those recognised in New Zealand. In Alžbeta Cejková's Krkonoše National Park (Czech Republic) and Sofia Lund's Norrland (Sweden) study sites they dealt with hundreds of species of *Hieraciinae*. In Molesworth we identified seven (*H. lepidulum*, *H. murorum*, *H. pollichiae*, *P. aurantiaca*, *P. caespitosa*, *P. officinarum* and *P. praealta*) of the nine found in New Zealand. *H. argillaceum* and *H. sabaudum* may also be on Molesworth, but we did not note them. There are several thousand species described in Europe, and the European botanists thought there would be many more than the six we found on Molesworth if they used the same criteria as they use at home. They

did not put up much of a fight adopting the kiwi way, which we used consistently. Only two *Hieracium* species were found in surveys before 2007, but there were likely more present.

***Pimelea* species – New Zealand daphne** Species of *Pimelea* were often difficult to ascribe to a species with hybridism and fluidity within the genera (Burrows, 2008, 2011). They are natives to Australia and New Zealand, with changing taxonomy over the past three decades. *P. concinna* and *P. traversii* are easily distinguished from the woolly-leaved species such as *P. mesoa*, or the less common *P. sericeovillosa*. *P. mesoa* was recognised by Burrows (2011), and is differentiated from *P. oreophila* and *P. sericeovillosa* by the amount of leaf hairs. It is unlikely that *P. suteri* or *P. pseudolyallii* were present in plots, although recorded in surveys prior to 2007. For analysis of Molesworth data, *P. mesoa*, *oreophila*, *pseudolyallii*, *sericeovillosa*, *suteri* were pooled into *P. mesoa*. *P. mesoa* tends to be found on valley floors and terraces, while *P. sericeovillosa* on steeper mountain sides.

**Introduced *Agrostis* species** Three exotic *Agrostis* were found in plots, and proved challenging to consistently differentiate. All have a membranous and translucent ligule, but with quite different size and shape between the species. *A. capillaris* has a short almost invisible ligule. *A. castellana* has a ligule 1–3.5 mm long. It was probably misidentified as *A. capillaris* by field teams prior to 2007 where it was prolific around the Sedgemere Tarns. *A. stolonifera* has a different growth habit and a ligule 2–6 mm long.

***Chionochloa flavescens* – broad leaved snow tussock** It is possible that forms resembling two sub-species are present on Molesworth. Hybrids with other tussock species are also known, which can make differentiation of the four tall tussock species on Molesworth tricky on some occasions. *C. flavescens* and *C. pallens* commonly

hybridise, but can be differentiated most consistently by the presence or absence of dis-articulating sheaths. *C. flavescens* is a tall dark green tussock. Leaf 60–120 cm × 10 mm, rolled, smooth throughout, sheath brownish, hairy. Ligule band of hair with tuft on blade. Culm 60-180 cm, smooth. Panicle open, lax, smooth throughout, awn long. It grows on steep, disturbed, rocky faces, which are upper shrubland to alpine. It is distinguished by broad leaf and sheath shavings in the tussock base.

Subspecies *flavescens* has a glabrous (smooth) sheath and short hairs at ligule (found Tararua ranges to Marlborough) and subspecies *brevis* with sheath hairy, short hairs at the ligule (found Marlborough to Canterbury). Sub-species *flavescens* is probably not present in Molesworth and confined in the South Island to Mt Stokes.

***Chionochloa macra* – slim snow tussock** Dense tussocks forming extensive grasslands.

Leaf 50-120 cm × 6-8 mm, stiff, flat, margins scabrid, mid-rib dark, poorly evident. Sheath hairy, dark brown. Ligule rim of hairs. Culm 60-100 cm. Panicle open. Awn long.

***Chionochloa oreophila* – snow hollow grass** Densely tufted, forming patches. Leaf 5–10 cm × 2–3 mm, flat or rolled, grooved, curved. Margins scabrid, sheath. Ligule short dense hairs. Culm 15–30 cm, smooth. Panicle open, awn long, bent. Confined to the western, higher parts of Molesworth in cirques and hollows.

North-west Nelson southwards, alpine grasslands, snow lie areas, especially in higher grasslands. Often covers large areas with scattered clumps.

***Chionochloa pallens* – mid-ribbed snow tussock** Leaf 80–150 cm × 6–8 mm, pale, Vee-shaped with strongly evident midrib, margin scabrid, upper dull, sheath straw coloured, persistent. Fine tuft of hairs at ligule. Ligule rim of very at short hairs. Culm 80–150 cm. Panicle open, awn long, twisted. Often main dominant. Strongly evident midrib is key character.

***Chionochloa rubra* – red tussock** Large reddish tussocks. Leaf to 100 × 1–4 mm, rigid, red-brown, arching, rolled. Sheath dark brown, with tuft at ligule. Ligule short rim of hairs. Culm 1–1.5 m, sometimes long hairy. Panicle open, shorter than leaves. Awn bent.

***Festuca matthewsii* – upland hard tussock** Sub-alpine to alpine grasslands throughout the South Island. Difficult to consistently distinguish from *F. novae-zelandiae* in the field at Molesworth because most plots are in the range of altitudes where both species overlap. In most regions of New Zealand *F. matthewsii* is distinctively smooth and glaucous blades, and *F. novae-zelandiae* scabrid, But there appear to be two forms of *F. matthewsii* at Molesworth. One glaucous and one scabrid. Leaf 10–30 cm, thin, rolled, pointed, smooth. Sheath also smooth. Ligule two lobed, acute, ciliolate. Culm 30–100 cm, smooth. Panicle open, few flowered, awn short.

***Festuca novae-zelandiae* – hard tussock** Erect fawn, perennial tussock. Leaf 10–40 cm × 0.4–0.7 mm, rough, erect, rigid, cylindric, hair-like, sharp pointed. Sheath fissured to the base. Ligule asymmetrical, hairy. Culm 20–100 cm, scabrid. Panicle open, few flowered. Awn short. Volcanic Plateau southwards, mostly east of the divide, montane to lower sub-alpine. Distinguished from *F. matthewsii* by scabrid leaves and panicle about equal to leaves.

***Koeleria* and *Deyeuxia* species – New Zealand oat grass** *Koeleria novozelandica* was unexpectedly absent from the 1987 recce data. This is surprising since it was commonly observed by Moore (1976). *Deyeuxia avenoides* (mountain oatgrass) was found in few plots prior to 2007. Field staff from the earlier survey probably had trouble finding and differentiating these two species. Both have slender, similarly distinctly ribbed leaf blades, although *K. novozelandica* tends to have blades 3–4 mm

wide and *D. avenoides* 1 mm wide. *K. novozelandica* has a shorter awn and a short even ligule, with a long and hairy sheath, *D. avenoides* has a smooth sheath, which is deeply grooved, brown and sometimes purple. Both were commonly observed in the 2016 survey.

***Poa colensoi* – blue tussock** Small stiff tussocks. Rolled leaf 5–30 cm × 0.5 mm, glabrous below, scabrid above. Margins scabrid. Sheath smooth, persistent, white, membranous. Ligule obtuse. Culm 5–10 cm, smooth. Panicle open. Widespread and often abundant on Molesworth, lowland to sub-alpine grasslands. Many varieties. Can be confused with rhizomatous *Poa hesperia*.

***Poa cita* – silver tussock** Dense, shiny tussock growing on fertile sites throughout New Zealand. Leaf 10–60 cm × 1–2.5 mm, tightly folded, leathery, smooth above, ciliate below, tip sharp. Sheath creamy brown, shiny, margin scabrid. Ligule very short even, ciliate. Culm 30–100 cm, equal to leaves. Smooth, scabrid near panicle. Panicle open, slender, scabrid, branches twisted.

***Rytidosperma setifolium* – bristle tussock** Perennial small tussocks. Leaf 25–35 cm, yellow to bright green, rolled, sharp pointed, smooth. Sheath pale, persistent, glabrous. Culm 50 cm, glabrous, node glabrous. Panicle erect, open, few flowered. Awn bent. Common throughout Molesworth grasslands, rocks places. Similar to *P. colensoi* but distinguished by hairs at the ligule and flowers. Usually drier places and blade not scabrid below like *P. colensoi*.

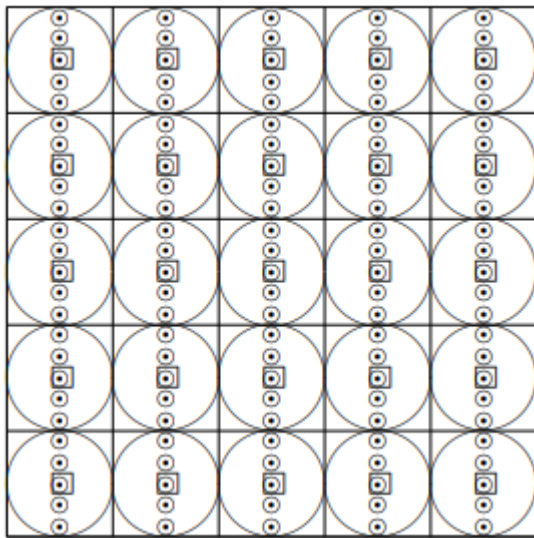
## 6. Relationship between HFI and biomass

A variety of methods have been employed for indexing shrub- and grassland biomass in New Zealand, usually without validation for measurement of biomass at a species level. There are some extensive plot networks including the LUCAS plot system (Beets and Brandon, 2011; Beets, 2012; Beets and Holt, 2012; Ministry for the Environment, 2013), DOCs repeatedly measured plots (Tier 1; Bellingham et al., 2014), and the former New Zealand Forest Service's grassland plot system (Wraight, 1960, 1962, 1963, 1966; Holloway et al., 1963; Tanentzap et al., 2009). We also used uncalibrated and unsubstantiated methods to estimate biomass and cover of grassland and shrub vegetation on Molesworth. To improve the credibility of future tussock grassland and shrubland plot surveys, calibration exercises using direct measurement of biomass should be undertaken. For Molesworth, HFI data seemed to provide a sensible measure of biomass. As long as growth forms are considered separately, point intercept correlate very well with biomass. (Bråthen et al., 2004; Ravolainen et al., 2010; Pottier and Jabot, 2017; Barkaoui et al., 2013). Rough assumptions of the relationship between plant biomass and frequency of occurrence were necessary in the absence of data on actual plant biomass. For an estimate of biomass to be reliable calibration work is required, which is a surprisingly rare exercise (Heady and Van Dyne, 1965). For calibration, several 5 m × 5 m plots could be repeatedly sampled for common measures of biomass (Wraight, 1960; Scott, 1965; Hurst and Allen, 2007a; Beets and Brandon, 2011; DOC, 2019), then harvested in 25 sub-plots (1 m × 1 m). Dry weights for each species, and for functional groups, can then be compared in order to develop allometric equations for predicting plant biomass from plot measurement data. Until that is done it is likely that the estimates of Molesworth biomass and net primary productivity are excessive. Methods can also be compared to determine the optimal protocol for shrub and grassland monitoring. Figure 3 shows a candidate harvest plot

layout. Other methods previously used to determine grassland biomass could also be included. For instance, Levy and Madden (1933) used 10 steel rods spaced at 50-mm intervals (point frame method, modified by (Heady and Rader, 1958; Smith, 1959)), or the discrete shrub method of Beets and Brandon (2011); Beets (2012) measures individual shrubs.

Future plot measurement work on Molesworth should also include the collection of better explanatory data at a plot scale. Measurements could include micro-climate and soil nutrient measurements. This may lead to improved statistical models on changes in vegetation at finer spatial and temporal scales, which in turn would lead to more credible predictions on where exotic plant invasion and cattle grazing have the greatest effect.

Figure 3: Example layout of 5 m × 5 m harvest plots for calibrating biomass measurements.



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