# Subtle foodscape displacement of a native ungulate by free-ranging livestock in a forest agroecosystem

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**Abstract.**   The prevalence of livestock grazing in wildlife areas is increasing. This transformation of ecosystems into agroecosystems is concerning because the introduction of new species may cause niche displacement of the functionally related native species. We used a large-scale fence scheme and fecal analyses to study the influence of free-ranging livestock on moose diet on three boreal forest ranges. We found low interspecific diet overlap between moose and livestock (mean Pianka's *O* across ranges = 0.21, SD = 0.104), and the diet overlap with livestock did not differ between moose in areas with livestock and in adjacent control areas without livestock. Still, moose sympatric with livestock had less fecal nitrogen (a proxy for diet quality) than moose in the control areas. Our findings suggest that interspecific interactions other than direct food competition contributed to reduce the moose' foraging opportunities, such as altered forage abundance and composition, or behavioral avoidance of livestock. We caution that displacement in the foodscape (i.e., spatiotemporal use of food) can occur through pathways not evident in niche indices based on composition of plant species in the diet.

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## Introduction

The prevalence of livestock grazing in wildlife areas is increasing because of expanding needs of food for humans (Tscharntke et al. 2012, Fynn et al. 2016). Such large-scale species introductions eventually transform ecosystems into agroecosystems, with potential loss of species and functional diversity (Zhang et al. 2007, Power 2010). However, the actual implications for the wildlife are largely unknown, partly due to difficulties of delimiting concurrent control areas for wide-roaming species (Petersen and Hastings 2001). This is concerning, as herbivores are both consumers and prey, and thereby a mediator link of ecosystem functioning (McLaren and Peterson 1994, Ripple et al. 2015).

Introduction of functionally related species into an ecosystem, for example within the same trophic level, is expected to displace the native species from its realized niche of resource use (Hutchinson 1957, Torchin and Mitchell 2004, Tingley et al. 2014). Interactions between species spatiotemporally seeking similar resources can involve both competition (negative impact) and facilitation (positive impact). According to the niche variation hypothesis (van Vaalen 1965), the most likely scenario is competition (but see Dodds 1997), whereupon the native species must use additional resources that are of lower value,

and thereby increases the width of its realized niche. However, competition can also decrease niche widths. In the case of diet niche, this occurs if the native species feeds even more selectively on the few species still of sufficient availability (Gordon and Illius 1989, Nicholson et al. 2006). A further complicating issue is that species partly compete and partly also facilitate food access for each other, for instance through pruning of plants (Cromsigt and Kuijper 2011).

Because we can observe the same shift in diet niche width for positive and negative displacement in the foodscape (i.e., spatiotemporal use of food resources in the landscape), niche indices based only on the composition of species in the diet can obscure the effect on animal fitness. What matters to the foraging animal is how much of which nutrients it is able to process without aversive effects, and this may largely vary even within a given plant species (Wam et al. 2017a). Unfortunately, obtaining comprehensive profiles of nutrient intake is challenging in natural settings (Felton et al. 2009). Wildlife biologists therefore have used various proxies for diet quality. One such is fecal nitrogen (N), which has been broadly applied as a non-invasive indicator of variation in protein intake by wild animals (Mattson 1980, McArt et al. 2009). Protein is considered a major nutritional driver for large herbivores such as ungulates, at least during the plant growing season (Parker et al. 2009). A recent meta-analysis confirmed that fecal N is useful and justified for intraspecific comparisons across areas with similar plant assemblies (Leslie et al. 2008, see also our *Discussion* section). If the fecal N of one ungulate species differs between areas, all else being equal apart from the presence of another ungulate species, we may attribute the difference to interspecific influences on food intake.

In this study, we used a large-scale fence scheme and fecal analyses to compare dietary data in summer for a large herbivore (the moose *Alces alces*) on three boreal forest ranges with free-ranging livestock (sheep *Ovis aries* and cattle *Bos taurus*) and in adjacent control areas being similar apart from absence of livestock. We used fecal N as a proxy for the diet quality of moose and related this to diet composition and diet overlap with the free-ranging livestock. Specifically, we postulated that moose would have low dietary overlap with sheep and cattle. Free-ranging cattle and sheep in boreal forests are essentially grazers (Mackie 1970, Uresk

and Paintner 1985, Putman et al. 1987, Beck and Peek 2005), while moose is more of a browser (Hofmann 1989) with grasses typically constituting <10% of moose summer diet on boreal ranges (Wam and Hjeljord 2010a). For this reason, we expected the diet composition and diet quality (fecal N) not to differ between moose sympatric with livestock and moose in control areas.

However, as outlined above, livestock can affect the foraging of moose through pathways other than direct food competition. Free-ranging livestock in forests are likely to occupy parts of the native ungulates' habitat (Stewart et al. 2002, Herfindal et al. 2017), which may cause them spatiotemporally to avoid these areas (Hibert et al. 2010). Livestock activity also is likely to affect the forage plants of native ungulates, but its outcome seems highly case dependent (e.g., increased grass abundance in Gordon 1988, reduced browse abundance in Hjeljord et al. 2014, divergent changes to abundances in Mysterud and Austrheim 2008, divergent changes to nutrient contents in Alpe et al. 1999). The outcome will depend on a series of site-specific factors, such as animal densities, soil fertility, and season, and is therefore difficult to predict from the scarce literature available. Yet, a comprehensive review of the influence of livestock grazing on native ungulates (their site use, food or foraging behavior, health, or demography) indicates that negative outcomes (N = 86) are more likely than positive (N = 34) or neutral (N = 35; Schieltz and Rubenstein 2016).

## MATERIALS AND METHODS

### Study area

We conducted field sampling during summer 2012 on three boreal forest ranges in southeastern Norway (Sande 59°42′ N, 10°7′ E; Nannestad 60°13′ N, 10°56′ E; and Ringsaker 60°57′ N, 10°53′ E) (Fig. 1). All ranges were situated in the lowlands (>50% of area <300 m above sea level), within the same climatic zone (i.e., continental, 2010–2012 mean temperature February −5.1°C and June 14.1°C, precipitation June + July 133 mm), to minimize environmental variability not related to animal activity. These forests are dominated by Norway spruce *Picea abies*, with Scots pine *Pinus sylvestris* on drier sites and deciduous trees intermixed along edges and natural clearings (Moen 1999).

Livestock (cattle and sheep) are free ranging in parts of the forests throughout the summer season (June–September). Because the ranges were large, and free-ranging livestock tend to aggregate in parts of the range, we used fecal counts to index livestock density and use of the areas where we collected fecal samples for our study (Table 1). To delimit livestock and control areas without livestock, we made use of a fence scheme established by livestock owners. The fence is constructed so that livestock cannot cross, but moose easily jumps (H. K. Wam, *personal observation*). The fence line follows property boundaries, which historically were settled by drawing straight lines on maps irrespectively of the terrain. There should therefore be no strong bias in topography or inherent soil fertility between livestock and control areas. The size of the fenced forested areas is approximately Sande: 110 km$^2$, Nannestad: 520 km$^2$, and Ringsaker: 250 km$^2$ (in Ringsaker, there is additional livestock area above the forest line). Field surveys in Sande and Ringsaker indicated that soil fertility was indeed largely similar in livestock and control areas, yet the vegetation abundance and vegetation composition differed (Table 2). Stem density of moose browse was lower in the livestock areas than in control areas. Also, in livestock areas, fewer of the plots had rowan and taller herbs, which are highly selected by moose (Wam and Hjeljord 2010*a*).

*Field work (fecal sampling)*

We counted feces from each of the three species (cattle, sheep, moose) along 2 m wide transects shaped as triangles (minimum 10 transects in each livestock or control area on a range,

Table 1. Animal density of sympatric cattle, sheep, and moose, as well as moose in adjacent control areas without livestock, on three boreal forest ranges in Norway in summer 2012, as found by fecal counts (mean ± 1 SD).†

| Range and species | Fecal density (feces/ha) | |
| --- | --- | --- |
| | Livestock areas | Control areas |
| Sande | | |
| Sheep | 24 ± 19 | 0 |
| Cattle | 59 ± 33 | 0 |
| Moose | 11 ± 6‡ | 5 ± 2‡ |
| Nannestad | | |
| Sheep | 50 ± 17 | 0 |
| Cattle | 83 ± 32 | 0 |
| Moose | 17 ± 7 | 20 ± 6 |
| Ringsaker | | |
| Sheep | 295 ± 54 | 0 |
| Cattle | 379 ± 62 | 0 |
| Moose | 13 ± 3 | 58 ± 14 |

† We counted feces along 2 m wide transects on randomly chosen young clear-cuts (dominant tree height <4 m, at least 10 transects in each livestock or control area on all ranges, mean length 300 m, SE = 24). Young clear-cuts are favored areas for both livestock and moose (Wam et al. 2010, Hjeljord et al. 2014).

‡ Note that in Sande, we found moose feces along few transects (3 out of 10 in livestock areas and 4 out of 10 in control areas).

Table 2. Site characteristics of livestock grazing areas and adjacent control areas without livestock on two boreal forest ranges in Norway (Sande and Ringsaker).

| Site characteristics | Sande livestock area | Sande control area | Ringsaker livestock area | Ringsaker control area |
| --- | --- | --- | --- | --- |
| Number of surveyed plots | 386 | 226 | 347 | 559 |
| Soil fertility (scale 0–4)† | 1.9 | 1.8 | 1.7 | 1.9 |
| Stem density deciduous‡ | 3.4 | 7.7 | 1.1 | 3.1 |
| % of plots with rowan | 31 | 70 | 6 | 34 |
| % of plots with birches | 35 | 37 | 20 | 23 |
| Vegetation cover field layer§ | 64 | 72 | 119 | 123 |
| % of plots with taller herbs | 1 | 7 | 6 | 23 |
| % of plots with raspberry | 16 | 7 | 17 | 22 |

*Notes:* Characteristics were mapped at 12-m$^2$ circular plots evenly distributed (every 25 m in young forest, i.e., height class <4 m, and every 75 m in older forest), along 2 m wide transects laid out as structured cross sections of the terrain (see Wam et al. 2010 for details). The numbers are averages across all plots per area.

† Soil fertility was classified as 0 = impediment, 1 = low soil fertility (6–8 in H40), 2 = intermediate soil fertility (11–14 in H40), and 3 = high soil fertility (17–20 in H40), where H40 is the height of trees at the age of 40 yr at breast height 1.3 m (Tveite 1977) and based on the dominating vegetation on 0.1 ha surrounding the plot. The proportion of bogs was similar between livestock and control areas in Sande (3% and 2%), while there were more bogs in livestock areas than in control areas in Ringsaker (7% and 1%). Impediment comprised <3% in all areas.

‡ Number of stems 0.3–3.0 m in tree height, that is, within reach of foraging moose (all deciduous species included).

§ Proportion of plot area covered by field-layer plants (all herbs, ferns, heathers, grasses, raspberry, and bilberry).

N = 95 transects in total, mean length 300 m, SE = 24; Fig. 1). The triangles were laid out on recently logged clear-cuts (dominant tree height <4 m) and randomly selected among all such clear-cuts available on the range. Our reason for sampling on clear-cuts was to facilitate and systematize observability of feces. We collected at least 15 fresh fecal samples from each animal species in all livestock and control areas on each range (mean = 17, SD = 4.1), which we placed in plastic bags on site, stored inside field cabins, and deep-froze within 2–3 d. To reduce the likelihood of pseudo-replication in diet samples, we collected only one fecal sample per transect from
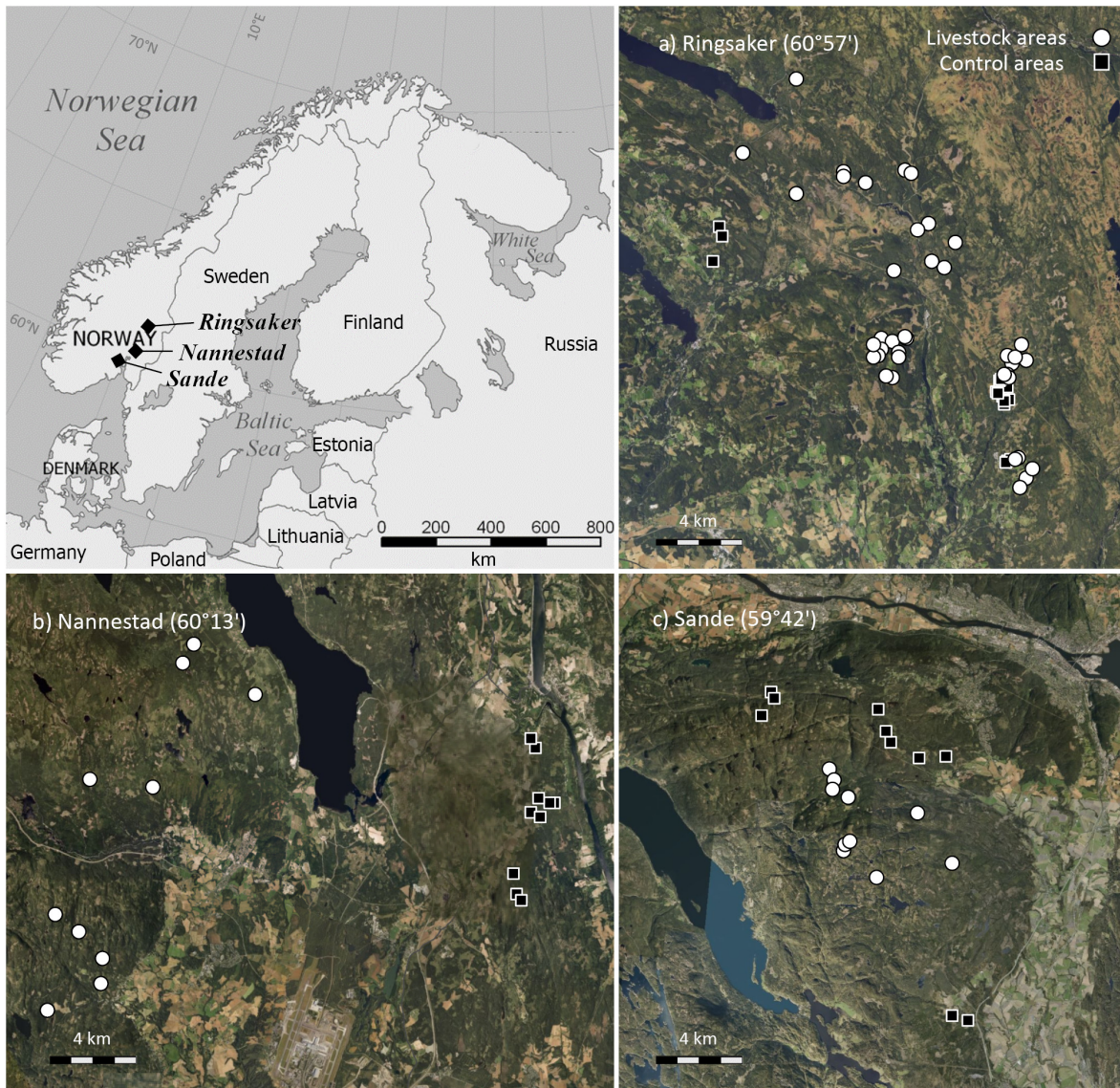


Fig. 1. Distribution of transects used to count and collect feces from livestock and moose sympatric with livestock, and moose in adjacent control areas without livestock. Sheep and cattle are free-ranged in summer within restricted areas on the three boreal forest ranges (a) Ringsaker, (b) Nannestad, and (c) Sande (numbers after range names are lattitudes). These areas are delimited by human-made fences (or natural obstacles) that follow property boundaries cutting arbitrarily through the terrain and its inherent site characteristics (soil fertility, topography, vegetation type).

each species. We found no livestock feces in the control areas, which confirm the expected barrier effect of the fence on livestock.

### Chemical analyses of feces

We determined diet composition using micro-histological analyses of epidermal fragments in the feces as outlined in Wam and Hjeljord (2010b). This gives a frequency measure of the occurrence of each plant species in the diet. Note that the method may underestimate more easily digested plants, such as certain herbs compared to grass or browse (Pulliam 1978). This applies equally to all areas, however. We also forced air-dried parts of each fecal sample at 30°C for 48 h and measured their total content of elemental nitrogen (fecal N) using a Micro Cube (Elementar Analysen, Hanau, Germany).

### Statistical analyses

We calculated diet width for moose using the Shannon–Wiener diversity index $e^{H'}$, rescaled to the number of species (Ricklefs 1973), where $H' = -\sum[p_i \times \ln(p_i)]$ and $p_i$ is the number of individuals of species $i$/total number of samples (at lowest taxonomical level; Appendix S1: Table S1). We tested for differences in diet width between sympatric moose and moose in control areas using a two-way ANCOVA (lm in R version 3.2.0, R Core Team 2017), with range and livestock (i.e., presence or absence of livestock) and their interaction as fixed explanatory variables. We did not treat range as random factor in a mixed model, because the low number of ranges (N = 3) is not sufficient to estimate the random variance component of such models.

We calculated diet overlap between animal groups according to Pianka (1973):

$$O_{A,B} = \frac{\sum(p_i q_i)}{\sqrt{\sum p_i^2 \sum q_i^2}}$$

where $p_i$ is the proportion of plant species $i$ in feces from animal group A, and $q_i$ is the proportion of plant species $i$ from animal group B. In our study, animal groups were sheep, cattle, sympatric moose (abbreviated "livestock" in the figures), or moose in control areas ("control" in the figures). An $O_{A,B}$ value of 1 indicates identical diet composition, whereas dissimilarity increases as $O_{A,B}$ approaches zero. $O_{A,B}$ was calculated both

for plant species grouped (browse = trees and taller shrubs; bilberry; raspberry; heather; grass = grasses, sedges; ferns = ferns, horsetails, club moss; herbs = herbaceous plants; and other = mosses, crops) and for the original plant classification (Appendix S1: Table S1).

We calculated diet overlap separately for each range using the mean diet for all samples from a given animal group. To account for potential differences in plant communities between ranges, we included only those plant species that were actually present in feces from a given range. We calculated 95% confidence interval (CI) based on bootstrapping (N = 1000). When we assessed whether moose fecal N (see next paragraph) was related to dietary overlap with livestock, we calculated $O_{\text{Moose, Sheep}}$ and $O_{\text{Moose, Cattle}}$ for each individual moose feces against the range averages of sheep and cattle.

We tested for differences in fecal N for sympatric moose compared to moose in control areas without livestock using a two-way ANCOVA with range and livestock (presence or absence of livestock) and their interaction as categorical fixed variables (lm in R version 3.2.0, R Core Team 2017). Next, we investigated whether variation in moose fecal N was related to dietary overlap between moose and livestock and to diet composition as found in the moose feces (Table 3). We also included the interactions between the dietary measure (overlap or content) and range and between the dietary measure and livestock. To reduce potential confounding effects due to collinearity between proportional variables (Graham 2003), we ran the procedure separately for each plant species or plant group in the diet. We used Akaike's information criterion, corrected for sample sizes (AIC$_c$) (Burnham and Anderson 2002) to rank candidate models. Candidate models were allowed to include any combination of the explanatory variables, but if an interaction was included, the two main variables were also retained (see Table 4 for lists of candidate models).

## Results

### Diet composition, diet width, and diet overlap of moose and livestock

Grasses dominated the diet of both cattle and sheep and to some extent also herbs for sheep, whereas the moose diet contained high

Table 3. Diet composition and diversity of sympatric cattle, sheep, and moose, as well as moose in adjacent control areas, on three boreal forest ranges in Norway in summer 2012, as found by micro-histological analyses of epidermal fragments in feces.†

| Range | Species | Browse | Bilberry | Raspberry | Herbs | Grasses | Ferns | Other | Diversity‡ |
|---|---|---|---|---|---|---|---|---|---|
| Sande | Cattle | 0.025 | 0.014 | 0.063 | 0.217 | 0.583 | 0.080 | 0.018 | 8.54 |
| | Sheep | 0.059 | 0.067 | 0.041 | 0.050 | 0.738 | 0.023 | 0.021 | 8.87 |
| | Moose | 0.309 | 0.271 | 0.163 | 0.008 | 0.064 | 0.168 | 0.017 | 5.17 |
| | Moose (control) | 0.342 | 0.340 | 0.065 | 0.044 | 0.070 | 0.093 | 0.054 | 5.76 |
| Nannestad | Cattle | 0.016 | 0.008 | 0.039 | 0.235 | 0.639 | 0.044 | 0.019 | 7.61 |
| | Sheep | 0.041 | 0.038 | 0.024 | 0.021 | 0.848 | 0.010 | 0.018 | 8.29 |
| | Moose | 0.397 | 0.272 | 0.104 | 0.003 | 0.114 | 0.092 | 0.017 | 5.37 |
| | Moose (control) | 0.455 | 0.210 | 0.121 | 0.003 | 0.119 | 0.087 | 0.005 | 5.42 |
| Ringsaker | Cattle | 0.009 | 0.036 | 0.083 | 0.012 | 0.825 | 0.018 | 0.017 | 6.20 |
| | Sheep | 0.012 | 0.044 | 0.034 | 0.005 | 0.854 | 0.018 | 0.032 | 6.60 |
| | Moose | 0.055 | 0.441 | 0.275 | 0.005 | 0.055 | 0.087 | 0.081 | 4.10 |
| | Moose (control) | 0.197 | 0.366 | 0.244 | 0.006 | 0.065 | 0.026 | 0.096 | 5.02 |

† At least 15 fresh samples/species in each livestock and control areas on all ranges (mean = 17, SD = 4.1). To increase the chance of sampling from unique individuals, we collected only one fecal sample/transect from each species. The mean distance between transects within a livestock or control area was 5161 m. Because not all areas yielded 15 samples from the transects, we also collected samples in the near vicinity of transects (up to approximately 200 m from the transect).

‡ Shannon–Wiener diversity index, rescaled to the number of species (Ricklefs 1973), where $H' = -\sum[p_i \times \ln(p_i)]$ and $p_i$ is the number of individuals of species $i$/total number of samples). We calculated the index from the lowest available taxonomic level of diet composition (Appendix S1: Table S1).

proportions of browse, bilberry, and raspberry (Table 3; Appendix S1: Table S1). The Shannon–Wiener index (diet width) for moose varied between ranges ($F_{2, 103} = 4.04$, $P = 0.020$), but was consistently lower for moose sympatric with livestock (mean = 4.6, SD = 1.38) than for moose in control areas without livestock (mean = 5.3, SD = 1.27; $F_{1, 103} = 3.96$, $P = 0.054$; interaction range and livestock; $F_{2, 103} = 0.82$, $P = 0.443$).

There was a high diet overlap between moose sympatric with livestock and moose in control areas without livestock, and there was a high diet overlap between sheep and cattle (Fig. 2). Both sympatric moose and moose in control areas had low diet overlap with sheep and cattle, and the diet overlap between sympatric moose and livestock did not differ significantly from the diet overlap between moose in control areas and livestock (all 95% CI of the difference in $O_{\text{Moose livestock, Livestock}}$ and $O_{\text{Moose control, Livestock}}$ included zero).

### Fecal N of moose in relation to free ranging of livestock

Feces from moose sympatric with livestock had significantly less nitrogen than feces from moose in the adjacent control areas without livestock ($F_{1,82} = 14.94$, $P \leq 0.001$, Fig. 3). Although the fecal N of moose varied between the three

ranges ($F_{2,82} = 8.52$, $P \leq 0.001$), the ranges had similar differences between sympatric moose and moose in control areas (interaction between range and livestock $F_{2,82} = 0.03$, $P = 0.969$).

### Moose fecal N in relation to diet composition and overlap with livestock

According to the AIC$_c$-based ranking of candidate models, moose fecal N was negatively related to diet overlap between moose and cattle $O_{\text{Moose, Cattle}}$, as well as the proportion of bilberry, grass, or other plants in the moose diet (Table 4, Fig. 4). In contrast, moose fecal N was positively related to the proportion of raspberry in the moose diet. All the highest ranked models included the explanatory variable livestock (i.e., whether samples were from moose sympatric with livestock or from moose in control areas without livestock), and models without the livestock variable consistently performed poorly in comparison (according to $\Delta$AIC$_c$ values). This suggests that the presence of livestock influenced moose fecal N.

## DISCUSSION

We found that a transformation of the forest ecosystems into agroecosystems by livestock grazing in our study areas likely has negative

Table 4. Models explaining variation in fecal N of moose sympatric with cattle and sheep, and moose in adjacent control areas without livestock on three boreal forest ranges in Norway, summer 2012 (N = 201 feces equally distributed among animal group and ranges).

| Diet measure | Diet | Range | Livestock | Diet × Livestock | Diet × Range | AIC$_c$ | ΔAIC$_c$ | $r^2$ |
|---|---|---|---|---|---|---|---|---|
| $O_{\text{Moose, Sheep}}$ |  | x | x |  |  | 36.70 | 0.00 | 0.334 |
|  | x | x | x |  |  | 38.91 | 2.22 | 0.335 |
|  | x | x | x | x |  | 40.06 | 3.36 | 0.334 |
|  |  | *x* |  |  |  | *55.64* | *18.94* | *0.151* |
| $O_{\text{Moose, Cattle}}$ | x | x | x |  |  | 36.01 | 0.00 | 0.357 |
|  | x | x | x | x |  | 36.37 | 0.36 | 0.372 |
|  |  | x | x |  |  | 36.70 | 0.69 | 0.324 |
|  | *x* | *x* |  |  |  | *53.04* | *17.04* | *0.197* |
| Browse |  | x | x |  |  | 36.70 | 0.00 | 0.334 |
|  | x | x | x |  |  | 38.78 | 2.09 | 0.336 |
|  | x | x | x |  | x | 39.53 | 2.83 | 0.366 |
|  | *x* | *x* |  |  | *x* | *52.32* | *15.62* | *0.245* |
| Bilberry | x | x | x |  |  | 28.64 | 0.00 | 0.409 |
|  | x | x | x | x |  | 31.01 | 2.36 | 0.409 |
|  | x | x | x |  | x | 31.81 | 3.17 | 0.420 |
|  | *x* | *x* |  |  |  | *44.94* | *16.30* | *0.268* |
| Raspberry | x | x | x |  |  | −3.86 | 0.00 | 0.593 |
|  | x | x | x | x |  | −1.72 | 2.14 | 0.594 |
|  | x | x | x |  | x | −0.62 | 3.24 | 0.600 |
|  | *x* | *x* |  |  |  | *31.81* | *35.67* | *0.371* |
| Herbs |  | x | x |  |  | 36.70 | 0.00 | 0.334 |
|  | x | x | x |  |  | 38.16 | 1.46 | 0.341 |
|  | x | x | x | x |  | 40.14 | 3.45 | 0.344 |
|  | *x* | *x* |  |  |  | *52.03* | *15.33* | *0.206* |
| Grasses | x | x | x |  |  | 35.69 | 0.00 | 0.359 |
|  |  | x | x |  |  | 36.70 | 1.00 | 0.334 |
|  | x | x | x | x |  | 38.36 | 1.67 | 0.364 |
|  | *x* | *x* |  |  |  | *55.20* | *19.51* | *0.176* |
| Ferns |  | x | x |  |  | 36.70 | 0.00 | 0.334 |
|  | x | x | x |  | x | 36.72 | 0.03 | 0.386 |
|  | x | x | x | x | x | 37.83 | 1.14 | 0.396 |
|  | *x* | *x* |  |  | *x* | *51.57* | *14.87* | *0.251* |
| Other | x | x | x |  |  | 27.92 | 0.00 | 0.414 |
|  | x | x | x |  | x | 28.67 | 0.75 | 0.441 |
|  | x | x | x | x |  | 30.12 | 2.20 | 0.415 |
|  | *x* | *x* |  |  | *x* | *48.20* | *20.28* | *0.280* |

*Notes:* AIC$_c$, Akaike's information criterion, corrected for sample sizes. Shown are the three highest AIC$_c$-ranked models for alternative diet measures (O = Pianka's overlap index, or content of specific plant groups). We also show the highest ranked model not including livestock (italic font), to highlight the influence of this important variable.

impact on a native ungulate. Moose sympatric with free-ranging cattle and sheep had lower fecal N than moose in control areas without livestock, indicating that sympatric moose obtained food of lower quality. As predicted from the different feeding strategy, moose (a browser) had low diet overlap with sheep and cattle (grazers). Furthermore, the diet composition of sympatric moose was almost identical to that of moose in control areas, apart from higher contents of ferns. Because

moose in the area generally do not select for ferns (Wam and Hjeljord 2010a), this suggests that sympatric moose had to make somewhat less optimal diet choices. Sympatric moose also had a narrower diet (Shannon–Wiener diversity index) than moose in control areas. Can these apparently minor diet differences explain the lower fecal N of sympatric moose?

The application of the fecal N index as an index of diet quality rests on the assumption that it is
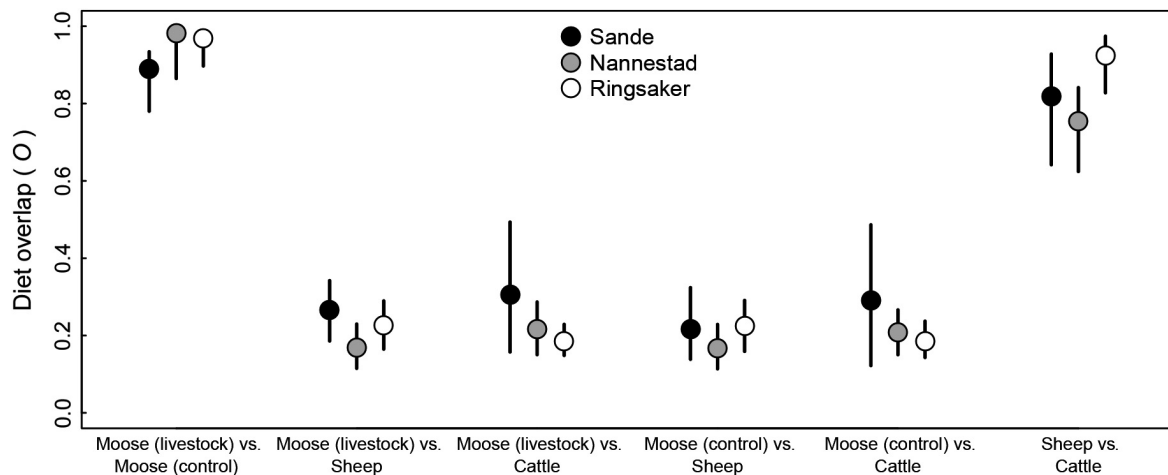
Fig. 2. Diet overlap in summer as measured by Pianka's $O$ (Pianka 1973) between livestock and moose on three boreal forest ranges in Norway 2012. Overlap is shown for moose sympatric with the livestock (livestock), and moose in adjacent control areas without livestock (control). Diet was estimated from micro-histological analyses of feces (N = 201, equally distributed among animal group, data in Appendix S1: Table S1). Bars represent 95% confidence interval based on bootstrapping (N = 1000).
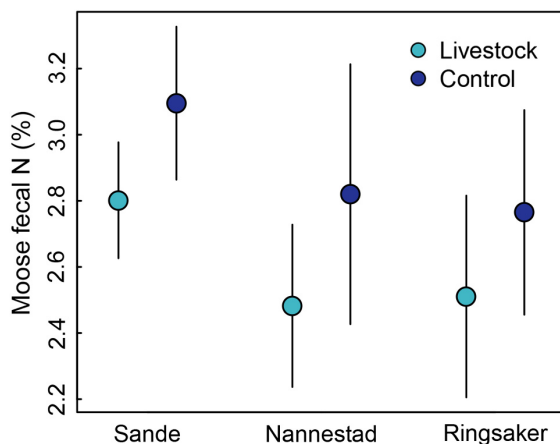


Fig. 3. Content of total nitrogen (mean ± 1 SD of dry matter) in summer feces of moose sympatric with cattle and sheep (livestock), and moose in adjacent control areas without livestock (control) on three boreal forest ranges in Norway 2012 (N = 201 feces equally distributed among animal group).

positively associated with higher protein intake, given that protein digestibility is not altered simultaneously (Leslie et al. 2008). Other food constituents in the diet affect protein digestibility, and particularly, protein precipitation of condensed tannins has received attention in the ungulate literature (Robbins et al. 1987, Spalinger et al. 2010). Condensed tannins are large molecules at the end of biosynthetic pathways of carbon-based plant secondary metabolites (Winkel-Shirley 2002). They are therefore generally of larger concentrations in older plant material (Riipi et al. 2002, Wam et al. 2017*a*, *b*). In our study, we did observe a slightly higher diet content of browse for moose in control areas compared to sympatric moose, potentially explaining their higher fecal N. It could be that because browse includes more perennial plant parts, they also have more condensed tannins than other plant groups. However, tannin concentrations in summer diets with similar browse levels as in our study have been found to comprise only trace amounts (Hodgman et al. 1996). It is also increasingly recognized that condensed tannins may even enhance rather than inhibit protein digestibility, depending on intake thresholds determined by complex dietary interactions (Makkar 2003, DeGabriel et al. 2014). In our data, there was no significant relationship between individual fecal N and proportion of browse in the diet (Fig. 4). Furthermore, the highest ranked models explaining variation in fecal N always included livestock and range, irrespective of which dietary measures we included (Table 4). It appears evident that the difference in fecal N between
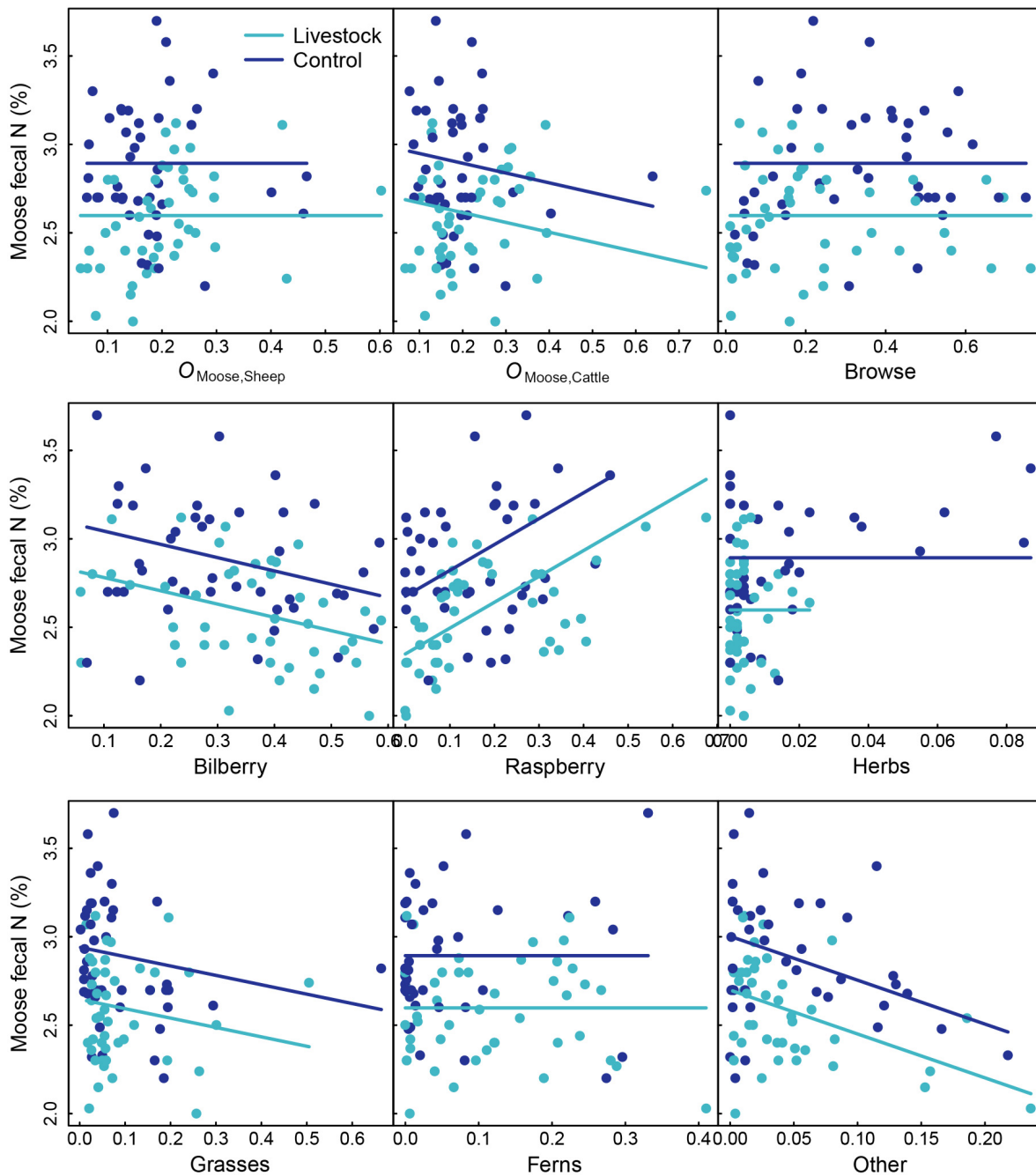
Fig. 4. Fecal N in relation to diet content (proportion of epidermal fragments in N = 201 feces equally distributed among animal group, data in Appendix S1: Table S1) and diet overlap (Pianka's *O*) for moose sympatric with livestock (livestock) or moose in adjacent control areas without livestock (control) on three boreal forest ranges in Norway 2012. Lines show the relationships between diet and fecal N based on the highest ranked models in Table 4, and for average values of fecal N across ranges (relationship between diet and fecal N did not differ between ranges, Table 4).

sympatric and control moose was not a result of differences in diet composition as measured by plant species.

We see two likely, and not mutually exclusive, explanations for why moose had lower fecal N in the presence of livestock despite their low dietary overlap: (1) moose behavioral avoidance of livestock and (2) changes to the vegetation caused by livestock activity (grazing, trampling, etc.). Moose may avoid areas used by livestock and thereby experience a spatial reduction in availability of resources. In a study on moose–livestock interactions based on GPS collared animals in one of our study areas (Nannestad), we found that moose indeed had a narrower habitat niche breadth when the habitat overlap with livestock increased, suggesting that moose habitat utilization is constrained in periods when livestock uses the same habitats (Herfindal et al. 2017). Behavioral avoidance between wild and domestic ungulates is expected to favor the domestic species (Krämer 1973, Coe et al. 2001, Cooper et al. 2008). Domestication selects for less fearful animals (Price 1999, Welp et al. 2004), which possibly explains why avoidance through fear responses may be more prevalent in moose than in livestock. Both cattle and sheep are more gregarious than moose, which could also factor in on which will be the most avoidant (McNaughton 1984). Such spatial displacement would incur a nutritional cost to moose in terms of lower intake rates, as it would have to spend more time on locomotion or vigilance (Charnov 1976, WallisDeVries et al. 1999, Massé and Côté 2013). Rather than travelling the longer distances between foraging patches without livestock, the moose may increase resource exploitation in a patch, eventually accepting plant tissue of lower quality (Sæther and Andersen 1990). In summer, large herbivores may select for plant tissue with certain nutritional characteristics rather than for plant species (Hjeljord et al. 1990, Verheyden-Tixier et al. 2008, Wam and Hjeljord 2010a, Redjadj et al. 2014). Moose can therefore experience quite a reduction in optimal foraging without it showing as changes to its diet composition.

In addition to affecting the foraging behavior of the wild herbivore, livestock may also alter the abundance of plants (Mysterud and Austrheim 2008, Foster et al. 2014, Hjeljord et al. 2014) and/or the nutritional composition of plants (Alpe

et al. 1999, Wagoner et al. 2013, Treydte et al. 2014). Although we found few compositional differences in the moose diet between livestock and control areas, the altered plant abundances (Table 2) may still influence the moose' intake rates of nutrients. For instance, Wagoner et al. (2013) found that deer spent the same time foraging when placed in areas not grazed by cattle compared to in grazed areas but obtained a 39% lower intake of digestible energy. Herbivory may improve nutrient contents of plants by delaying phenology (e.g., more digestible fiber structure, more protein; Westenskow-Wall et al. 1994, Alpe et al. 1999). However, this highly depends on the grazing intensity (Cook et al. 1953), which in our study varied considerably between ranges (Table 1). Plant species adapted to low-resource environments such as boreal forests are more sensitive to herbivory, which generally have a negative effect on the plants' nutritional value to the animals (Bryant et al. 1981, 1983).

Our fecal counts add to the indication that moose responded behaviorally to the presence or the vegetational influence of livestock by moving to areas without livestock (as did mule deer in Loft et al. 1991). Higher fecal density of livestock on our study ranges appeared to be associated with lower fecal density of moose (relative to the adjacent control area). On the range most densely populated by livestock, we observed more than four times as many moose feces outside compared to inside the livestock fence. It is unlikely that the lower density of moose feces in livestock areas was an artifact of sampling procedures. Fecal counts are highly influenced by observability (Persson 2003), but feces are easier to detect in more open (like inside the livestock fence) than in more structured vegetation (like outside the fence).

Our results confirm that interspecific interactions with free-ranging livestock are likely to alter the foraging opportunities of native large herbivores. Most importantly, our study shows that these alterations may occur through subtle foodscape displacements that are not evident in diet compositions, yet they can potentially have substantial impact on nutrient intake. It is easy to disregard minor diet changes as insignificant, but one should not forget that even small diet perturbations may generate strong fitness consequences (the multiplier effect, White 1983). Fitness-related

traits in moose are closely related to summer foraging conditions (Sæther et al. 1996, Herfindal et al. 2006, 2014), which corresponds to the time of the year when livestock is on the forest ranges. Furthermore, if moose avoid livestock areas, it may influence migratory behavior, which is another important factor for their fitness (Rolandsen et al. 2017). Given locally and globally increasing transformations of ecosystems into agroecosystems, we call for more research on the large-scale effects of livestock–herbivore interactions.

## ACKNOWLEDGMENTS

## LITERATURE CITED

Alpe, M. J., J. L. Kingery, and J. C. Mosley. 1999. Effects of summer sheep grazing on browse nutritive quality in autumn and winter. Journal of Wildlife Management 63:346–354.

Beck, J. L., and J. M. Peek. 2005. Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen-sagebrush summer range. Rangeland Ecology & Management 58:135–147.

Bryant, J. P., F. S. Chapin III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357–368.

Bryant, F. C., C. A. Taylor, and L. B. Merrill. 1981. White-tailed deer diets from pastures in excellent and poor range condition. Journal of Range Management 34:193–200.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129–136.

Coe, P. K., B. K. Johnson, S. L. Kern, S. L. Findholt, J. G. Kie, and M. J. Wisdom. 2001. Responses of elk and mule deer to cattle in summer. Journal of Range Management 54:205, A51–A76.

Cook, C. W., L. E. Stoddart, and L. E. Harris. 1953. Effects of grazing intensity upon the nutritive value of range forage. Journal of Range Management 6:51–54.

Cooper, S. M., H. L. Perotto-Baldivieso, M. K. Owens, M. G. Meek, and M. Figueroa-Pagán. 2008. Distribution and interaction of while-tailed deer and cattle in a semi-arid grazing system. Agriculture, Ecosystems & Environment 127:85–92.

Cromsigt, J. P. G. M., and D. P. J. Kuijper. 2011. Revisiting the browsing lawn concept: Evolutionary interactions or pruning herbivores? Perspectives in Plant Ecology, Evolution and Systematics 13:207–215.

DeGabriel, J. L., B. D. Moore, A. M. Felton, J. U. Ganzhorn, C. Stolter, I. R. Wallis, C. N. Johnson, and W. J. Foley. 2014. Translating nutritional ecology from the laboratory to the field: milestones in linking plant chemistry to population regulation in mammalian browsers. Oikos 123:298–308.

Dodds, W. K. 1997. Interspecific interactions: constructing a general neutral model for interaction type. Oikos 78:377–383.

Felton, A. M., A. Felton, D. B. Lindenmayer, and W. J. Foley. 2009. Nutritional goals of wild primates. Functional Ecology 23:70–78.

Foster, C. N., P. S. Barton, and D. B. Lindenmayer. 2014. Effects of large native herbivores on other animals. Journal of Applied Ecology 51:929–938.

Fynn, R. W. S., D. J. Augustine, M. J. S. Peel, and M. de Garine-Wichatitsky. 2016. Review: strategic management of livestock to improve biodiversity conservation in African savannahs: a conceptual basis for wildlife-livestock coexistence. Journal of Applied Ecology 53:388–397.

Gordon, I. J. 1988. Facilitation of red deer grazing by cattle and its impact on red deer performance. Journal of Applied Ecology 25:1–9.

Gordon, I. J., and A. W. Illius. 1989. Resource partitioning by ungulates on the Isle of Rhum. Oecologia 79:383–389.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815.

Herfindal, I., H. Haanes, E. J. Solberg, K. H. Røed, K. A. Høgda, and B.-E. Sæther. 2014. Moose body mass variation revisited: disentangling effects of environmental conditions and genetics. Oecologia 174:447–458.

Herfindal, I., U. S. Lande, E. J. Solberg, C. M. Roland-sen, O. Roer, and H. K. Wam. 2017. Weather affects temporal niche partitioning between moose and livestock. Wildlife Biology. https://doi.org/10.2981/wlb.00275

Herfindal, I., B.-E. Sæther, E. J. Solberg, R. Andersen, and K. A. Høgda. 2006. Population characteristics predict responses in moose body mass to temporal variation in the environment. Journal of Animal Ecology 75:1110–1118.

Hibert, F., C. Calenge, H. Fritz, D. Maillard, P. Bouché, A. Ipavec, A. Convers, D. Ombredane, and M.-N. de Visscher. 2010. Spatial avoidance of invading pastoral cattle by wild ungulates: insights from using point process statistics. Biodiversity and Conservation 19:2003–2024.

Hjeljord, O., T. Histøl, and H. K. Wam. 2014. Forest pasturing of livestock in Norway: effects on spruce regeneration. Journal of Forest Research 25:941–945.

Hjeljord, O., N. Hövik, and H. B. Pedersen. 1990. Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. Ecography 13:281–292.

Hodgman, T. P., B. B. Davitt, and J. R. Nelson. 1996. Monitoring mule deer diet quality and intake with fecal indices. Journal of Range Management 49:215–222.

Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants – a comparative view of their digestive system. Oecologia 78:443–457.

Hutchinson, G. E. 1957. Concluding remarks. Population studies: animal ecology and demography. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Krämer, A. 1973. Interspecific behavior and dispersion of two sympatric deer species. Journal of Wildlife Management 37:288–300.

Leslie, D. M., R. T. Bowyer, and J. A. Jenks. 2008. Facts from feces: Nitrogen still measures up as a nutritional index for mammalian herbivores. Journal of Wildlife Management 72:1420–1433.

Loft, E. R., J. W. Menke, and J. G. Kie. 1991. Habitat shifts by mule deer: the influence of cattle grazing. Journal of Wildlife Management 55:16–26.

Mackie, R. J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. Wildlife Monographs 20:1–79.

Makkar, H. P. S. 2003. Effects and fate of tannins in ruminant animals, adaptation to tannins, and strategies to overcome detrimental effects of feeding tannin-rich feeds. Small Ruminant Research 49:241–256.

Massé, A., and S. D. Côté. 2013. Spatiotemporal variations in resources affect activity and movement patterns of white-tailed deer (*Odocoileus virginianus*) at high density. Canadian Journal of Zoology 91:252–263.

Mattson Jr., W. J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11:119–161.

McArt, S. H., D. E. Spalinger, W. B. Collins, E. R. Schoen, T. Stevenson, and M. Bucho. 2009. Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska. Ecology 90:1400–1411.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266:1555–1558.

McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist 124:863–886.

Moen, A. 1999. National atlas of Norway – vegetation. Norwegian Mapping Authority, Hønefoss, Norway.

Mysterud, A., and G. Austrheim. 2008. The effect of domestic sheep on forage plants of wild reindeer; a landscape scale experiment. European Journal of Wildlife Research 54:461–468.

Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 2006. Forage selection by mule deer: Does niche breadth increase with population density? Journal of Zoology 269:39–49.

Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57–69.

Persson, I.-L. 2003. Seasonal and habitat differences in visibility of moose pellets. Alces 39:233–241.

Petersen, J. E., and A. Hastings. 2001. Dimensional approaches to scaling experimental ecosystems: designing mousetraps to catch elephants. American Naturalist 157:324–333.

Pianka, E. R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4:53–74.

Power, A. G. 2010. Ecosystem services and agriculture: tradeoffs and synergies. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2959–2971.

Price, E. O. 1999. Behavioural development in animals undergoing domestication. Applied Animal Behaviour Science 65:245–271.

Pulliam, D. E. 1978. Determination of digestibility coefficients for quantification of elk fecal analysis. Dissertation. Washington State University, Pullman, Washington, USA.

Putman, R. J., R. Pratt, J. Ekins, and P. J. Edwards. 1987. Food and feeding behaviour of cattle and

ponies in the New Forest, Hampshire. Journal of Applied Ecology 24:369–380.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Redjadj, C., G. Darmon, D. Maillard, T. Chevrier, D. Bastianelli, H. Verheyden, A. Loison, and S. Saïd. 2014. Intra- and interspecific differences in diet quality and composition in a large herbivore community. PLoS ONE 9:e84756.

Ricklefs, R. E. 1973. Ecology. Chiron Press, Newton, Massachusetts, USA.

Riipi, M., V. Ossipov, K. Lempa, E. Haukioja, J. Koricheva, S. Ossipova, and K. Pihlaja. 2002. Seasonal changes in birch leaf chemistry: Are there trade-offs between leaf growth and accumulation of phenolics? Oecologia 130:380–390.

Ripple, W. J., et al. 2015. Collapse of the world's largest herbivores. Science Advances 1:e1400103.

Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D. L. Baker, C. C. Schwartz, and W. W. Mautz. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology 68:98–107.

Rolandsen, C. M., E. J. Solberg, B.-E. Sæther, B. V. Moorter, I. Herfindal, and K. Bjørneraas. 2017. On fitness and partial migration in a large herbivore—migrant females have higher reproductive performance than resident females. Oikos 126:547–555.

Sæther, B.-E., and R. Andersen. 1990. Resource limitation in a generalist herbivore, the moose *Alces alces*: ecological constraints on behavioural decisions. Canadian Journal of Zoology 68:993–999.

Sæther, B.-E., R. Andersen, O. Hjeljord, and M. Heim. 1996. Ecological correlates of regional variation in life history of the moose *Alces alces*. Ecology 77:1493–1500.

Schieltz, J. M., and D. I. Rubenstein. 2016. Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know? Environmental Research Letters 11:1133.

Spalinger, D. E., W. B. Collins, T. A. Hanley, N. E. Casara, and A. M. Carnahan. 2010. The impact of tannins on protein, dry matter, and energy digestion in moose (*Alces alces gigas*). Canadian Journal of Zoology 88:977–987.

Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83:229–244.

Tingley, R., M. Vallinoto, F. Sequeira, and M. R. Kearney. 2014. Realized niche shift during a global biological invasion. Proceedings of the National Academy of Sciences USA 111:10233–10238.

Torchin, M. E., and C. E. Mitchell. 2004. Parasites, pathogens, and invasions by plants and animals. Frontiers in Ecology and the Environment 2:183–190.

Treydte, A. C., S. Baumgartner, I. M. A. Heitkonig, C. C. Grant, and W. M. Getz. 2014. Herbaceous forage and selection patterns by ungulates across varying herbivore assemblages in a South African savanna. PLoS ONE 8:e82831.

Tscharntke, T., Y. Clough, T. C. Wanger, L. Jackson, I. Motzke, I. Perfecto, J. Vandermeer, and A. Whitbread. 2012. Global food security, biodiversity conservation and the future of agricultural intensification. Biological Conservation 151:53–59.

Tveite, B. 1977. Site-index curves for Norway spruce (*Picea abies* (L.) Karst.). Report Norwegian Forest Research Institute 33. Pages 1–84.

Uresk, D. W., and W. W. Paintner. 1985. Cattle diets in a ponderosa pine forest in the northern Black Hills. Journal of Range Management 38:440–442.

van Vaalen, L. 1965. Morphological variation and width of ecological niche. American Naturalist 99:377–390.

Verheyden-Tixier, H., P. C. Renaud, N. Morellet, J. Jamot, J. M. Besle, and B. Dumont. 2008. Selection for nutrients by red deer hinds feeding on a mixed forest edge. Oecologia 156:715–726.

Wagoner, S. J., L. A. Shipley, R. C. Cook, and L. Hardesty. 2013. Spring cattle grazing and mule deer nutrition in a bluebunch wheatgrass community. Journal of Wildlife Management 77:897–907.

WallisDeVries, M. F., E. A. Laca, and M. W. Demment. 1999. The importance of scale of patchiness for selectivity in grazing herbivores. Oecologia 121:355–363.

Wam, H. K., and O. Hjeljord. 2010a. Moose summer and winter diets along a large scale gradient of forage availability in southern Norway. European Journal of Wildlife Research 56:745–755.

Wam, H. K., A. Felton, C. Stolter, L. Nybakken, and O. Hjeljord. 2017b. Moose selecting for specific nutritional composition of birch places limits on food acceptability. Ecology & Evolution 8:1117–1130.

Wam, H. K., C. Stolter, and L. Nybakken. 2017b. Compositional changes in foliage phenolics with plant age, a natural experiment in boreal forests. Journal of Chemical Ecology 43:920–928.

Wam, H. K., and O. Hjeljord. 2010b. Moose summer diet from feces and field-surveys: a comparative study. Rangeland Ecology & Management 63:387–395.

Wam, H. K., O. Hjeljord, and E. J. Solberg. 2010. Differential forage use makes carrying capacity equivocal on ranges of Scandinavian moose *Alces alces*. Canadian Journal of Zoology 88:1179–1191.

Welp, T., J. Rushen, D. L. Kramer, M. Festa-Bianchet, and A. M. de Passile. 2004. Vigilance as a measure of fear in dairy cattle. Applied Animal Behaviour Science 87:1–13.

Westenskow-Wall, K. J., W. C. Krueger, L. D. Bryant, and D. R. Thomas. 1994. Nutrient quality of bluebunch wheatgrass regrowth on elk winter range in relation to defoliation. Journal of Range Management 47:240–244.

White, R. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377–384.

Winkel-Shirley, B. 2002. Biosynthesis of flavonoids and effects of stress. Current Opinion in Plant Biology 5:218–223.

Zhang, W., T. H. Ricketts, C. Kremen, K. Carney, and S. M. Swinton. 2007. Ecosystem services and dis-services to agriculture. Ecological Economics 64:253–260.

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Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2280/full