

Leaf trait–palatability relationships differ between ungulate species: evidence from cafeteria experiments using naïve tussock grasses

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Abstract: Leaf functional traits have been proposed as general indicators of plant palatability to ungulate herbivores, identifying which species are likely to be most at risk from ungulates, and how ungulate grazing may change ecosystem processes. However, few studies have tested whether leaf trait–palatability relationships are consistent across different ungulate species. The palatability of 44 native New Zealand grass taxa (from the genera *Festuca* and *Chionochloa*) to two ungulate herbivores (sheep *Ovis aries* and red deer *Cervus elaphus scoticus*) was assessed in cafeteria experiments. There were significant differences between sheep and deer in the selection or avoidance of grass taxa, in part related to differences in response to variation in leaf functional traits. Deer had a greater tendency than sheep to select grasses with a higher specific leaf area (SLA) and to avoid taxa with a low SLA, suggesting that it is not possible to generalise leaf trait–palatability relationships across different ungulate species. Results suggest different ungulate species are likely to have additive effects on the biodiversity and ecosystem functioning of New Zealand's native grasslands. These findings indicate that the impacts of ungulate herbivory on ecosystem processes will depend on which grass species are present.

Keywords: *Cervus elaphus scoticus*; *Chionochloa*; *Festuca*; grazing; herbivory preference; *Ovis aries*

Introduction

Leaf functional traits have been widely proposed as useful predictors of plant palatability to ungulate herbivores (e.g. Coley et al. 1985; Herms & Matson 1992; Grime et al. 1996; Cornelissen et al. 1999). Consequently, they are potentially useful in predicting the vulnerability of plants to herbivory by ungulates, and herbivore impacts on ecosystem function (Wardle et al. 2001). However, there is a lack of research testing the generality of leaf trait–palatability relationships across several ungulate species under experimental conditions. This article presents the results of cafeteria experiments measuring the palatability of native New Zealand grasses to two ungulate species in an attempt to isolate relationships between leaf functional traits and palatability.

Evidence suggests leaves become more palatable as nitrogen content and specific leaf area increase and fibre content and tensile strength decrease (e.g. Coley et al. 1985; Wright & Illius 1995). Generally, ungulate herbivory results in a decrease in the abundance of palatable species (Augustine & McNaughton 1998). Because leaf traits contribute to palatability and litter decomposition rates (e.g. Grime et al. 1996), leaf functional traits could potentially predict the impact of ungulate herbivory on below-ground ecosystem properties and processes (e.g. Wardle et al. 2001), as well as changes in plant species composition.

Much of the existing work linking leaf functional traits to palatability is based on field observations of herbivore plant selection (e.g. Forsyth et al. 2005), and has often compared plant species of highly differing architecture and stature (e.g. Diaz et al. 2001; Pollock et al. 2007). Field studies are complicated by difficulty in assessing relative availability of forage species, possible confounding effects of animal behaviour (e.g. to avoid predators), and patchiness in the distribution of palatable species within the landscape (e.g. Forsyth et al. 2002, 2005). Architecture and stature have been identified as controlling factors in ungulate herbivory in grassland communities (e.g. Illius et al. 1999) and might confound leaf trait–palatability relationships. Cafeteria experiments using species with similar architecture, but differing leaf functional traits, avoid some of the confounding factors associated with field studies.

Ungulate species differ widely in their nutritional requirements and their ability to digest fibrous material (e.g. Morand-Fehr 2005),

so it might be expected that leaf trait–palatability relationships will vary between ungulate species. Consequently, research aiming to examine the potential of leaf functional traits as general predictors of palatability needs to consider several ungulate species. Most cafeteria experiments only include a single ungulate species (e.g. Deguchi et al. 2001; Renaud et al. 2003; Parsons et al. 2006; but see Pollock et al. 2007), and a small range of plant taxa (e.g. Iason et al. 1996; Illius et al. 1999; Renaud et al. 2003) when assessing preferences in herbivory.

New Zealand's native flora evolved in the absence of ungulate herbivores (although a wide range of avian herbivores were present), but numerous studies have noted considerable variation in the palatability of native plant species to ungulates despite this naïveté (e.g. Forsyth et al. 2002; 2005). Research linking leaf traits and palatability to ungulates within New Zealand has focused on native forest ecosystems (e.g. Wardle et al. 2001; Forsyth et al. 2005), but extensive areas of indigenous grassland are grazed by farm stock, and wild deer species, and changes in grassland structure have occurred in response to grazing (e.g. Lee et al. 2000; Rose and Platt 1992; Rose et al. 1995; Grove et al. 2002). The relationship between ungulate grazing and leaf functional traits in grassland species has been poorly documented in New Zealand, and further information is needed to understand the causes of grassland change, and to assess the threats to indigenous grass species from introduced browsing animals.

Here we present results from cafeteria experiments examining the palatability of 44 indigenous New Zealand tussock-forming grass taxa (from the genera *Chionochloa* and *Festuca*) to two ungulate species (sheep *Ovis aries* and red deer *Cervus elaphus scoticus*)¹. Sheep are primarily domestic animals in New Zealand and graze indigenous grasslands extensively in eastern South Island rangelands, while wild deer can be significant browsers of palatable native plants both in forests and in the distinctive alpine grasslands on New Zealand's axial ranges. Together, the distribution of these ungulate browsers covers the entire range of New Zealand's indigenous grasslands.

The aim of the cafeteria experiments was to test the generality of leaf functional trait – palatability relationships, using New Zealand's indigenous grasses as an example. Species of *Chionochloa* and *Festuca* are the structural dominants of most native grassland ecosystems within New Zealand (Wardle 2002). These species offer considerable variability in functional traits (e.g. growth rate, foliar

nutrient content, specific leaf area) and mostly share a tussock-forming habit. Consequently, these two grass genera enable us to assess the potential of leaf functional traits as predictors of New Zealand grass species' vulnerability to ungulate herbivores. This, to our knowledge, is the first study that uses cafeteria experiments to test relationships between leaf functional traits and palatability for more than one ungulate herbivore across such a large number of structurally similar plant taxa.

Methods

Sourcing of plant material

The collection localities of each grass taxon are given in Marx et al. (2004). For each taxon 10–20 individual plants were collected, and daughter tillers propagated under common garden conditions to remove any effects of phenotypic plasticity arising from environmental conditions at the collection locality.

Cafeteria experiment and data analyses

For each indigenous taxon of *Chionochloa* ($n = 32$) and *Festuca* ($n = 12$)², five similarly sized plants were selected from propagated material. Young plants were used to avoid differences in structure that may arise from accumulation of dead leaves, sheaths and stems in older tussocks. Several studies have demonstrated that herbivory on younger individuals severely limits recruitment in tussock-forming grasslands (Rose & Platt 1992; Lee et al. 1993), demonstrating that palatability during the juvenile stage is highly relevant in predicting long-term threats from herbivory. For each plant, the initial number of tillers and maximum plant height were measured. One plant was retained as a control plant, which was harvested at ground level, dried at 70°C for at least 48 h, and weighed. The other plants were placed in random order at equal spacing along the margin of the paddock or enclosure within which the ungulate grazers were held.

For the red deer experiment, a relatively large number of individual animals (c. 40) were available, and all replicates were exposed to grazing at the same time, with no restriction to deer movement within the paddock. For the sheep experiment, the target plants of each replicate were placed on the margins of a circular enclosure of 5-m diameter, after which nine sheep (one ram and eight ewes) were introduced. Replicates were exposed to sheep grazing sequentially. The different herbivores were allowed to graze for sufficient time (generally 0.5 h per replicate) as required to show a range of grazing damage across the different plants. Four replicate trials were performed for sheep, with five performed using deer. Each trial contained one plant from each grass taxon.

After each trial, the grazed plants were harvested at ground level, dried, and weighed. Mean tiller weights of the control plants were used to estimate initial above-ground biomass of the grazed plants, by multiplying mean tiller weight by initial number of tillers. Biomass reduction was calculated for each of the treated plants.

Since the grazing pressure was not standardised across herbivore species (due to differences in numbers of animals) it may be misleading to compare biomass loss for a given plant taxon across herbivore species. Further, analysis of variance (ANOVA) revealed a significant block (replicate) effect on the percentage of biomass lost for each of the ungulate herbivores considered. To correct for possible biases, biomass loss for each individual plant (P_i) was expressed as a proportion of total biomass loss within the replicate (following Pollock et al. 2007):

$$P_i = \frac{x_i}{\sum_{j=1}^n x_j} - \frac{1}{n}$$

where x_i is the estimated biomass loss of an individual plant and n is the number of plants included in the replicate.

We used one-way ANOVA to determine if grass species differed significantly in P_i within each herbivore species, and two-way ANOVA to test for an interaction between herbivore species and plant species. Because of non-normality in the data and problems associated with log transformation (Wilson 2007), randomisation tests were used to calculate P -values for the F -statistics, following the recommendations of Anderson and ter Braak (2003). The observed F -statistic was compared with that expected when P_i values were randomised. Unrestricted randomisation of raw P_i values between tussock species was used in one-way ANOVA. In two-way ANOVA, F -statistics associated with main effects (i.e. plant species and herbivore species) were compared with those expected with randomisation of treatment groups (i.e. each combination of plant species and herbivore species). Finally, the F -statistic for the plant–herbivore interaction effect was compared with that expected from unrestricted randomisation of residuals. Anderson and ter Braak (2003) provide a detailed description of these methods and demonstrate that these maintain statistical power and appropriate Type I error rates when data are non-normal.

Herbivore plant preferences were examined using Spearman's rank correlation coefficient (r_{sp}) because we were interested in similarities in the palatability rank of grass species across herbivores.

This experimental design does not allow quantification of variation in preferences between individuals. This may be an important source of variation and would be interesting to examine in future studies. Nevertheless our approach does allow quantification of differences in mean preferences of each ungulate species.

Functional trait measurements

Leaf functional traits either demonstrated or suggested to be related to palatability were measured for each of the 44 grass taxa. The tensile strength of leaves influences resistance to defoliation (Illius et al. 1995) and was measured on 10 mature leaves for each grass taxon. Tensile strength was determined by clamping the base of an excised leaf section (taken from the middle of the leaf) into a vice and the upper part of the leaf into a vice grip attached to a dynamometer (Bond et al. 2004), and pulling slowly until leaf breakage occurred. If a leaf broke where it was clamped, the trial was discarded. Specific leaf area (SLA) was calculated as leaf area divided by leaf dry mass. Leaf area was calculated as the length of the leaf section multiplied by its width. In all statistical analyses, the square-root of SLA was used, since area is the square of two linear dimensions and consequently exhibits large variation (i.e. the same convention followed in previous studies, e.g. Pollock et al. 2007).

Samples of leaf were collected from the control plants, oven-dried at 70°C for 48 h, and ground using a Cyclone sample mill (Udy Corp, Fort Collins, CO, USA). Nitrogen and phosphorus concentrations were determined using a continuous flow analyser following modified Kjeldahl digestion (Bremner & Mulvaney 1982; Blakemore et al. 1987).

Leaf opal phytoliths are silicon-rich deposits extruded into the leaves of many grass species and may act as a defence against herbivory (Massey & Hartley 2006). Data on leaf opal phytoliths were obtained from Marx et al. (2004). Here the mass of phytoliths (as a proportion of leaf dry weight) and the proportion of different phytolith classes (from a total of 200 phytoliths examined) were recorded for two individuals of each taxon. The resulting data were summarised in a detrended correspondence analysis (DCA) ordination. The first two axes of this ordination were used in the present study. The primary DCA axis separates taxa with abundant panicoid-type phytoliths from those with abundant chloroid phytoliths. The second axis separates taxa with abundant chionochloid phytoliths from those lacking this type.

¹ Nomenclature for ungulates follows King (2005).

² Nomenclature follows Edgar & Connor (2000) and Connor & Lloyd (2004).

Relationships between plant functional traits and palatability

Functional traits were selected for their proven or suggested relationship to at least one species of herbivore in the published literature. There is no a priori reason to assume that any single trait or combination of traits is more likely to be related to palatability than other traits or trait combinations. Further, each of the traits provides independent information, and they are not easily separated into groups. Comparison of a large number of models with no a priori selection of candidate models is increasingly discouraged (Burnham & Anderson 2002). Consequently, we sought to reduce the number of candidate traits before testing trait–palatability relationships.

Selecting candidate traits

The number of candidate traits was reduced by examining the ability of functional traits to predict P_i values across models including all combinations of functional traits, using linear least-squares regression. A corrected Akaike Information Criterion (AICc) value was calculated for each model (Burnham & Anderson 2002). The best-performing model is considered to be the one with the lowest AICc value. AICc was chosen since it remains accurate when sample size is small-to-moderate relative to the number of unknown parameters fitted (Burnham & Anderson 2002). An Akaike weight, which gives an estimate of the probability that a model gives the most parsimonious fit to the data among the models considered, was calculated for each model (i.e. each combination of functional traits) following the method described by Johnson and Omland (2004). A w_i value of >0.9 provides a high degree of confidence (i.e. $>90\%$ confidence) that the model in question is the best-performing among those considered:

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{j=1}^R \exp\left(-\frac{1}{2}\Delta_j\right)}$$

where R is the number of models under consideration and Δ_i is the difference between the AICc value of model i and the minimum AICc value across all models. The sum of w_i values across all models adds to unity. The number of variables was initially reduced by examining the summed Akaike weight of each variable:

$$w_k = \sum_{i=1}^{R_k} w_i$$

where w_k is the Akaike weight of predictor variable k and R_k is the number of models including k (this is the same for all variables when all possible combinations of variables are examined). This weighting provides a measure of the probability that a variable is in the set of variables giving maximum explanatory power. The variables with a w_k of c. 0.6 or greater were retained (normally a higher value would be used but the large number of possible combinations results in a greater chance of spuriously rejecting predictor variables).

The potential for non-linear relationships between functional traits and P_i was examined by comparing the predictive ability of simple and quadratic linear regressions and the non-linear power function ($y = c + ax^b$). This was done by comparing w_i values of the types of relationship, where the quadratic and power relationships each had an extra fitted parameter. In no instance was there evidence that either quadratic regression or the power function provided a significant increase in predictive ability.

Testing trait–palatability relationships using a reduced candidate set of variables

Since our aim was not to identify a single optimal model (i.e. a model with much lower AIC than all other models), but rather the functional traits most strongly related to palatability, we report the w_k for each of the retained predictor variables across all possible combinations of these variables. For descriptive purposes, the decrease in R^2 caused by the removal of each variable from the full regression model was calculated, with a P -value then being found for the associated

t -statistic (using error degrees of freedom, since in both cases this is same as testing the significance of R^2 for a regression model including a single variable). To check whether any single observation had an unduly large effect on regression coefficients, Cook's distance was examined for each data point in the regression model including all retained functional traits. Any points found to have a significantly large Cook's distance value were removed from the dataset and the regression repeated to assess if this altered the sign of regression coefficients and the significance of the overall model.

Relationships between differences in palatability and plant functional traits

The framework described above was also used to determine whether differences in plant species preferred by herbivores were related to different responses to plant functional traits. Here, difference in P_i of plant species between pairs of herbivores was regressed on plant functional traits.

Results

Defoliation patterns were examined between herbivores and across the different *Chionochloa* and *Festuca* taxa. Between-grass taxa variation in P_i (the biomass loss of species i as a proportion of total biomass loss for the replicate) was significantly greater than within-taxa variation for all herbivore species, indicating that each herbivore preferentially ate certain species while avoiding others (Table 1). The herbivore \times grass species interaction term was significant (Table 1), indicating that herbivores tended to select and avoid different grass species. This is supported by the lack of evidence for correlation of P_i scores between different herbivore species (Fig. 1). Deer were the most selective of the herbivore species, having the highest F -value for P_i across grass species.

Leaf traits and palatability

Plant functional traits were tested for independence. No pair of traits had a Pearson $r > 0.6$ and r was much lower for most pairs (Table 2). Consequently principal components analysis (PCA) failed to yield any easily interpretable axes. Thus, each of the functional traits was treated separately in subsequent analyses.

Not all traits were significantly related to biomass loss. Leaf tensile strength, the square-root of specific leaf area (SLA) (Fig. 2), and leaf nitrogen concentration were retained as candidate variables for P_i for sheep (Table 3), with each having comparable explanatory power. SLA was by far the best predictor of P_i for deer (Fig. 2), with

Table 1. One-way ANOVA results for biomass loss by grass taxa for each herbivore species and results for two-way ANOVA with grass taxa and herbivore species as factors. F_{obs} is the observed F -statistic, F_{exp} is the mean F -value obtained from 10^5 randomisations, and Prop. is the proportion of randomisations giving an F -value equal to or greater than F_{obs} .

Variance source	F_{obs}	F_{exp}	Prop.
<i>Deer</i>			
Plant species	4.529	1.016	<0.001
<i>Sheep</i>			
Plant species	2.469	1.007	<0.001
<i>Two-way : Plant–Herbivore</i>			
Herbivore species	3.652	2.002	0.173
Plant species	3.213	2.992	0.312
Plant–Herbivore interaction	0.948	0.772	0.046

Table 3. Results for multiple regression of biomass loss to herbivory by sheep and deer on leaf functional traits. ‘Sign’ = sign of the regression coefficient; ‘AIC weight’ = w_k value; ‘Change in R^2 ’ and ‘Change in AICc’ refer to the change caused by adding the variable in question from a regression model including all other retained variables; * = included in optimal model; Sqrt SLA = square root of specific leaf area; POP% = weight of plant opal phytoliths as a percentage of leaf dry weight. Overall results for the optimal regression in each case were sheep $R^2 = 0.22$, $P = 0.015$, $w_i = 0.33$ and deer $R^2 = 0.31$, $P = 0.001$, $w_i = 0.60$.

	AIC		R ²		
	Sign	weight	ΔR^2	P-value	$\Delta AICc$
<i>Sheep</i>					
Sqrt SLA*	+	0.712	0.085	0.084	-1.31
Leaf tensile strength*	-	0.648	0.059	0.154	-0.16
Nitrogen content	+	0.509	0.022	0.389	1.51
<i>Deer</i>					
Sqrt SLA*	+	0.996	0.302	0.001	-9.92
POP%*	-	0.601	0.069	0.134	-0.81

Table 5. Pairwise comparison between different herbivore species of percent weight loss through herbivory in each of the grass taxa studied. ‘sig.’ refers to significance calculated according to the Mann–Whitney U test.

Plant taxon	$P_i(\text{deer}) - P_i(\text{sheep})$	sig
<i>Chionochloa acicularis</i>	0.012	
<i>C. antarctica</i>	-0.005	
<i>C. beddiei</i>	0.022	<0.05
<i>C. cheesemanii</i>	-0.004	
<i>C. conspicua</i> subsp. <i>conspicua</i>	0.007	
<i>C. conspicua</i> subsp. <i>cunninghamii</i>	0.000	
<i>C. crassiuscula</i> subsp. <i>crassiuscula</i>	0.028	<0.05
<i>C. crassiuscula</i> subsp. <i>directa</i>	-0.004	
<i>C. crassiuscula</i> subsp. <i>torta</i>	0.015	
<i>C. flavescens</i> subsp. <i>brevis</i>	0.007	
<i>C. flavescens</i> subsp. <i>lupeola</i>	0.013	
<i>C. flavicans</i>	0.021	<0.05
<i>C. lanea</i>	-0.003	
<i>C. macra</i>	0.016	<0.1
<i>C. nivifera</i>		
<i>C. oreophila</i>		
<i>C. ovata</i>	0.014	
<i>C. pallens</i> subsp. <i>pilosa</i>	0.008	
<i>C. rigida</i> subsp. <i>amara</i>	0.016	<0.05
<i>C. rigida</i> subsp. <i>rigida</i>	-0.022	
<i>C. rubra</i> subsp. <i>cuprea</i>	-0.004	
<i>C. rubra</i> subsp. <i>occulta</i>	-0.022	<0.05
<i>C. rubra</i> subsp. <i>rubra</i>	0.003	
<i>C. spiralis</i>	0.002	
<i>C. teretifolia</i>	-0.012	
<i>C. vireta</i>	0.006	
<i>Festuca actae</i>	0.001	
<i>F. coxii</i>	-0.006	
<i>F. deflexa</i>	-0.011	
<i>F. matthewsii</i> subsp. <i>aquilonia</i>	0.001	
<i>F. matthewsii</i> subsp. <i>latifundii</i>	-0.023	<0.1
<i>F. matthewsii</i> subsp. <i>matthewsii</i>	-0.029	<0.05
<i>F. novae-zelandiae</i>	0.012	
<i>F. ultramafica</i>	-0.017	

Table 4. Results for multiple regression of differences in biomass loss to herbivory (P_i) between deer and sheep. * = included in optimal model. Overall results for the optimal regression in each case were $R^2 = 0.13$, $P = 0.049$, $w_i = 1.00$.

$P_i(\text{deer}) - P_i(\text{sheep})$	Sign	AIC weight	ΔR^2	R ² P-value	$\Delta AICc$
Sqrt SLA*	+	1.00	0.132	0.049	-253.77

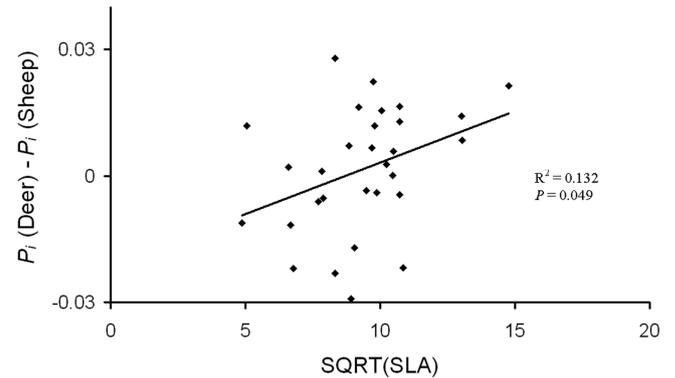


Figure 3. Differences in P_i of grass taxa between deer and sheep versus the square root of SLA.

Discussion

Our results demonstrate remarkable differences in the grass species preferred by sheep and red deer. Herbivore differences seem to have their basis at least partially in responses to leaf functional trait variation across the grass taxa. These results raise questions about the validity of using leaf functional traits as general indicators of palatability.

The lesser degree of selectivity displayed by sheep relative to deer seems to be due in part to lower sensitivity to variation in leaf functional traits, especially SLA. However, while leaf functional traits may be less useful in predicting the impacts of sheep grazing on native grasslands than for deer, it seems that leaf traits still influence sheep preferences. In the New Zealand context, emphasis has been placed on the physiognomic shifts in native grasslands caused by sheep grazing, especially in combination with repeated burning. Most work has demonstrated that long-term sheep grazing results in a transition from grasslands dominated by *Chionochloa* or *Festuca* tussocks to those dominated by grazing avoiders, such as flat rosette-forming and prostrate perennials, annual species, and grazing-tolerant, stoloniferous exotic grasses (e.g. Rose et al. 2004). There appears to be no work demonstrating whether these physiognomic shifts are associated with changes in the dominant leaf functional traits of these grasslands, though there is some evidence that grazing causes a decrease in plant biomass nutrient concentrations (McIntosh 1997; Scott et al. 2001). Our results suggest sheep grazing might be expected to result in leaf trait shifts (especially in SLA, leaf nitrogen concentration and leaf tensile strength). Since leaf traits are known to affect below-ground ecosystem processes (e.g. Wardle et al. 2001), it is possible that leaf trait shifts might partially explain the drastic changes in ecosystem properties (e.g. McIntosh 1997; Scott et al. 2001) that are induced by long-term sheep grazing of native grasslands.

Deer showed a strong tendency to prefer grass species with greater specific leaf area (SLA) and avoid species with a low SLA (Fig. 2). This disagrees with previous work (Forsyth et al. 2005) on deer browse, which found in a temperate forest ecosystem that while red deer preferred plants with lower leaf fibre content, there was no evidence of a preference for high SLA. This probably reflects

either a difference in approach (field vs experimental) or the fact that these authors dealt with woody plant species differing greatly in architecture and leaf structural type, since both studies covered a similar range of SLA values.

That deer were more selective than sheep concurs with observations of deer browsing in forests. Forsyth et al. (2005) showed that deer browsed preferentially on certain plant species even when these species were in very low abundance throughout the study area. Recently Bee et al. (2009) found that deer in the Murchison Mountains, Fiordland, select vegetation patches within a landscape based on the overall patch quality, and at a fine-grain level choose among individual plants of different species based on relative palatability.

Elsewhere in New Zealand, the selectivity of deer browsing has repeatedly been considered responsible for the decline of palatable species (e.g. Wardle et al. 2001). Further, the high selectivity of deer browsing has been shown to alter below-ground ecosystem processes in native forests, since leaf palatability and decomposition rates tend to be positively related (Wardle et al. 2001). Our results suggest deer may be equally selective within grasslands as they are when browsing forests. This may cause similar shifts in grassland functional composition and ecosystem processes as have been observed for forests.

The selectivity of deer herbivory in New Zealand's subalpine and montane grasslands has frequently been attributed to foliar nutrient levels. Mills et al. (1991) found that deer preferred *Chionochloa pallens* in an alpine grassland, with the authors citing the higher nitrogen content of *C. pallens* relative to co-occurring species as the reason for this. Other work in similar grasslands (Rose & Platt 1987) observed that deer selected *C. pallens* and large-leaved forbs, particularly when they occurred on high fertility sites, which would support the role of nitrogen content. However, our results suggest that mechanical aspects of leaf structure might actually be more important in plant selection by deer when a broader suite of tussock species is considered. There is little work available examining the effects of long-term deer herbivory on the functional composition or ecosystem processes of New Zealand's subalpine and montane grasslands. Lee et al. (2000) showed that *C. pallens* tussocks took more than 20 years to recover from simulated deer browsing, suggesting that deer herbivory might substantially reduce the abundance of palatable tussock-forming species in the long term.

Cafeteria-style preference experiments have several obvious limitations for deriving predictions on the effects of herbivory in the field (Pollock et al. 2007). Herbivore preferences may be influenced by the nutritional regime prior to experimentation and dominance behaviour within the group. One limitation of our study is that we were unable to quantify individual-level differences in plant preferences within ungulate species, yet this might be an important source of variation. The functional traits of juvenile plants grown in common garden conditions may not reflect those of adult plants in the wild, which may alter herbivore preferences in the field relative to cafeteria experiments. A cafeteria experiment does not provide herbivores with the range of palatabilities that occur in the field. Some of the least palatable species in the experiment may be at the more palatable end of the scale in the grasslands where they occur.

Finally, it is important to note that palatability does not necessarily reflect vulnerability to herbivory. Some species may be better able to recover from herbivory, so that selection by herbivores may have variable consequences. For example deer-preferred *Chionochloa pallens* in Fiordland also has the highest relative growth rate of tall tussock species in the region, which may ameliorate the impact of deer foraging (Lloyd et al. 2003). We tried to control for this by studying species of similar growth form and life-history characteristics, but some interspecific variation in tolerance of herbivory is inevitable. Consequently, the results presented here should be interpreted with some caution in anticipating herbivore impacts in the field.

Despite these caveats, field observations of population decline in response to grazing, where available, generally support our experimental results. For several of the grass taxa with the highest mean P_i values taken across herbivores (*Chionochloa beddiei*, *C. conspicua* subsp. *conspicua*, *C. flavicans*, *C. macra*, and *Festuca*

coxii; Appendix 1), the evidence of generally higher vulnerability to ungulate herbivory is supported by field observations. Early depletion of high elevation *Chionochloa macra* populations in Central Otago has been related to the rapid growth in stock numbers during this period (O'Connor 1982), and frequent evidence of grazing is noted as a distinguishing feature of this species (Edgar & Connor 2000). *Chionochloa conspicua* subsp. *conspicua* appears to have decreased in abundance due to deer browse in some parts of Fiordland (Mark and Baylis 1982). *Chionochloa flavicans* and *C. beddiei* are largely restricted to inaccessible sites on rock outcrops and cliffs in the eastern and southern North Island (Edgar & Connor 2000), which also suggests an intolerance of ungulate browsing. In contrast several of the taxa with the lowest P_i values (both subspecies of *Chionochloa rigida*, two subspecies of *Festuca mathewsii*, and *Festuca novae-zelandiae*; Appendix 1) are known to persist in grazed snow tussock grasslands under extensive pastoral management (e.g. Connor 1964).

Overall, the observed inconsistency in herbivore preferences is at least partially attributable to differences in herbivore response to leaf functional traits. This suggests leaf traits may not be able to provide a general index of plant palatability across different ungulate species, and that leaf trait–palatability relationships may need to be examined for each ungulate species separately. Our results also imply sheep and deer may threaten different native plant species, so the potential impacts of ungulate species on native grasslands might need to be assessed on a species-by-species basis. In particular, differences in selectivity and differences in response to leaf functional traits suggest that where different ungulate species coexist they may have additive effects on grassland functional composition and ecosystem processes. Further cafeteria experiments including a broader range of ungulate species may provide new insights into variation in trait–palatability relationships.

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Appendix 1. Mean biomass lost to herbivory as a proportion of the total lost for the replicates (P_i) values for each grass taxon, for each of the herbivore species studied.

Plant taxon	P_i (sheep)	P_i (deer)	Mean
<i>Chionochloa acicularis</i>	-0.008	0.004	-0.001
<i>C. antarctica</i>	0.000	-0.005	0.000
<i>C. beddiei</i>	-0.002	0.021	0.008
<i>C. cheesemanii</i>	0.003	-0.001	-0.004
<i>C. conspicua</i> subsp. <i>conspicua</i>	0.002	0.008	0.005
<i>C. conspicua</i> subsp. <i>cunninghamii</i>	0.003	0.003	0.004
<i>C. crassiuscula</i> subsp. <i>crassiuscula</i>	-0.004	0.024	0.004
<i>C. crassiuscula</i> subsp. <i>directa</i>	-0.004	-0.007	-0.002
<i>C. crassiuscula</i> subsp. <i>torta</i>	0.003	0.019	0.009
<i>C. defracta</i>	NA	-0.009	-0.005
<i>C. flavescens</i> subsp. <i>brevis</i>	0.001	0.008	0.003
<i>C. flavescens</i> subsp. <i>flavescens</i>	NA	0.002	0.001
<i>C. flavescens</i> subsp. <i>hirta</i>	NA	-0.009	0.000
<i>C. flavescens</i> subsp. <i>lupeola</i>	-0.006	0.007	0.002
<i>C. flavicans</i>	0.006	0.027	0.011
<i>C. juncea</i>	-0.005	NA	-0.006
<i>C. lanea</i>	NA	NA	0.005
<i>C. macra</i>	0.005	0.021	0.006
<i>C. nivifera</i>	0.010	NA	0.000
<i>C. oreophila</i>	0.003	NA	0.002
<i>C. ovata</i>	0.000	0.014	0.005
<i>C. pallens</i> subsp. <i>cadens</i>	-0.003	NA	0.002
<i>C. pallens</i> subsp. <i>pallens</i>	0.009	NA	0.004
<i>C. pallens</i> subsp. <i>pilosa</i>	-0.003	0.005	0.001
<i>C. rigida</i> subsp. <i>amara</i>	-0.022	-0.005	-0.008
<i>C. rigida</i> subsp. <i>rigida</i>	-0.002	-0.024	-0.011
<i>C. rubra</i> subsp. <i>cuprea</i>	0.009	0.005	0.007
<i>C. rubra</i> subsp. <i>occulta</i>	-0.002	-0.024	-0.010
<i>C. rubra</i> subsp. <i>rubra</i>	0.000	0.002	0.000
<i>C. spiralis</i>	-0.002	0.000	0.000
<i>C. teretifolia</i>	-0.013	-0.024	-0.013
<i>C. vireta</i>	0.008	0.014	0.009
<i>Festuca actae</i>	-0.002	-0.001	0.001
<i>F. coxii</i>	0.008	0.002	0.005
<i>F. deflexa</i>	0.000	-0.011	-0.002
<i>F. luciarum</i>	NA	0.015	0.003
<i>F. madida</i>	0.007	NA	0.005
<i>F. matthewsii</i> subsp. <i>aquilonia</i>	-0.010	-0.010	-0.010
<i>F. matthewsii</i> subsp. <i>latifundii</i>	0.007	-0.016	-0.003
<i>F. matthewsii</i> subsp. <i>matthewsii</i>	0.007	-0.022	-0.003
<i>F. matthewsii</i> subsp. <i>pisamontis</i>	0.002	NA	-0.007
<i>F. multinodis</i>	0.010	NA	0.005
<i>F. novae-zelandiae</i>	-0.011	0.001	-0.005
<i>F. ultramafica</i>	0.005	-0.012	-0.003

NA = no data available