

Are trampling effects by wild tundra reindeer understudied?

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Abstract: Grazing and trampling by the wide-ranging wild tundra reindeer may have major top down landscape effects by causing vegetation changes. Grazing, as the collective effect of eating, trampling, defecation, and urination, has been studied extensively. In contrast, trampling effects *per se* are rarely studied, and almost never quantified, even though considered very important. The main reason appears to be methodological; effects of trampling imprints are difficult to measure and quantify systematically. In particular, in winter reindeer may largely subsist on slow-growing ground lichens. They grow in habitats with little snow cover and extensive soil frost, and dry lichen may be particularly susceptible to trampling, generating a likely substantial forage loss.

Key words: grazing; trampling; reindeer; lichen; forage loss.

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Introduction

Grazing and trampling by large herbivores like northern reindeer (*Rangifer tarandus L.*) can have extensive top down landscape effects on tundra and alpine vegetation through generating vegetation changes (e.g. Suominen & Olofsson, 2000; Austrheim & Eriksson, 2001; Cairns & Moen, 2004; Wehn *et al.*, 2011; Holtmeier, 2015). Thus, herbivores can be ecosystem keystone species (e.g. Naiman & Rogers, 1997; Suominen & Olofsson, 2000; Eby *et al.*, 2014). This type of ecological changes are often referred to as generated by a single process, 'grazing' or 'browsing' (e.g. Olf *et al.*, 1999; Albon *et al.*, 2007; Tremblay *et al.*, 2007; Mysterud & Austrheim, 2008). However, this is meant to collectively cover the

two concomitants but different processes of *eating* and *trampling* of vegetation (e.g. Pellerin *et al.*, 2006). The directed and selective *eating* of plants, including effects of defecation and urination, and to some extent also spill (material not eaten, but spilled) on soil, has been studied extensively in herbivores, with several different and well developed methods both in the field and the laboratory (e.g. Stewart, 1967; Holechek *et al.*, 1982; Dove & Mayes, 1991), and including reindeer (Skogland, 1984; Sormo *et al.*, 1999; Stark *et al.*, 2000; Stark *et al.*, 2007; Finstad & Kielland, 2011; Ophof *et al.*, 2013; Zielinska *et al.*, 2016). However, the necessarily associated but undirected *trampling* of vegetation may be as important in generating vegetation changes, but is an additional eco-

logical mechanism that likely depends on different ecological factors, e.g. reindeer hoofs and movement behaviours and ambient climatic conditions like air humidity. For example, in 1911 the Norwegian High Mountain Grazing Commission (Hardangervidda) (Hirsch *et al.*, 1911) stated. 'In summer, the reindeer herders are afraid of letting the herds onto areas where there is lush winter forage, that is where the ground is covered by lichen. In summer when the lichens are dry and brittle, it is devastating when a herd tramples back and forth over it'. Although perceived to be of such major importance, it appears to us that one hundred years later trampling remains a challenge to study and quantify, and is still understudied. Open alpine grazing systems is a particularly good model for studying trampling effects, because chionofobic oligotrophic vegetation, like lichen, may be exposed to trampling year round (e. g. Skogland, 1984). More forested grazing systems, e.g. northern pine *Pinus sylvestris* and birch *Betula pubescens* forests, may also be used as reindeer pasture in summer or year-round, but is often more snow-covered in winter, and therefore more susceptible to trampling during the summer season (e. g. Kumpula *et al.*, 2011; Pekkarinen *et al.*, 2015).

Methodological challenges in the study of trampling

Thus, in a recent review of low-intensity grazing, Rosenthal *et al.* (2012) concluded that the impact of trampling even by domestic herbivores on plant species composition and richness, is underestimated. The direct and easily observable mechanical disruption of vegetation cover and soil, including soil compaction, infiltration of water, and nutrient cycling, have to some extent been studied and quantified in some herbivores (Stark *et al.*, 2000; Pellerin *et al.*, 2006; Schrama *et al.*, 2013; Xu *et al.*, 2013; Ludvikova *et al.*, 2014) (but for different results see Plumptre, 1994; Cumming & Cumming,

2003; Van Uytvanck & Hoffmann, 2009). However, the more subtle preceding effects on the vegetation appear to be rather understudied. This is likely due to methodological difficulties: how can we quantify trampling effects on not eaten (not removed), but still trampled vegetation? Although trampling is frequently referred to as important in studies of interactive herbivore-vegetation effects, it is still stated in a non-quantitative and often rather anecdotal way (Persson *et al.*, 2000; Austrheim *et al.*, 2008; Suominen *et al.*, 2008), including for the northern reindeer living in fragile and vulnerable cold high-latitude alpine and Arctic ecosystems (Skogland, 1983; Skogland, 1984; Körner, 2003). During the critical winter, reindeer may eat substantial amounts of lichen (Skogland, 1984; Kumpula, 2001; Storeheier *et al.*, 2002; Vistnes & Nellemann, 2008; Hansen *et al.*, 2010) which may be the most important and easily available forage. Slow-growing ground lichens are weak competitors, mainly found on sites where the environmental conditions are challenging to most vascular plants. Alpine lichen heaths are dominated by chionofobic species growing mainly on exposed, nutrient poor habitats where wind blows the snow away, resulting in extensive frost (Dahl, 1956; Odland & Munkejord, 2008). Dry, brittle lichen in exposed habitats will likely be subject to trampling, and, importantly, maintain hoof footprints. Combined with their ecological significance, lichen may present a model more suitable for quantitative trampling studies than the more pliable, and therefore resilient, vascular plants. Total lichen cover and biomass vary greatly, from a total dry biomass of 2 kg m⁻² in undisturbed *Pine* forests and 1.2 kg m⁻² in undisturbed exposed alpine heaths (e.g. Kumpula, 2001), to less than 0.1 kg m⁻² in heavily grazed, and necessarily also trampled alpine heaths (Odland *et al.*, 2014). Desiccated and brittle lichen will be particularly susceptible to trampling (Holtmeier *et al.*, 2003; Kumpula *et*

al., 2011). New high-resolution 3D laser technology may prove helpful to quantify lichen loss in experimental studies (Heggenes *et al.*, 2017).

Reindeer, with their large body, graze extensively, live in herds, are nearly always on the move, with some of the longest ungulate migrations known, are known to take a toll on the typically low production and patchy distribution of high quality vegetation resources in the Alpine and Arctic landscapes. Thus, vegetation eating and trampling are major ecological processes affecting these fragile ecosystems. But how well studied is reindeer trampling *per se*?

Qualitative and understudied reindeer trampling relative to eating of vegetation

During the long northern winters, reindeer often depend on lichen forage (Skogland, 1989; Ferguson *et al.*, 2001; Vikhamar-Schuler *et al.*, 2013). As for other ungulate-grazing ecosystems, it is common knowledge that the two main factors plant eating and trampling dictate the quantity and quality of the vegetation grazing resource (Gaare & Skogland, 1975; Gaare & Skogland, 1980; Koster *et al.*, 2013; Holtmeier, 2015). Unfortunately, also for reindeer this is conveniently often seen as a single process (e.g. den Herder *et al.*, 2003; Boudreau & Payette, 2004; Kumpula *et al.*, 2014), likely because they are difficult to separate (Olofsson *et al.*, 2001). In reported studies, the negative effects of trampling on fruticose lichens may qualitatively be stated as substantial and important (Pegau, 1970; Suominen & Olofsson, 2000; Cooper & Wooley, 2001; Moen & Danell, 2003; Cairns & Moen, 2004; Olofsson *et al.*, 2004; Cooper, 2006; Moen & Lagerstrom, 2008; Kittl *et al.*, 2009; Olofsson, 2009; Kumpula *et al.*, 2011; Koster *et al.*, 2013). Trampling has even recently been speculated to be more important than grazing (Vistnes & Nellemann, 2008; Kumpula *et al.*, 2011), and especially for lichen winter forage. The effects

of trampling on lichen have been suggested to depend on abiotic and biotic ecological factors (Sorensen *et al.*, 2009), in particular humidity (Cooper *et al.*, 2001; Moen *et al.*, 2009; Kumpula *et al.*, 2011) and species (Bayfield *et al.*, 1981; Sorensen *et al.*, 2009). However, few studies try to estimate such trampling effects *per se*. Thus, for example Vistnes & Nellemann (2008) in a recent study on reindeer winter grazing suggest an estimated “spillage” factor of 10 (‘times consumption’), not based on presenting any original data, but with reference to a study by Gaare & Skogland (1975). “Spillage” is not specified, but likely includes trampling as a major factor, but also additional waste that may be associated with plant eating, e.g. selective feeding and dislodged vegetation, and spill during winter crater digging and feeding. During the summer season, trampling will by far be more important, whereas in winter, when snow cover partly protects ground lichen, trampling will be less, and spill may be relatively more important. If a spillage factor of 10 was the case, i.e. trampling is even more important than plant eating (Kumpula *et al.*, 2011), would not the ecological effects of how reindeer behave and move (causing spill and trampling), and vegetation sensitivity to trampling, be far more important than how and how much reindeer eat? If so, the widespread focus on grazing as a collective effect of reindeer on vegetation in relevant literature (e.g. Moen & Danell, 2003; Olofsson, 2006; Olofsson *et al.*, 2010; Kumpula *et al.*, 2014) may benefit from a separation and better understanding of the effects of different activities by reindeer. A conceptual model of vegetation loss due to plant eating and trampling versus reindeer density (Fig. 1) is necessarily speculative and bold, because data are so few or lacking. However, we suggest a linear relationship when forage is abundant and reindeer forage at maximum level, but with decreasing removal of vegetation per head as higher reindeer density increases food compe-

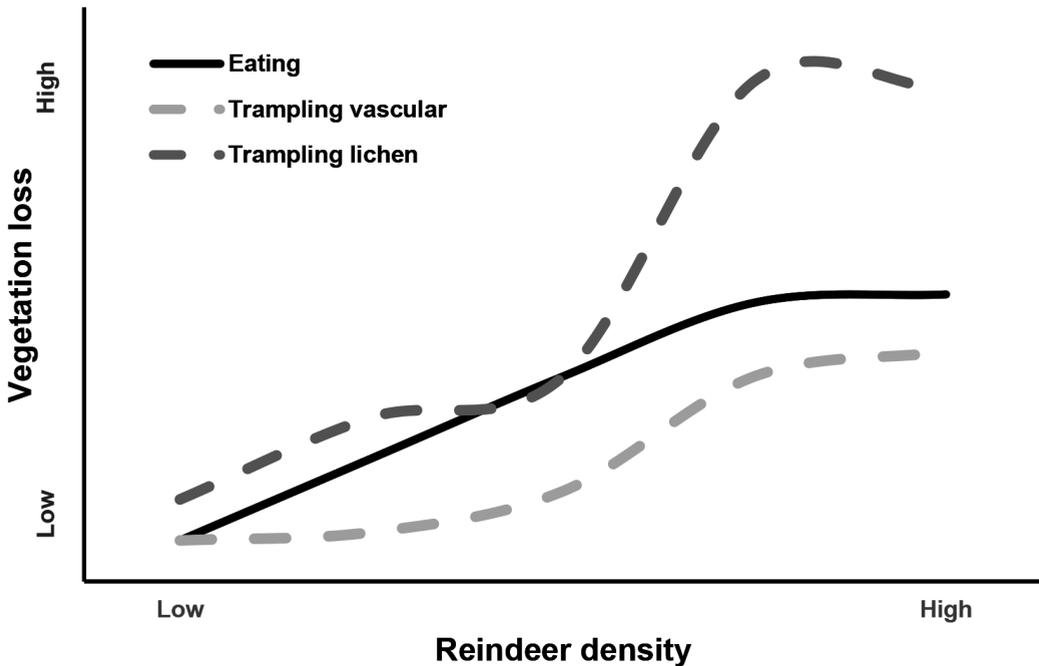


Figure 1. A conceptual model of vegetation loss due to eating and trampling by reindeer. Trampling generates more vegetation loss than eating, but the relationship is likely underestimated in the figure (illustration purposes). A near linear relationship may exist for plant eating (black line) and reindeer density when forage is abundant, but decreasing as competition for food increases, and depending on annual production of forage. Trampling loss may be low at low reindeer densities for pliable vascular plants (light grey dashed line), but likely more linear in lichen (dark grey dashed line), in particular in dry lichen, and considerably more than vegetation eaten. Step overlap may perhaps initially decrease loss rate of lichen as reindeer density increases. Loss will increase until vegetation cover is reduced, and eventually approaches mechanical disruption, when loss will obviously drop sharply (not modelled here).

tion. Trampling effects may be relatively low for more pliable, i.e. resilient vascular plants. This relationship is likely more linear in particular in dry, brittle lichen, but will decrease when increased reindeer density results in more repeat footprints. Loss will increase sharply when vegetation cover approaches mechanical disruption (Fig. 1) with additional loads of water and soil erosion. Once the vegetation cover disrupts, vegetation loss will obviously drop sharply (not included in the figure).

Understudied and overrated reindeer trampling: gossip snowballing?

The food requirements and diet of reindeer are extensively studied and research methods well established (e.g. Gaare & Skogland, 1975;

Holleman *et al.*, 1979; Skogland, 1980; Adamczewski *et al.*, 1988; Ferguson *et al.*, 2001; Storeheier *et al.*, 2003; Ophof *et al.*, 2013). Similarly, the extent and consequences of active grazing by reindeer are well documented (e.g. Gaio-Oliveira *et al.*, 2006; Moen *et al.*, 2009; Kumpula *et al.*, 2011; Tommervik *et al.*, 2012; Thompson & Barboza, 2013; Turunen *et al.*, 2013). However, trampling is not, in spite of being considered so important (Kumpula *et al.*, 2011), with a potential “spillage” factor of up to 10 (Gaare & Skogland, 1975; Vistnes & Nellemann, 2008). We are only aware of one relatively old quantitative report on this, which is also the basis for the suggested (summer trampling) factor of 10. From measurements of trampling and material removed, but

not eaten by six domestic reindeer on relatively thick lichen mats, Gaare & Skogland (1975) estimated a loss factor of 10, relative to what the animals actually consumed during the snow season (103 g \pm SD 71 DM m⁻² versus 10 g DM m⁻²). Clearly, this factor will depend on season, and when, how, and how much reindeer graze on lichen ranges. In Alpine habitats this may be year round (e. g. Skogland, 1980; Skogland, 1984), in forested habitats variable, but often more in summer (Stark *et al.*, 2000; Stark *et al.*, 2007; Kumpula *et al.*, 2011). In a later publication (Gaare & Skogland, 1980) this is restated as a 'wastage' factor varying positively with available lichen biomass, of '10 times intake at available biomass near the K-value' that 'declines to a factor of 2 at a biomass of 0.09 K' (K=maximum lichen biomass, with reference to Alpine habitats with lichen as primary winter forage). Here 'wastage' is attributed to reindeer selective feeding, which vary, for example with biomass, plant composition, and the degree of snow cover, and results in 'spillage of rejected lichen species dismantled from the mat in the process of digging and extracting'. Trampling *per se* was apparently not included here. Consequently, in addition to trampling, there may be substantial spill, i.e. reindeer appear to be not very efficient winter foragers. Already more than thirty years ago, Gaare & Skogland (1980) also stated that "The wastage factor appeared the most uncertain and critical value...". The substantial scale of such a 'wastage' factor is supported by a recent experimental study of reindeer trampling effects in dry, brittle lichen, i.e. a worst case scenario (Heggenes *et al.*, 2017). Indeed, with reference to Gaare & Skogland (1980) recent attempts to build population models for reindeer (e. g. Moxnes *et al.*, 2001; Tahvonen *et al.*, 2014; Pekkarinen *et al.*, 2015) have included "...removal is increased by wastage of lichen caused by grazing reindeer.the fraction of lichen that is really lost to grazing, for instance by ending up

in lakes and rivers. It does not include lichen, which fastens in a new location and continues to grow there" (Moxnes *et al.*, 2001). Estimated loss factor was set to vary from 0.5 to 4.5 (times intake) depending on density of lichen. Again, type of grazing system may be important, likely with the highest loss factor in open alpine areas. Tahvonen *et al.* (2014) modelled lower, forested grazing systems with considerable snow depth, and modified the loss factor, taken from Moxnes *et al.* (2001), to 1.3 lichen removed (intake plus loss). Recently, Pekkarinen *et al.* (2015), again with reference to Moxnes *et al.* (2001), used seasonal wastage factors for lower, forested grazing systems, lowest (=1.3; intake plus loss in all factors) in winter due to snow cover, increasing during spring (=1.6) to a maximum in summer (=3.0), and then decreasing again in the fall (=1.6). Since all factors are more than one, the assumption is again that reindeer in summer waste considerably more lichen than they eat.

In an early observational field study, Pegau (1970) herded approximately 500 reindeer over a non-utilized portion of a large dwarf shrub meadow during moist and dry conditions, i.e. a rainy and foggy day and a dry, warm day after 24 hours without rain. The amount of dislodged and shattered lichens roughly doubled. After one summer, 68 % of the lichens were dislodged and 16 % were shattered into segments less than ½ inch. It was concluded that 'on summer ranges where lichens comprise at least 30 % of available forage, at least 15 % of the lichens should be considered as unavailable because of trampling by reindeer'. To the best of our knowledge, this paper is the only one that describes the damage of trampling in more detail, suggesting that trampling may cause substantial loss of lichen, but depending on moisture. Observed differences of lichen biomass between different seasonal forested grazing areas (Kumpula *et al.*, 2011, Kumpula *et al.*, 2014) suggest major lichen waste,

depending on season, weather conditions and moisture. It is, however, important to note that whereas shattered lichen may be unavailable as food for reindeer, this lichen is not necessarily lost or dead to the ecosystem. Such disturbance may also facilitate lichen spreading.

Conclusion

The common idea that reindeer trampling may be a major cause of lichen forage losses appears to be based on anecdotal observations, and does not seem well substantiated or quantified scientifically. However, vegetation loss due to 'wastage' appears to be much more important than vegetation eaten by reindeer, at least during certain ecological conditions, i.e. dry weather, in summer. Therefore, more studies and experiments are required that disentangle the important 'wastage' effects of different activities of reindeer. It appears difficult to state on a general basis that the 'wastage' of forage is 2-10 times the consumed forage, at least when it comes to trampling. The additional spill associated with selective vegetation eating, also remains to be studied in more detail.

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References

- Adamczewski, J. Z., Gates, C. C., Soutar, B. M. & Hudson, R. J.** 1988. Limiting effect of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus-goenlandicus*) on Coat Island, Northwest Territories, Canada. — *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 66: 1986-1996. <https://doi.org/10.1139/z88-291>
- Albon, S. D., Brewer, M. J., O'Brien, S., Nolan, A. J. & Cope, D.** 2007. Quantifying the grazing impacts associated with different herbivores on rangelands. — *Journal of Applied Ecology* 44: 1176-1187. <https://doi.org/10.1111/j.1365-2664.2007.01318.x>
- Austrheim, G. & Eriksson, O.** 2001. Plant species diversity and grazing in the Scandinavian mountains - patterns and processes at different spatial scales. — *Ecography* 24: 683-695. <https://doi.org/10.1111/j.1600-0587.2001.tb00530.x>
- Austrheim, G., Mysterud, A., Pedersen, B., Halvorsen, R., Hassel, K. & Evju, M.** 2008. Large scale experimental effects of three levels of sheep densities on an alpine ecosystem. — *Oikos* 117: 837-846. <https://doi.org/10.1111/j.0030-1299.2008.16543.x>
- Bayfield, N. G., Urquhart, U. H. & Cooper, S. M.** 1981. Susceptibility of 4 species of *Cladonia* to disturbance by trampling in the Caringorm Mountains, Scotland. — *Journal of Applied Ecology* 18: 303-310. <https://doi.org/10.2307/2402497>
- Boudreau, S. & Payette, S.** 2004. Growth performance of *Cladonia stellaris* following caribou disturbance in subarctic Quebec. — *Ecoscience* 11: 347-355. <https://doi.org/10.1080/11956860.2004.11682842>
- Cairns, D. M. & Moen, J.** 2004. Herbivory influences tree lines. — *Journal of Ecology* 92: 1019-1024. <https://doi.org/10.1111/j.1365-2745.2004.00945.x>
- Cooper, E. J.** 2006. Reindeer grazing reduces seed and propagule bank in the High Arctic.

- *Canadian Journal of Botany-Revue Canadienne De Botanique* 84: 1740-1752. <https://doi.org/10.1139/b06-127>
- Cooper, E. J., Smith, F. M. & Wookey, P. A.** 2001. Increased rainfall ameliorates the negative effect of trampling on the growth of High Arctic forage lichens. — *Symbiosis* 31: 153-171.
- Cooper, E. J. & Wookey, P. A.** 2001. Field measurements of the growth rates of forage lichens, and the implications of grazing by Svalbard Reindeer. — *Symbiosis* 31: 173-186.
- Cumming, D. H. M. & Cumming, G. S.** 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. — *Oecologia* 134: 560-568. <https://doi.org/10.1007/s00442-002-1149-4>
- Dahl, E.** 1956. Rondane: Mountain Vegetation in South Norway and its Relation to the Environment. — *Skrifter Norske Videnskapsakademi i Oslo, Matematisk-naturvidenskapelig Klasse 3*: 1-374.
- den Herder, M., Kytoviita, M. M. & Niemela, P.** 2003. Growth of reindeer lichens and effects of reindeer grazing on ground cover vegetation in a Scots pine forest and a subarctic heathland in Finnish Lapland. — *Ecography* 26: 3-12. <https://doi.org/10.1034/j.1600-0587.2003.03211.x>
- Dove, H. & Mayes, R. W.** 1991. The use of plant wax alkanes as marker substances in studies of the nutrition of herbivores - A review. — *Australian Journal of Agricultural Research* 42: 913-952. <https://doi.org/10.1071/AR9910913>
- Eby, S., Burkepile, D. E., Fynn, R. W. S., Burns, C. E., Govender, N., Hagenah, N., Koerner, S. E., Matchett, K. J., Thompson, D. I., Wilcox, K. R., Collins, S. L., Kirkman, K. P., Knapp, A. K. & Smith, M. D.** 2014. Loss of a large grazer impacts savanna grassland plant communities similarly in North America and South Africa. — *Oecologia* 175: 293-303. <https://doi.org/10.1007/s00442-014-2895-9>
- Ferguson, M. A. D., Gauthier, L. & Messier, F.** 2001. Range shift and winter foraging ecology of a population of Arctic tundra caribou. — *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 79: 746-758. <https://doi.org/10.1139/z01-013>
- Finstad, G. L. & Kielland, K.** 2011. Landscape Variation in the Diet and Productivity of Reindeer in Alaska Based on Stable Isotope Analyses. — *Arctic Antarctic and Alpine Research* 43: 543-554. <https://doi.org/10.1657/1938-4246-43.4.543>
- Gaare, E. & Skogland, T.** 1975. Wild reindeer food habits and range use at Hardangervidda. In: *Ecological Studies 17 Fennoscandian Tundra Ecosystems Part 2.* (ed), F. E. W. Berlin, Springer Verlag: 195-205.
- Gaare, E. & Skogland, T.** 1980. Lichen-reindeer interaction studied in a simple case model. *Proceedings of 2nd International Reindeer/Caribou Symposium, Røros, Norway, 1979.* Reimers, E., Gaare, E. & Skjenneberg, S. Trondheim, Direktoratet for vilt og ferskvannsfisk: 47-56.
- Gaio-Oliveira, G., Moen, J., Danell, O. & Palmqvist, K.** 2006. Effect of simulated reindeer grazing on the re-growth capacity of mat-forming lichens. — *Basic and Applied Ecology* 7: 109-121. <https://doi.org/10.1016/j.baae.2005.05.007>
- Hansen, B. B., Aanes, R. & Saether, B. E.** 2010. Feeding-crater selection by high-arctic reindeer facing ice-blocked pastures. — *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 88: 170-177. <https://doi.org/10.1139/Z09-130>
- Heggenes, J., Odland, A., Chevalier, T., Ahlberg, J., Berg, A., Larsson, H. & Bjerketvedt, D. K.** 2017. Herbivore grazing - or trampling? Trampling effects by a large ungulate in cold high-latitude ecosystems. —

- Ecology and Evolution* 7: 6423-6431. <https://doi.org/10.1002/ece3.3130>
- Hirsch, J. L., Lægread, O. & Aasberg, G.** 1911. Indstilling fra Fjeldbeitekomiteen om Hardangerviddens Utnyttelse. Centraltrykkeriet Kristianina, Landbruksdepartementet: 78.
- Holechek, J. L., Vavra, M. & Pieper, R. D.** 1982. Botanical composition determination of range herbivore diets - A review. — *Journal of Range Management* 35: 309-315. <https://doi.org/10.2307/3898308>
- Holleman, D. F., Luick, J. R. & White, R. G.** 1979. Lichen intake estimates for reindeer and caribou during winter. — *Journal of Wildlife Management* 43: 192-201. <https://doi.org/10.2307/3800651>
- Holtmeier, F.-K.** 2015. *Animals' Influence on the Landscape and Ecological Importance - Natives, Newcomers, Homecomers*. Dordrecht, Springer.
- Holtmeier, F.-K., Broll, G., Mutertshies, A. & Anschlag, K.** 2003. Regeneration of trees in the treeline ecotone: Northern Finnish Lapland. — *Fennia* 181: 103-128.
- Kitti, H., Forbes, B. C. & Oksanen, J.** 2009. Long- and short-term effects of reindeer grazing on tundra wetland vegetation. — *Polar Biology* 32: 253-261. <https://doi.org/10.1007/s00300-008-0526-9>
- Koster, E., Koster, K., Aurela, M., Laurila, T., Berninger, F., Lohila, A. & Pumpanen, J.** 2013. Impact of reindeer herding on vegetation biomass and soil carbon content: a case study from Sodankylä, Finland. — *Boreal Environment Research* 18: 35-42.
- Kumpula, J.** 2001. Winter grazing of reindeer in woodland lichen pasture Effect of lichen availability on the condition of reindeer. — *Small Ruminant Research* 39: 121-130. [https://doi.org/10.1016/S0921-4488\(00\)00179-6](https://doi.org/10.1016/S0921-4488(00)00179-6)
- Kumpula, J., Kurkilahti, M., Helle, T. & Colpaert, A.** 2014. Both reindeer management and several other land use factors explain the reduction in ground lichens (*Cladonia* spp.) in pastures grazed by semi-domesticated reindeer in Finland. — *Regional Environmental Change* 14: 541-559. <https://doi.org/10.1007/s10113-013-0566-8>
- Kumpula, J., Stark, S. & Holand, O.** 2011. Seasonal grazing effects by semi-domesticated reindeer on subarctic mountain birch forests. — *Polar Biology* 34: 441-453. <https://doi.org/10.1007/s00300-010-0899-4>
- Körner, C.** 2003. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Berlin Heidelberg, Springer Verlag. <https://doi.org/10.1007/978-3-642-18970-8>
- Ludvikova, V., Pavlu, V. V., Gaisler, J., Hejzman, M. & Pavlu, L.** 2014. Long term defoliation by cattle grazing with and without trampling differently affects soil penetration resistance and plant species composition in *Agrostis capillaris* grassland. — *Agriculture Ecosystems & Environment* 197: 204-211. <https://doi.org/10.1016/j.agee.2014.07.017>
- Moen, J., Boogerd, C. & Skarin, A.** 2009. Variations in mountain vegetation use by reindeer (*Rangifer tarandus*) affects dry heath but not grass heath. — *Journal of Vegetation Science* 20: 805-813. <https://doi.org/10.1111/j.1654-1103.2009.01074.x>
- Moen, J. & Danell, O.** 2003. Reindeer in the Swedish mountains: An assessment of grazing impacts. — *Ambio* 32: 397-402. <https://doi.org/10.1579/0044-7447-32.6.397>
- Moen, J. & Lagerstrom, A.** 2008. High species turnover and decreasing plant species richness on mountain summits in Sweden: Reindeer grazing overrides climate change? — *Arctic Antarctic and Alpine Research* 40: 382-395. [https://doi.org/10.1657/1523-0430\(07-031\)\[MOEN\]2.0.CO;2](https://doi.org/10.1657/1523-0430(07-031)[MOEN]2.0.CO;2)
- Moxnes, E., Danell, O., Gaare, E. & Kumpula, J.** 2001. Optimal strategies for the use of reindeer rangelands. — *Ecological Modelling* 145: 225-241. <https://doi.org/10.1016/>

- Mysterud, A. & Austrheim, G.** 2008. The effect of domestic sheep on forage plants of wild reindeer; a landscape scale experiment. — *European Journal of Wildlife Research* 54: 461-468. <https://doi.org/10.1007/s10344-008-0171-1>
- Naiman, R. J. & Rogers, K. H.** 1997. Large animals and system level characteristics in river corridors. — *Bioscience* 47: 521-529. <https://doi.org/10.2307/1313120>
- Odland, A. & Munkejord, H. K.** 2008. The importance of date of snowmelt for the separation of different oligotrophic and mesotrophic mountain vegetation types in Southern Norway. — *Phytocoenologia* 38: 3-21. <https://doi.org/10.1127/0340-269X/2008/0038-0003>
- Odland, A., S.M., S., Bjerketvedt, D. K. & Myrvold, L. L.** 2014. Estimation of lichen biomass with emphasis on reindeer winter pastures at Hardangervidda, S Norway. — *Rangifer* 34: 95-110. <https://doi.org/10.7557/2.34.1.2852>
- Olf, H., Vera, F. W. M., Bokdam, J., Bakker, E. S., Gleichman, J. M., de Maeyer, K. & Smit, R.** 1999. Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. — *Plant Biology* 1: 127-137. <https://doi.org/10.1111/j.1438-8677.1999.tb00236.x>
- Olofsson, J.** 2006. Plant diversity and resilience to reindeer grazing. — *Arctic Antarctic and Alpine Research* 38: 131-135. [https://doi.org/10.1657/1523-0430\(2006\)038\[0131:PDARTR\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2006)038[0131:PDARTR]2.0.CO;2)
- Olofsson, J.** 2009. Effects of Simulated Reindeer Grazing, Trampling, and Waste Products on Nitrogen Mineralization and Primary Production. — *Arctic Antarctic and Alpine Research* 41: 330-338. <https://doi.org/10.1657/1938-4246-41.3.330>
- Olofsson, J., Hulme, P. E., Oksanen, L. & Suominen, O.** 2004. Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. — *Oikos* 106: 324-334. <https://doi.org/10.1111/j.0030-1299.2004.13224.x>
- Olofsson, J., Kitti, H., Rautiainen, P., Stark, S. & Oksanen, L.** 2001. Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. — *Ecography* 24: 13-24. <https://doi.org/10.1034/j.1600-0587.2001.240103.x>
- Olofsson, J., Moen, J. & Ostlund, L.** 2010. Effects of reindeer on boreal forest floor vegetation: Does grazing cause vegetation state transitions? — *Basic and Applied Ecology* 11: 550-557. <https://doi.org/10.1016/j.baec.2010.03.004>
- Ophof, A. A., Oldeboer, K. W. & Kumpula, J.** 2013. Intake and chemical composition of winter and spring forage plants consumed by semi-domesticated reindeer (*Rangifer tarandus tarandus*) in Northern Finland. — *Animal Feed Science and Technology* 185: 190-195. <https://doi.org/10.1016/j.anifeedsci.2013.08.005>
- Pegau, R. E.** 1970. Effect of reindeer trampling and grazing on lichens. — *Journal of Range Management* 23: 95-97. <https://doi.org/10.2307/3896107>
- Pekkarinen, A. J., Kumpula, J. & Tahvonen, O.** 2015. Reindeer management and winter pastures in the presence of supplementary feeding and government subsidies. — *Ecological Modelling* 312: 256-271. <https://doi.org/10.1016/j.ecolmodel.2015.05.030>
- Pellerin, S., Huot, J. & Cote, S. D.** 2006. Long term effects of deer browsing and trampling on the vegetation of peatlands. — *Biological Conservation* 128: 316-326. <https://doi.org/10.1016/j.biocon.2005.09.039>
- Persson, I. L., Danell, K. & Bergstrom, R.** 2000. Disturbance by large herbivores in boreal forests with special reference to moose. — *Annales Zoologici Fennici* 37: 251-263.
- Plumptre, A. J.** 1994. The effects of trampling

- damage by herbivores on the vegetation of the Parc-National-Des-Volcans, Rwanda. — *African Journal of Ecology* 32: 115-129. <https://doi.org/10.1111/j.1365-2028.1994.tb00563.x>
- Rosenthal, G., Schrautzer, J. & Eichberg, C.** 2012. Low-intensity grazing with domestic herbivores: A tool for maintaining and restoring plant diversity in temperate Europe. — *Tuexenia*: 167-205.
- Schrama, M., Heijning, P., Bakker, J. P., van Wijnen, H. J., Berg, M. P. & Olf, H.** 2013. Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. — *Oecologia* 172: 231-243. <https://doi.org/10.1007/s00442-012-2484-8>
- Skogland, T.** 1980. Comparative summer feeding strategies of arctic and alpine *Rangifer*. — *Journal of Animal Ecology* 49: 81-98. <https://doi.org/10.2307/4278>
- Skogland, T.** 1983. The effects of density dependent resource limitation on size of wild reindeer. — *Oecologia* 60: 156-168. <https://doi.org/10.1007/BF00379517>
- Skogland, T.** 1984. Wild reindeer foraging-niche organization. — *Holarctic Ecology* 7: 345-379. <https://doi.org/10.1111/j.1600-0587.1984.tb01138.x>
- Skogland, T.** 1989. Natural selection of wild reindeer life-history traits by food limitation and predation. — *Oikos* 55: 101-110. <https://doi.org/10.2307/3565879>
- Sorensen, L. I., Mikola, J., Kytoviita, M. M. & Olofsson, J.** 2009. Trampling and Spatial Heterogeneity Explain Decomposer Abundances in a Sub-Arctic Grassland Subjected to Simulated Reindeer Grazing. — *Ecosystems* 12: 830-842. <https://doi.org/10.1007/s10021-009-9260-6>
- Sormo, W., Haga, O. E., Gaare, E., Langvatn, R. & Mathiesen, S. D.** 1999. Forage chemistry and fermentation chambers in Svalbard reindeer (*Rangifer tarandus platyrhynchus*). — *Journal of Zoology* 247: 247-256. <https://doi.org/10.1111/j.1469-7998.1999.tb00988.x>
- Stark, S., Julkunen-Tiitto, R. & Kumpula, J.** 2007. Ecological role of reindeer summer browsing in the mountain birch (*Betula pubescens* ssp. *czerepanovii*) forests: effects on plant defense, litter decomposition, and soil nutrient cycling. — *Oecologia* 151: 486-498. <https://doi.org/10.1007/s00442-006-0593-y>
- Stark, S., Wardle, D. A., Ohtonen, R., Helle, T. & Yeates, G. W.** 2000. The effect of reindeer grazing on decomposition, mineralization and soil biota in a dry oligotrophic Scots pine forest. — *Oikos* 90: 301-310. <https://doi.org/10.1034/j.1600-0706.2000.900210.x>
- Stewart, D. R. M.** 1967. Analysis of plant epidermis in faeces - A technique for studying food preferences of grazing herbivores. — *Journal of Applied Ecology* 4: 83-111. <https://doi.org/10.2307/2401411>
- Storeheier, P. V., Mathiesen, S. D., Tyler, N. J. C. & Olsen, M. A.** 2002. Nutritive value of terricolous lichens for reindeer in winter. — *Lichenologist* 34: 247-257. <https://doi.org/10.1006/lich.2002.0394>
- Storeheier, P. V., Mathiesen, S. D., Tyler, N. J. C., Schjelderup, I. & Olsen, M. A.** 2003. Utilization of nitrogen- and mineral-rich vascular forage plants by reindeer in winter (vol 139, pg 151, 2002). — *Journal of Agricultural Science* 140: 128. <https://doi.org/10.1017/S002185960300995X>
- Suominen, O. & Olofsson, J.** 2000. Impacts of semi-domesticated reindeer on structure of tundra and forest communities in Fennoscandia: a review. — *Annales Zoologici Fennici* 37: 233-249.
- Suominen, O., Persson, I.-L., Danell, K., Bergstrom, R. & Pastor, J.** 2008. Impact of simulated moose densities on abundance and richness of vegetation, herbivorous and pred-

- atory arthropods along a productivity gradient. — *Ecography* 31: 636-645. <https://doi.org/10.1111/j.0906-7590.2008.05480.x>
- Tahvonon, O., Kumpula, J. & Pekkarinen, A. J.** 2014. Optimal harvesting of an age-structured, two-sex herbivore-plant system. — *Ecological Modelling* 272: 348-361. <https://doi.org/10.1016/j.ecolmodel.2013.09.029>
- Thompson, D. P. & Barboza, P. S.** 2013. Responses of caribou and reindeer (*Rangifer tarandus*) to acute food shortages in spring. — *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 91: 610-618. <https://doi.org/10.1139/cjz-2013-0047>
- Tommervik, H., Bjerke, J. W., Gaare, E., Johansen, B. & Thannheiser, D.** 2012. Rapid recovery of recently overexploited winter grazing pastures for reindeer in northern Norway. — *Fungal Ecology* 5: 3-15. <https://doi.org/10.1016/j.funeco.2011.08.002>
- Tremblay, J. P., Huot, J. & Potvin, F.** 2007. Density-related effects of deer browsing on the regeneration dynamics of boreal forests. — *Journal of Applied Ecology* 44: 552-562. <https://doi.org/10.1111/j.1365-2664.2007.01290.x>
- Turunen, M., Oksanen, P., Vuojala-Magga, T., Markkula, I., Sutinen, M. L. & Hyvonen, J.** 2013. Impacts of winter feeding of reindeer on vegetation and soil in the sub-Arctic: insights from a feeding experiment. — *Polar Research* 32: 12. <https://doi.org/10.3402/polar.v32i0.18610>
- Van Uytvanck, J. & Hoffmann, M.** 2009. Impact of grazing management with large herbivores on forest ground flora and bramble understorey. — *Acta Oecologica-International Journal of Ecology* 35: 523-532. <https://doi.org/10.1016/j.actao.2009.04.001>
- Vikhamar-Schuler, D., Hanssen-Bauer, I., Schuler, T. V., Mathiesen, S. D. & Lehnig, M.** 2013. Use of a multilayer snow model to assess grazing conditions for reindeer. — *Annals of Glaciology* 54: 214-226. <https://doi.org/10.3189/2013AoG62A306>
- Vistnes, I. I. & Nellemann, C.** 2008. Reindeer winter grazing in alpine tundra: Impacts on ridge community composition in Norway. — *Arctic Antarctic and Alpine Research* 40: 215-224. [https://doi.org/10.1657/1523-0430\(07-001\)\[VISTNES\]2.0.CO;2](https://doi.org/10.1657/1523-0430(07-001)[VISTNES]2.0.CO;2)
- Wehn, S., Pedersen, B. & Hanssen, S. K.** 2011. A comparison of influences of cattle, goat, sheep and reindeer on vegetation changes in mountain cultural landscapes in Norway. — *Landscape and Urban Planning* 102: 177-187. <https://doi.org/10.1016/j.landurbplan.2011.04.003>
- Xu, L., Freitas, S. M. A., Yu, F. H., Dong, M., Anten, N. P. R. & Werger, M. J. A.** 2013. Effects of Trampling on Morphological and Mechanical Traits of Dryland Shrub Species Do Not Depend on Water Availability. — *Plos One* 8: 8. <https://doi.org/10.1371/journal.pone.0053021>
- Zielinska, S., Kidawa, D., Stempniewicz, L., Los, M. & Los, J. M.** 2016. New Insights into the Microbiota of the Svalbard Reindeer *Rangifer tarandus platyrhynchus*. — *Frontiers in Microbiology* 7: 9. <https://doi.org/10.3389/fmicb.2016.00170>

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