1   **Stomping in silence: Conceptualizing trampling effects on soils in polar tundra**

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Author Contributions

MV, MT, CGB and FQB designed the workshop, and MT and CGB chaired the workshop. ICB, KAB, IE, BCF, ISJ, ALK, PM, MPB, JDMS, SS, KS and JH participated in the workshop and/or contributed otherwise in development of the conceptual model. MT conducted the literature search and MT and MV analysed the review results. MT and MV wrote the paper, to which CGB, HY and FQB contributed significantly. All authors provided comments to the manuscript drafts.

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Abstract

1. Ungulate trampling modifies soils and interlinked ecosystem functions across biomes. Until today, most research has focused on temperate ecosystems and mineral soils, while trampling effects on cold and organic matter rich tundra soils remain largely unknown.

2. We aimed to develop a general model of trampling effects on soil structure, biota, microclimate and biogeochemical processes, with a particular focus on polar tundra soils. To reach this goal, we reviewed literature about the effects of trampling and physical disturbances on soils across biomes and used this to discuss the knowns and unknowns of trampling effects on tundra soils.

3. We identified four pathways through which trampling affects soils: 1) soil compaction, 2) reductions in soil fauna and fungi, 3) rapid losses in vegetation biomass and cover, and 4) longer-term shifts in vegetation community composition.

4. We found that, in polar tundra, soil responses to trampling pathways 1 and 3 could be characterized by non-linear dynamics and tundra-specific context-dependencies that we formulated into testable hypotheses.

5. In conclusion, trampling may affect tundra soil significantly but many direct, interacting and cascading responses remain unknown. We call for research to advance understanding of trampling effects on soils to support informed efforts to manage and predict the functioning of tundra systems under global changes.

1 Introduction

Across terrestrial ecosystems, ungulate herbivores play a key role in shaping vegetation (Diaz et al., 2007), soil nutrient dynamics (Augustine & McNaughton, 2006), and the global carbon (C) cycle (Schmitz et al., 2018; Tanentzap & Coomes, 2012), thus granting these complex herbivore-plant-soil interactions a focal role in ecosystem research and management. Ungulates influence ecosystems directly by consuming biomass, by excreting urine and faeces, and by trampling. Despite the fact that ungulates trample constantly, while they defoliate and fertilize only occasionally, the latter forces have been long considered as primary mechanisms through which ungulates, and *sensu lato* vertebrate herbivores, affect soil food webs and biogeochemistry (Bardgett & Wardle, 2003; Cherif & Loreau, 2013). Yet, trampling is slowly becoming recognized as an important non-trophic force shaping ecosystems (Forbes & Kumpula, 2009; Heggenes, Odland, & Bjerketvedt, 2018; Kéfi et al., 2012; Schmidt, Näsholm, & Rentsch, 2014), and a few recent models identify trampling as a prominent mechanism by which ungulates affect soil biogeochemical cycles and organisms (Andriuzzi & Wall, 2017; Howison, Olff, van de Koppel, & Smit, 2017; Schrama et al., 2013a, 2013b). These models, even though progressive, focus on temperate-tropical ecosystems dominated by mineral soils, and therefore might not apply to cold tundra and permafrost soils with typically high organic matter content and cryogenic processes. Notably, we are currently lacking a generalized conceptual model for herbivore trampling effects on soils and ecosystem functioning. These would be analogous to herbivore feeding and excretion models that have greatly facilitated herbivory research ever since their launch (Bardgett & Wardle, 2003; Wardle & Bardgett, 2004). This essential knowledge gap hinders future developments in the research of non-trophic interactions in tundra ecosystems and beyond.

In agricultural/managed grassland systems, physical disturbances like trampling are often associated with changes in soil structure, biota and functioning and these changes can either be intertwined or occur independently of each other (Beylich, Oberholzer, Schrader, Höper, & Wilke, 2010; Finlayson et al., 2002; Hoorman, de Moraes, & Reeder, 2011). Similar effects can be expected in systems with wild ungulates although environmental conditions may strongly mediate and constrain the consequences of trampling on soils. For example, trampling by cattle compacts mineral soils and subsequently decreases soil pore volume and nitrogen (N) mineralization (Schrama et al., 2013b). Importantly, this chain of events happens only when soils are either very dry or very wet, and is stronger in clay (loamy) soils than in sandy soils, pointing towards soil moisture and texture as key context variables that can mediate the impacts of trampling (Schrama et al., 2013b). In addition to changes in N mineralization, in mineral soils with <20% organic matter, trampling may also cause a

decline in abundance of soil engineering fauna, concomitant with trampling-induced soil (bio)compaction, whereas "*little compaction is expected on [...] organic, or frozen soils*" (Howison et al., 2017 p. 374). Despite this expectation, in organic and cold tundra soils, herbivory reduces soil fauna and soil respiration, with trampling-induced soil compaction as the proposed main mechanism behind these changes (Andriuzzi & Wall, 2017). Put together, these findings indicate that soil responses to trampling may be multiplex and vary between soils.

A pivotal role of trampling for tundra ecosystem functioning has been previously inferred based on late Pleistocene state transitions. Following large herbivore extinctions 50 000–10 000 years ago, productive steppe dominated by trampling tolerant forbs and grasses transitioned to contemporary, low productivity tundra dominated by trampling sensitive bryophytes (hereafter referred to as mosses) and dwarf or low-erect shrubs (Olofsson & Post, 2018; Willerslev et al., 2014; Zimov et al., 1995). Today, relative to the Pleistocene, the Arctic tundra is home to greatly reduced diversity and density of large native herbivores that are reindeer (*Rangifer tarandus*, caribou in North America) and musk ox (*Ovibos moschatus*, Olofsson & Post, 2018). Dall sheep (*Ovis dalli*), snow sheep (*Ovis nivicola*) and elk (*Alces alces*) inhabit only lower latitude sub-Arctic, alpine and boreal areas (Barrio et al., 2016a). While transient trampling effects of these ungulates may be subtle in comparison to past Pleistocene megafauna, their ability to locally drive graminoid-moss state transitions accompanied by shifts in ecosystem and soil processes and albedo has been reported, especially for Old World reindeer (Forbes & Kumpula, 2009; Olofsson, Stark, & Oksanen, 2004; van der Wal, 2006). Indeed, much of the complex vegetation and ecosystem responses to herbivores in tundra may be driven by trampling either alone or in concert with defoliation and fertilization that alone usually do not recreate the observed changes in vegetation or ecosystem processes caused by ungulate presence (Egelkraut, Barthelemy, & Olofsson, 2020; Falk, Schmidt, & Ström, 2014; Falk, Schmidt, Christensen, & Ström, 2015; Olofsson, 2009). In tundra, climate warming is rapidly shifting species pools, altering biogeochemical cycles (Abbott et al., 2016; IPCC, 2014; Meredith et al., 2019) and changing the populations and behaviour of ungulates (Cuyler et al., 2020; Mallory & Boyce, 2017; Mysterud, 2013; Uboni et al., 2016). Moreover, any prospective efforts to re-wild tundra (Andriuzzi & Wall, 2018; Olofsson & Post, 2018) or use natural climate solutions (Macias-Fauria, Jepson, Zimov, & Malhi, 2019) should anticipate both trophic and non-trophic forces that shape these ecosystems through time. Given these multiple co-occurring phenomena, incorporating trampling-soil interactions into tundra ecosystem research is particularly pressing for informed management of these ecosystems.

Here, we propose a general conceptual model of trampling effects on soils, including soil structure, biota, microclimate and biogeochemical processes, with a specific emphasis on polar

tundra soils (hereafter referred to as tundra). In addition, we propose new, testable hypotheses about the cascading effects of trampling that we believe are integral especially for tundra. We develop the model and the hypotheses by synthesizing trampling (i.e. ungulates, humans, simulated) and physical disturbance (i.e. small vehicles, cf. Forbes, Ebersole, & Strandberg, 2001) literature from all managed and natural ecosystems and, specifically, by reviewing empirical findings from tundra (Supplementary Information 1). We finally highlight some salient knowledge gaps and provide suggestions for future research.

2 Towards a general conceptual model of trampling pathways for polar tundra soils

We propose a general conceptual model to outline major mechanistic links by which trampling can affect soil characteristics (Fig. 1). The proposed model integrates both recent (temperate) conceptual models (Andriuzzi & Wall, 2017; Howison et al., 2017; Schrama et al., 2013a), older conceptualizations from tundra (Chapin & Shaver, 1981) and empirical evidence from natural and agricultural contexts, including temperate, boreal, alpine and arctic ecosystems (Suppl. Information 2). This integrated model identifies four trampling-effect pathways (Fig. 1): *via changes in soil structure* (A) *and biota* (B); and *via changes in plant cover* (C) *and plant functional composition* (D). These trampling-effect pathways are likely to co-occur (Piñeiro, Paruelo, Oesterheld, & Jobbágy, 2010), interact and cascade down to soil microclimate, biogeochemistry and SOM dynamics with context-dependent outcomes that may further vary over time (E, Fig. 1). In the case of ungulates, trampling effects can be mitigated or intensified by the effects of ungulate excretion and defoliation. Below, we first introduce the mechanisms linked with pathways A–D and then, for each pathway, identify its consequences on soil.

2.1 Pathway A: direct structural changes in soil

Trampling-induced soil compaction Trampling impacts soil via compression, which changes soil structural properties, such as soil aggregate formation and porosity and alters soil bulk density (Fig. 1, pathway A), as repeatedly observed in agricultural and rangeland systems (Beylich et al., 2010; Hoorman et al., 2011; Six, Bossuyt, Degryze, & Denef, 2004). Accordingly, ungulate presence associates with compacted soils in grassland ecosystems with mineral soils (Howison et al., 2017; Ludvíková, Pavlů, Gaisler, Hejcman, & Pavlů, 2014) as well as in cold ecosystems with organic soils, such as alpine and arctic-alpine tundra (Liu, Kan, Yang, & Zhang, 2015; Stark, Strömmer, & Tuomi, 2002) and boreal forests (Donkor et al., 2002; Kolstad et al., 2018; Stark, Tuomi, Strömmer, & Helle, 2003). Also in tundra, ungulate trampling (Ylänne, Olofsson, Oksanen, & Stark, 2018), vehicle

184 disturbances (Chapin & Shaver, 1985) and trampling by humans often link with more compacted

185 soils but can also have negligible effects and even induce soil loosening (Bryan, 1977; Gellatly,

186 Whalley, & Gordon, 1986a; Gellatly, Whalley, Gordon, & Ferguson, 1986b; Suppl. Fig. S2).

187 In tundra, trampling-induced varying responses in soil structure may be contingent on

188 trampling intensity, i.e. the sum of pressure and frequency of trampling within a certain time, and,

189 further, show nonlinear relationships with increasing trampling intensity (Fig. 2). More precisely, at

190 low trampling intensities, soils could be insensitive to trampling-induced soil compaction, which

191 begins only after trampling intensity surpasses a threshold. Once trampling intensity further increases,

192 another threshold is surpassed and soils start to loosen up and erode. These kind of nonlinear threshold

193 dynamics have been reported from subarctic tundra, where soil structural responses shift from

194 compaction to loosening (erosion) with (human) trampling intensity, which ranged from 20 to 200

195 tramples per day (Gellatly et al., 1986a, 1986b; Fig. 2). Similarly, compaction followed by loosening

196 and erosion may associate with game paths, migration routes of caribou in North America (Nicholson,

197 Arthur, Horne, Garton, & Del Vecchio, 2016) and along reindeer herding fences in Scandinavia

198 (Moen & Danell, 2003). We propose that nonlinear relationships between trampling intensity and soil

199 structure could be pertinent across trampled ecosystems.

200 In addition to trampling intensity, vegetation could modulate compaction dynamics

201 (Fig. 2). Generally, abundant plant shoots and aboveground litter buffer soils against compaction

202 (Hoorman et al. 2011; Howison et al., 2017) especially under low trampling intensity. Increasing

203 trampling intensity damages plants that gradually lose their (aboveground) buffering capacity, which

204 may allow the initiation and advancement of compaction (Gellatly et al., 1986b; Monz, 2002; Fig. 2)

205 in susceptible tundra soils (see also discussion below). Eventually, root mats start to dismantle

206 triggering loosening of soil (Bryan, 1977; Fig. 2). However, plant functional groups, such as dwarf

207 shrubs, grasses and mosses, vary in their sensitivity to trampling-induced damages as well as in their

208 capacity to buffer soil, owing to their differences in brittleness, shoot and root architecture and

209 production of litter (Cole, 1995). Consequently, plant communities differ in their capacity to buffer

210 soil against compaction (Mingyu, Hens, Xiaokun, & Wulf, 2009; Willard & Marr, 1970). For

211 example, dwarf shrub (e.g. *Empetrum nigrum*, *Betula nana*) dominated vegetation and its creeping

212 woody stems could protect tundra soils against compaction even though dwarf shrubs themselves are

213 sensitive to (intensive) trampling. On the contrary, even though graminoids can better recover from

214 trampling, their erect and brittle shoots might pose much weaker buffer for soil that further decreases

215 as ungulates eat and thus remove graminoid biomass. Thus, we hypothesize that increasing trampling

216 intensity induces varying progression of compaction depending on local vegetation (Fig. 2).

217   Susceptibility to compaction may vary across tundra sites with similar vegetation
218 (Crisfield, MacDonald, & Gould, 2012; Gisladottir, 2006; Monz, 2002), pointing towards other
219 modulators, such as soil organic matter (OM) content and moisture (Fig. 3). In temperate and
220 agricultural systems, abundant OM buffers soils against compaction, making soils "incompressible"
221 (Hoorman et al., 2011; Howison et al., 2017). Organic tundra soils are more cohesive and may be less
222 sensitive to compaction or erosion than soils with a large fraction of fine particles (Tejedo et al., 2012)
223 or with low aggregate density, e.g. some volcanic soils (Orradottir, Archer, Arnalds, Wilding, &
224 Thurow, 2008). However, while OM can reduce soil compaction, it simultaneously increases soil
225 water holding capacity turning more OM-rich soils potentially also moister (Gisladottir, 2006; Stark
226 et al., 2003; Fig. 3A). Moisture, in turn, strongly increases susceptibility to compaction in Andosols
227 (Dec, Dörner, Balocchi, & López, 2012 and references therein) as in tundra (Bryan, 1977; Chapin &
228 Shaver, 1981; Monz, 2002; Fig 3A) and variation between wet and dry states may also promote soil
229 structural recuperation after compaction (Dec et al., 2012). In tundra, moisture conditions shift due
230 to seasonality (snowmelt), habitat heterogeneity (wet/moist snow beds and hollows *versus*
231 dry/exposed ridges and hummocks), water table level (freely draining systems *versus* saturated
232 systems) and, in the case of ungulate presence, due to urination. These shifting moisture conditions
233 could, consequently, introduce variation in the compaction susceptibility of organic tundra soils. We
234 hypothesize that dry systems are in general resistant to trampling-induced compaction and regain
235 their shape when pressure is lifted but, under wet conditions, turn susceptible to trampling-induced
236 compaction (Willard & Marr, 1970; Fig. 3B). Further, we hypothesize that wet systems, such as
237 peatlands, are in general susceptible to trampling-induced compaction but, under dry conditions, they
238 could be resistant to compaction (Bryan, 1977; Chapin & Shaver, 1981; Racine & Ahlstrand, 1991;
239 Fig. 3B).

240

241 **Consequences of compaction** Trampling-induced changes in aggregate formation and porosity
242 affect soil aeration and water infiltration that may alter nutrient mineralization and long-term C
243 dynamics (Hoorman et al., 2011; Schrama et al., 2013b; Six et al., 2004). Changes in soil porosity
244 may reduce roots and mycorrhizal fungi (Hartmann et al., 2014; Hoorman et al., 2011), availability
245 and quality of microhabitats for soil fauna, and protect microbes from multicellular predators
246 (Breland & Hansen, 1996). Consequently, the abundance and assemblages of soil animals,
247 microorganisms and, ultimately, soil food webs and biotic soil processes may all change (Beylich et
248 al., 2010; Hoorman et al., 2011; Six et al., 2004; see 2.2). Over longer term, compaction and
249 associated changes in aeration and water regime may modulate plant species composition (Lezama
250 & Paruelo, 2016; Veldhuis, Howison, Fokkema, Tielens, & Olff, 2014). These causal links may apply

to tundra but confirming them calls for new empirical work that combines soil structural, biotic and biogeochemical parameters (Suppl. table S1). Importantly, trampling-induced soil compaction may result in outcomes that are unique to tundra. Compaction may induce soil warming and deepening of thaw front, since denser soil increases water content and thereby thermal conductivity (Racine & Ahlstrand, 1991) or, conversely, may induce soil cooling via increasing water table height (Mosbacher, Michelsen, Stelvig, Hjermstad-Sollerud, & Schmidt, 2018; see also 2.3). These could feedback to microbial mineralization rates, which are controlled by temperature, oxygen availability and active layer depth (Davidson & Janssens, 2006; Schuur et al., 2015).

2.2 Pathway B: changes in soil biota

Trampling-induced mortality and shifts in resources Trampling and physical disturbances may reduce soil fauna and microbes directly through cutting- and compression-induced mortality but also indirectly through shifts in resources, such as habitable macro-pore spaces and forage (Fig. 1 pathway B; Andriuzzi & Wall, 2017; Beylich et al., 2010; Hoorman et al., 2011; Six et al., 2004; see also 2.1). Across biomes, trampling and biocompaction have been linked with declined abundance of soil fauna (Howison et al., 2017; Sørensen, Mikola, Kytöviita, & Olofsson, 2009; Tejedo et al., 2012) but these declines may occur only after trampling intensity surpasses a threshold, as was found with increasing human trampling in tundra (Ayres et al., 2008). However, ungulate exclosure experiments that control ungulate trampling, defoliation and excretion have reported only weak responses in soil fauna (Andriuzzi & Wall, 2017). These weak responses could stem from too low trampling intensity that does not surpass the threshold or, alternatively, ungulate excreta could provide nutrients and forage for soil fauna to counteract the negative effects of trampling. In addition, in tundra, fauna traits, such as life-history strategies, may also dictate responses to both human (Ayres et al., 2008; Tejedo et al., 2012) and simulated trampling (Sørensen et al., 2009) and, for example, parthenogenic soil fauna were more common in tundra soils disturbed by vehicles than in adjacent undisturbed soils (Kevan, Forbes, Kevan, & Behan-Pelletier, 1995).

Trampling and physical disturbances shift faunal forage, microbial biomass and plant litter, with expected feedbacks to soil fauna (i.e. altered bottom-up regulation) representing different feeding groups (Veen, Olff, Duyts, & van der Putten, 2010). Firstly, bacteria have been found to be more resistant to trampling and physical disturbances than fungi in boreal and tundra ecosystems (Hartmann et al., 2014; Sørensen et al., 2009) and, consequently, declines in soil fungi may decrease fungal feeding soil fauna. Secondly, trampling induces vegetation changes (see also 2.3 and 2.4) that range from (rapid) declines in plant litter and altered root growth to vegetation community shifts that

feedback to tundra microbes, such as mycorrhizal fungi (Eskelinen, Stark, & Männistö, 2009; but see Chu, Neufeld, Walker, & Grogan, 2011). All these, consequently alter the availability of forage for litter, root and fungal feeding fauna.

Consequences of biota declines Trampling-induced changes in soil fungi, bacteria and fauna could, firstly, alter soil trophic interactions and biodiversity. In addition, reductions of fungi may feedback to soil structure, as fungi promote soil macro-aggregation and porosity (Six et al., 2004). Changes in soil fauna composition can also alter soil structure (Schrader, Langmaack, & Helming, 1997), biogeochemistry and SOM dynamics, as fauna translocate particulate organic matter and feed on litter and microbial decomposers (Filser et al., 2016; Osler & Sommerkorn, 2007).

2.3 Pathway C – trampling effects mediated via plant loss

Loss of insulating plant layer modulating tundra soil thermal regime Trampling and physical disturbances directly damage and decrease aboveground plant biomass and cover in tundra (Gisladottir, 2006; Kevan et al., 1995; Monz, 2002; Starr, Seefeldt, Zhang, & Rowell, 2018) as in other systems (Cole, 1995). In tundra, mosses dominate many vegetation types and their cover, biomass and thickness often decrease due to trampling (Gisladottir, 2006; Monz, 2002; Sørensen, Mikola, & Kytöviita, 2008). The trampling-induced loss of mosses may play a critical role (Fig. 1 pathway C), since mosses control soil thermal and moisture regime and heat flux, although these effects vary among moss species depending on e.g. their moss layer thickness and moisture holding capacity (Blok et al., 2011; Soudzilovskaia, van Bodegom, & Cornelissen, 2013). Indeed, in tundra, trampling-induced declines in mosses occur often in synchrony with increased soil temperature (Olofsson, 2009; van der Wal & Brooker, 2004).

Trampling via moss thinning may exert non-linear effects on soil temperature that are contingent on air temperature and moisture (O'Donnell, Romanovsky, Harden, & McGuire, 2009; Soudzilovskaia et al., 2013) and the thickness of moss layer. For example, in freely draining tundra, trampling-induced moss thinning induces a linear increase in summer soil temperature but only after moss layer becomes shallow enough or, in other words, passes underneath a threshold moss thickness (Fig. 4 panel B). Any changes in the moss thickness above the threshold do not change soil temperature (van der Wal & Brooker, 2004). Further, soil temperature differences between thin and thick moss carpet may intensify with increasing summer air temperature (van der Wal & Brooker, 2004). Therefore, soil can remain significantly cooler under thicker than shallower moss carpet when air is warm (Fig. 4 panel B) but moss control over soil temperature may become negligible when air

is cold (Fig. 4 panel A). In contrast to freely-draining tundra, in waterlogged tundra (Fig. 4 panel C) with continuous surface-water flow, trampling-induced thinning of moss carpet may cool soil during summer (Falk et al., 2015) as a consequence of increased surface-water flow rates with reduced moss biomass, and subsequently a higher convectional heat loss (Mosbacher et al., 2018). We hypothesize that trampling decreases moss thickness, which after surpassing a threshold results in soil warming under warm and dry conditions. Under waterlogged conditions, moss thinning induces a consistent soil cooling.

Consequences of plant loss Trampling-induced reductions in aboveground plant biomass may alter shading and albedo, evapotranspiration, root exudation and belowground productivity (Bernier et al., 2011; Blok et al., 2011; Hafner et al., 2012; Olofsson, 2009) that cascade down to soil microclimate, labile nutrient and C pools, and modulate soil compaction (see 2.1). Trampling-induced loss of N_2-fixing mosses (Alexander & Schell, 1973) could reduce N inputs to the system and hence decrease soil N availability. Alternatively, N availability could also increase, if reduced moss layer is less able to intercept nutrients from ungulate excreta (Barthelemy, Stark, Michelsen, & Olofsson, 2018).

Trampling-induced moss thinning and the consequent shifts in soil temperature can cascade down to tundra soil and ecosystem functions in unique ways (Fig. 1). Firstly, moss thinning and associated soil warming link with increased soil N mineralization rates and plant N availability (Fig. 4; Olofsson, 2009; van der Wal, van Lieshout, & Loonen, 2001) that could further interact with soil biota and soil OM dynamics (Fig. 1). Secondly, a thinner moss layer may advance spring thaw and thus vascular plant and microbial phenology in comparison to thick moss carpet (Gornall, Jónsdóttir, Woodin, & van der Wal, 2007). Thirdly, a thinner moss layer may also allow permafrost thawing (active layer deepening) that may support microbial encroachment and root growth into deeper soil horizons (Fig. 4; Blok et al., 2011; Chapin & Shaver, 1981; Kevan et al., 1995; Krzyszowska, 1989; van der Wal et al., 2001).

2.4 Pathway D – trampling effects mediated via plant community shifts

Longer-term vegetation shift Trampling may drive shifts in plant functional or species composition towards species with higher resilience and resistance to mechanical damage (Cole, 1995; Forbes et al., 2001; Jónsdóttir, 1991; Lezama & Paruelo, 2016). These vegetation shifts may arise via direct trampling damages altering plant fitness and survival and could further intensify due to ungulate defoliation and excretion (Egelkraut et al., 2020). Alternatively, vegetation shifts may arise via trampling-induced changes in soil resource availability and plant-soil-feedbacks (Egelkraut, Kardol,

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Long, & Olofsson, 2018) and these changes likely emerge and evolve as the different trampling-effect pathways act alone and in interaction over time (Fig. 1A–C). In tundra, both ungulate presence (*i.e.* trampling, defoliation and excretion) as well as other physical disturbances have been repeatedly linked with decreases in dwarf shrubs, mosses and tall forbs, as opposed to increases in graminoids (Bryan, 1977; Chapin & Shaver, 1981; Kevan et al., 1995; van der Wal et al., 2001). These vegetation compositional shifts induce changes in litter that feedback to plant-soil interactions (Fig. 1D; Bardgett & Wardle, 2003) and, in tundra, these shifts have been suggested to induce local ecosystem state transitions (*sensu* van der Wal, 2006),

Consequences of vegetation shift A trampling-induced vegetation shift towards graminoid-dominance may parallel with lower soil moisture content (Ricca, Miles, Van Vuren, & Eviner, 2016; Zimov et al., 1995) and alter surface albedo and microclimate (te Beest, Sitters, Ménard, & Olofsson, 2016). Increased dominance of graminoids may also cascade down to soil microbial assemblages and processes with consequences on soil OM dynamics (Fig. 1). For example, the increased abundance of non-mycorrhizal graminoids links with reduced fungal dominance in soil (Männistö, Ganzert, Tiirola, Häggblom, & Stark, 2016), with higher root: shoot ratios (Ylänne et al., 2018) and with increased microbial decomposition of cellulose (Stark & Väisänen, 2014).

3 Outlook

Trampling can have significant and pervasive effects on ecosystem functions and services, such as C sequestration, but in tundra, the trampling-induced cascades in soil structure, biota, microclimate and biogeochemical flows as well as the interactions between the different trampling-effect pathways remain empirically largely unverified. Likewise, threshold dynamics of trampling effects on tundra soil and their dependency on environmental context remain understudied. We propose that empirical efforts should be taken to identify these interactions and threshold dynamics. To reach this goal, we recommend supplementing ungulate-plant-soil research with systematic measurements of trampling indicators, such as moss layer thickness, soil bulk density, temperature and N. In addition, we recommend to measure contextual parameters, such as index of trampling intensity, vegetation composition, and soil moisture. These parameters would support the primary parameters, such as soil faunal and microbial communities, roots and soil C dynamics that we consider requiring most acutely investigation. The proposed measurements could be applied in different experimental setups, such as ungulate experiments including exclosures and/or sites with different ungulate densities. In these cases, it is advisable to record feeding marks and pellets to evaluate the role of trampling in

383 comparison to feeding and excretion. In addition, the protocol could be applied in trampling
384 simulation experiments (e.g. Egelkraut et al., 2020) and along game paths and migration routes. We
385 hope that the proposed conceptual models and testable hypotheses will facilitate further empirism by
386 providing tools for formulating research question(s) and interpreting data.

387 In tundra, the ongoing climate change and permafrost thaw are rapidly shifting air
388 temperature, hydrology and vegetation composition (IPCC, 2014; Myers-Smith et al., 2011; Olefeldt
389 et al., 2016) that, in turn, modulate trampling effects on soils. Importantly, trampling effects on soils
390 could either reinforce or mitigate the consequences of climate change on tundra ecosystems. As an
391 example, trampling-induced moss thinning triggers soil warming and active layer deepening that are
392 expected to increase soil C mineralization and greenhouse gas emissions (Davidson & Janssens,
393 2006). These responses could amplify in a warming climate, as the effects of moss thinning exhibit
394 thresholds with air temperature. As another example, trampling effects on soil water dynamics,
395 temperature and N mineralization could either facilitate or suppress tundra shrubification (Myers-
396 Smith et al., 2015). Concomitantly, proposed rewilding of tundra (e.g. Macias-Fauria et al., 2019)
397 stands to (re-)introduce a substantial non-trophic force, with relatively poorly understood
398 consequences. To conclude, we highlight the urgent need to develop a better understanding of locally,
399 regionally and geographically widespread trampling effects on soils and ecosystem functioning to
400 support more informed management of changing tundra systems.

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Figure legends

Figure 1. A general conceptual model of trampling effect pathways (boxes A–D) on soils, including
trampling effects through changes in (**A**) soil structure, (**B**) soil biota, (**C**) plant cover and (**D**)
vegetation community shifts. Effect pathways **A–C** include rapid responses to trampling, while
pathway **D** involves slower shifts through herbivore-plant-soil feedbacks. Driving processes of each
effect pathway are indicated in italics. Effect pathways **A–D** drive cascading changes in the soil
matrix (**E**), through sets of pathway-specific mechanisms (indicated inside arrows) that depend on
the environmental context. The soil matrix (**E**) includes soil structure, biota (decomposer organisms,
roots) and microclimate (temperature, moisture), which interact and further modulate biogeochemical
cycles and soil organic matter (SOM) dynamics. For example, trampling induced changes in soil biota
may occur directly (pathway B) or via effects of compaction (pathway A); changes in soil fauna or
root biomass may, in turn, affect soil aggregation processes and hence soil structure.

Figure 2. Proposed non-linear relationships between trampling intensity and soil compaction
(measured often as bulk density) and cohesion, modulated by local vegetation composition. Low
intensity trampling hardly induces compaction but increasing trampling intensity induces compaction
due to loss of local buffering vegetation, until a threshold of peak compaction is reached (dashed
orange box). Peak soil compaction is followed by the disintegration of soil aggregates and roots
resulting in loosening of the soil. If vegetation is dominated by plants with high buffering capacity,
such as dwarf shrubs, soil compaction may start and advance only at higher trampling intensity (dark
green solid line). If vegetation is dominated by plants with low buffering capacity, such as grasses,
compaction may start and advance already at low trampling intensity (light green dashed line),
whereas if vegetation consists evenly of dwarf shrubs and grasses, compaction may follow
intermediate pattern (green long-dashed line). Vegetation composition also modulates the location of
peak compaction and the subsequent soil loosening along the trampling intensity gradient.

Figure 3. Proposed relationships between (**A**) soil water holding capacity and soil organic matter
content (SOM%), as well as soil moisture (%) and soil sensitivity to compaction and (**B**) SOM content
and sensitivity to compaction modulated by soil moisture regime. Along a soil moisture gradient from
wet to dry, the effect of (high) SOM content in modulating soil sensitivity to compaction changes:
under wet conditions, high SOM enhances compaction sensitivity but, under dry conditions, high
SOM mitigates compaction sensitivity.

733   **Figure 4.** Proposed relationships between trampling intensity, moss thickness and growing season

734   soil temperature modulated by local air temperature and drainage conditions, as well as their

735   cascading effects on N mineralization, active layer thickness and rooting depth. Increasing trampling

736   intensity leads to reduced moss thickness, and increasing coupling of air and soil temperature. **(A)** If

737   air temperature is low, loss of the insulating effect of the moss layer does not lead to increased soil

738   temperature. **(B)** If air temperature is high, reducing moss thickness below an insulation threshold

739   leads to increasing growing season soil temperature. Changes in soil temperature alter thermally

740   sensitive N-mineralization, active layer depth and rooting depth. **(C)** Water saturated soils may

741   deviate from dynamics outlined for freely draining systems if thinning moss layer leads to increasing

742   surface water flow, and hence increasing heat loss due to thermal conductivity.

Conceptual model of the trampling – soil system

No temporal lag or short lag time

Long lag time

Trampling effect pathways

A Direct pathway via soil structure

Compression, mixing

B Direct pathway via soil biota

Damage-induced mortality

C Indirect pathway via plant cover

Damage-induced loss of biomass

D Indirect pathway via plant community shift

Damage-induced changes in long-term fitness

Environmental context

Changes in: porosity/aggregation, bulk density, water holding capacity, O_2

Changes in: soil mixing, decomposition, trophic interactions

Changes in: insulation, albedo/insolation, evapotranspiration, roots (soil stability, exudation)

Changes in: litter quantity and quality, mycorrhiza, root profile

Soil characteristics affected by trampling

E

Structure   **Biota**   **Microclimate**

Biogeochemistry & SOM dynamics

744

Figure 1.
745

746

747 **Figure 2.**

748

749

750 **Figure 3.**

FREELY-DRAINING SYSTEM   SATURATED SYSTEM

A   COLD AIR   B   WARM AIR   C

Trampling intensity

moss layer (cm)

temperature

N miner.

active layer & rooting depth

loss of insulation

Increased surface water-flow

ABOVE GROUND

BELOW GROUND

751
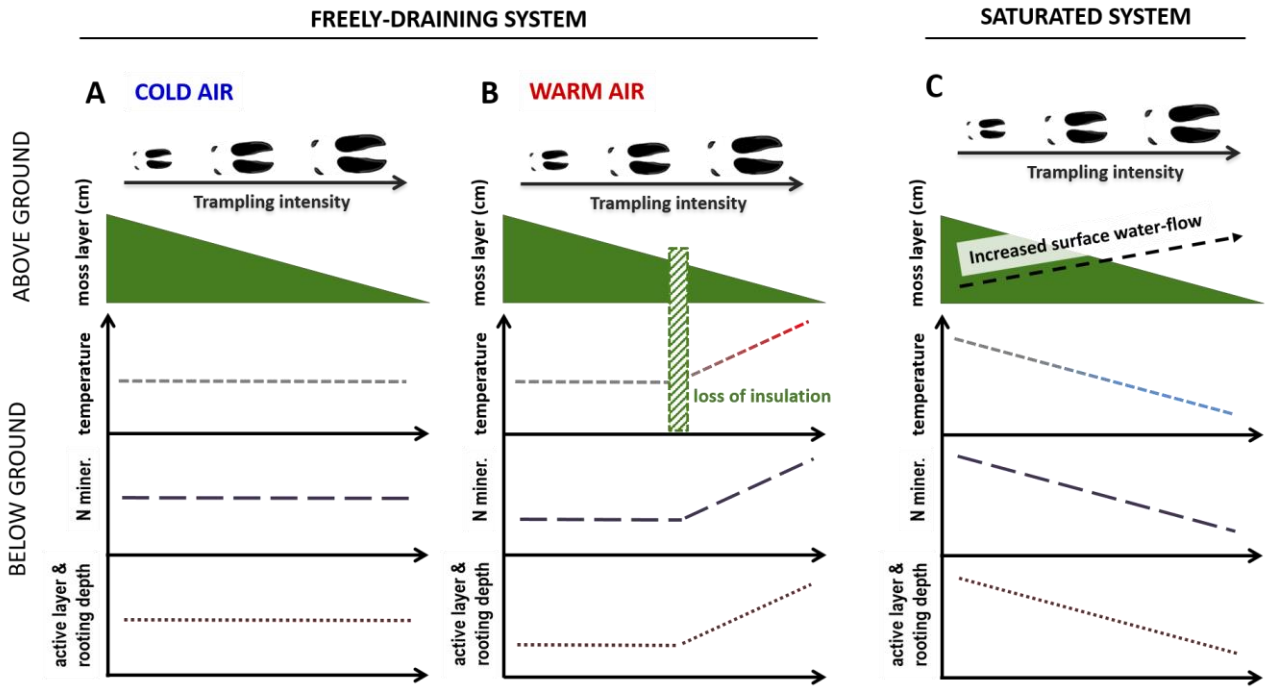
Figure 4.

753   Supplementary Materials of:

754   **Stomping in silence: Conceptualizing trampling effects on soils in polar tundra**

755 **Contents**

762

763 **Supplementary Information 1: Literature search and qualitative data analysis**

764 We used the scientific databases Web of Science and Scopus for our literature search (October 4th

765 2018, updated March 11th 2019) with a search string 'trampling OR trample AND subarctic OR arctic

766 OR tundra OR polar' that covered article title, abstract and keywords. The search resulted in 68

767 articles, which were filtered based on the criteria that the study was conducted in circumpolar tundra

768 >60 degrees latitude around the poles (i.e. Arctic, subarctic, or Antarctic systems), the study reported

769 results on soil parameter(s) and included a 'trampling agent' (trampling by large herbivores or an

770 equivalent ground pressure and disturbance, e.g. simulated trampling, trampling by humans) in the

771 experimental design. When trampling agent was trampling by large herbivores, we included papers

772 that had experimentally controlled ungulate presence. Thus, these papers did not isolate trampling,

773 defoliation and fertilization but, instead, inferred the role of trampling. This kind of approach,

774 inference using e.g. soil compaction as an indicator of trampling, has been used also in studies that

775 have proposed causalities between trampling and soil nitrogen cycling (Schrama et al., 2013) and soil

776 fauna (Howison, Olff, van de Koppel, & Smit, 2017). The resulting 13 papers were supplemented by

777 three means. First, we ran an additional search on Google Scholar with the above string but added the

778 word "soil" and identified four original research papers not found through Scopus or Web of Science.

779 Second, as ground pressure exerted by wheels had been used to simulate herbivore trampling (Starr,

780 Seefeldt, Zhang, & Rowell, 2018), we searched papers about ATV (all-terrain vehicle; 'trampling

781 agent' being vehicle) effects on tundra soil. For this, we carried out a separate search on Google

782 Scholar with "vehicle OR rut AND soil AND arctic OR subarctic OR tundra OR polar" (November

783 27th 2018, updated March 21st 2019), which resulted in ten papers although we were able to obtain

full texts only for nine papers. Third, we searched through the reference lists of all those papers that fulfilled the filtering criteria, which resulted in two additional papers.

These steps yielded 28 original research papers for the review. Of these, we extracted 203 observations of different measured soil parameters (hereafter *observations*) that we assigned into four categories as follows: 'structure' (e.g. compaction), 'biota' (e.g. mesofauna), 'microclimate' (e.g. temperature), and 'biogeochemistry' (e.g. soil nutrients and mineralization, including soil respiration and nitrogen mineralization, Suppl. Table S1). Some of the studies included more than one site in their design (e.g. Chapin & Shaver, 1981; Ylänne, Olofsson, Oksanen, & Stark, 2018) and, in these cases, we extracted observations for each site separately. The number of observations can thus exceed the number of retrieved papers. For each observation, we extracted the direction of the trampling effect (increase, neutral, decrease). We consider statistically significant results, as well as trends with high effect sizes, where p-value < 0.1 due to high levels of variation (Amrhein, Greenland, & McShane, 2019). We acknowledge that this practice requires care, but can avoid undue conservative inference in the data (Amrhein et al., 2019), as soils are highly heterogeneous in scales from centimetres to hundreds of meters (Ettema & Wardle, 2002). We also extracted study site characteristics (Suppl. Table S1).

We chose to use a qualitative analysis of trampling effects from the retrieved literature. Even though the low number of studies as such does not exclude the possibility of a formal meta-analysis (Koricheva, Gurevitch, & Mengersen, 2013), the few retrieved studies here were so variable in their methodologies, trampling agents, study designs and ecological contexts, causing any quantitative comparison to be meaningless. First, different analytical methods and metrics were often used to quantify trampling effects on soil variables: compaction was measured through bulk density, penetration resistance and surface depression (e.g. Gellatly, Whalley, & Gordon, 1986a; Racine & Ahlstrand, 1991), root responses were recorded through six different metrics (Chapin & Shaver, 1981; Harper & Kershaw, 1997; Olofsson, 2009; van der Wal, van Lieshout, & Loonen, 2001; Ylänne et al., 2018), and soils CO_2 release was measured both in the field and in lab incubations (e.g. Falk, Schmidt, Christensen, & Ström, 2015; Starr et al., 2018). Second, there were interdependencies (autocorrelation) between trampling agent, study location and measured soil parameter. For instance, structural variables were often reported in footpath studies (Suppl. Table S1a), and all observations from the Antarctic were from footpath studies whereas all observations from the Siberian and Canadian Arctic were from vehicle studies.

The studies varied in their approach to how the level of trampling was controlled (i.e. "trampling agent"), and in the range of trampling intensities (ground pressure × frequency) that were

817 applied. The trampling agents included ungulate presence, simulated trampling, humans (i.e. footpath

818 studies) and vehicles. Trampling agents likely vary in their trampling intensity and qualitatively, in

819 terms of e.g. mixing of soil. For instance, the ground pressures reported for different trampling agents

820 range between 30–40 kPa for adult reindeer (Peth & Horn, 2006) and from ca. 7–18 kPa (Racine &

821 Ahlstrand, 1991; smaller vehicles) to 24 kPa (Buchkina, 1998; larger vehicles) for tracked vehicles.

822 The ground pressures induced by simulated livestock and reindeer trampling ranged from 70 kPa

823 (Starr et al., 2018) to 240 kPa (Olofsson, 2009), respectively. We report the results separately for each

824 trampling agent.

825 **Supplementary table S1a-d.** List of reviewed papers, the trampling agent, measured soil parameters [relating to soil structure, soil biota and
826 belowground net primary production (BNPP), soil microclimate, biogeochemistry and biogeochemical processes], as well as metadata (site climatic
827 and altitudinal characteristics and soil bulk density and organic matter content). The bibliographic information for each paper is available at the
828 end of the Supplementary Information, in the References.

1a		Soil structure			
Reference	trampling agent	compaction	horizon	aggregation	porosity
Ayres et al. 2008	human				
Buchkina et al. 1998	vehicle	bulk density	profile survey	micro-structure (microscope)	micro-structure, water retention
Bryan 1977	human	method NA	profile survey	aggregate stability	
Bölter et al. 2006	reindeer	bulk density			
Chapin & Shaver 1981	vehicle	bulk density			
Falk et al. 2015	muskox				
Forbes 1998	vehicle				
Gellatly et al. 1986a	human	penetration resistance			
Gellatly et al. 1986b	human	bulk density, penetration resistance			dry density
Gisladottir 2006	human	bulk density		inferred via clay content	
Greenslade et al. 2012	human				
Harper & Kershaw 1997	vehicle		profile survey		
Herbein & Neal 1990	vehicle				
Kevan et al. 1995	vehicle				
Krzyszowska 1989	human + vehicle	bulk density			
Monz 2002	human	penetration resistance[a]			
Mosbacher et al. 2018	muskox				
Neal & Herbein 1983	vehicle				
Niwranski et al 2002	vehicle				
Olofsson 2009	simulation				
Racine & Ahlstrand 1991	vehicle	surface depression			
Starr et al. 2018	simulation	bulk density, penetration resistance			
Sørensen et al. 2009	simulation				
Tejedo et al. 2009	human	penetration resistance, dry bulk density			
Tejedo et al. 2012	human	penetration resistance			
Van der Wal & Brooker 2004	reindeer				
Van der Wal et al. 2001	reindeer				
Ylänne et al. 2018	reindeer	bulk density			

829

830 [a] The study shows consistent increases in penetration resistance in all trampled sites, but due to high variation, the results are not significant for one
831 vegetation type.

1b		Soil biota			BNPP
Reference	trampling agent	mesofauna	Fungi	bacteria	roots
Ayres et al. 2008	human	nematodes, tardigrades, rotifers (count/kg soil)			
Buchkina et al. 1998	vehicle				
Bryan 1977	human				
Bölter et al. 2006	reindeer			count, biomass (epifluorescence microscopy)	
Chapin & Shaver 1981	vehicle				root biomass by depth
Falk et al. 2015	muskox				
Forbes 1998	vehicle				
Gellatly et al. 1986a	human				
Gellatly et al. 1986b	human				
Gisladottir 2006	human				
Greenslade et al. 2012	human				
Harper & Kershaw 1997	vehicle				depth of rooting zone
Herbein & Neal 1990	vehicle				
Kevan et al. 1995	vehicle	soil arthropods			
Krzyszowska 1989	human + vehicle				
Monz 2002	human				
Mosbacher et al. 2018	muskox				
Neal & Herbein 1983	vehicle				
Niwranski et al 2002	vehicle	Collembolan			
Olofsson 2009	simulation				root biomass, BNPP
Racine & Ahlstrand 1991	vehicle				
Starr et al. 2018	simulation				
Sørensen et al. 2009	simulation	nematodes, enchytraeids, collembola	biomass (PLFA)	biomass (PLFA)	
Tejedo et al. 2009	human	soil arthropods			
Tejedo et al. 2012	human	collembola			
Van der Wal & Brooker 2004	reindeer				
Van der Wal et al. 2001	reindeer				*Poa* root profile
Ylänne et al. 2018	reindeer				root biomass, C and N

832

833

1c		microclimate		biogeochemistry		
Reference	trampling agent	temperature (depth/timing of measurement)	Moisture	SOM/SOC (LOI temp., duration)	N, P	pH
Ayres et al. 2008	human	soil surface (?) / summer, day	gravimetric moisture content			
Buchkina et al. 1998	vehicle		water retention curves	SOC g/kg^{-1} (LOI: NA)		
Bryan 1977	human			SOM (LOI: NA)		
Bölter et al. 2006	reindeer	2, 5, 10 and 15cm / summer		SOC (LOI: 540°C, NA)		
Chapin & Shaver 1981	vehicle	10cm / summer, afternoon; thaw depth	moisture content	SOC % (LOI: 600°C, 6h)	available P	pH
Falk et al. 2015	muskox	10cm below moss surface; active layer thickness	water table depth			
Forbes 1998	vehicle	5,10 and 15cm in mineral soil / summer diurnal				
Gellatly et al. 1986a	human					
Gellatly et al. 1986b	human		moisture content (wet-dry mass)	SOC (LOI: NA)		
Gisladottir 2006	human		moisture content (wet-dry mass)	SOC (LOI: 985°C, NA)	available PO$_4$, N	pH
Greenslade et al. 2012	human					
Harper & Kershaw 1997	vehicle	5 cm / summer continuous	moisture content, hygroscopic water[b]	SOM (LOI: 550°C, 4h)[b]		pH
Herbein & Neal 1990	vehicle		gravimetric moisture content[c]	SOC (dichromate wet oxidation)		
Kevan et al. 1995	vehicle	depth of the active layer	moisture content	SOC content (LOI: 600°C; NA)	P, NH$_4$,NO$_3$	pH
Krzyszowska 1989	human + vehicle	thaw depth				
Monz 2002	human				N,NH$_4$,NO$_3$	
Mosbacher et al. 2018	muskox	5cm below green moss /year; active layer thickness	water table depth			
Neal & Herbein 1983	vehicle					
Niwranski et al 2002	vehicle					
Olofsson 2009	simulation	10cm / summer				
Racine & Ahlstrand 1991	vehicle	thaw depth				
Starr et al. 2018	simulation			SOM (method NA)	NH$_4$, NO$_3$, PO$_4$, C:N	
Sørensen et al. 2009	simulation			SOM (LOI: 460°C, 5h)		
Tejedo et al. 2009	human					
Tejedo et al. 2012	human					
Van der Wal & Brooker 2004	reindeer	below moss layer/summer point measurement			NH$_4$, NO$_3$	
Van der Wal et al. 2001	reindeer	below moss layer / summer				
Ylänne et al. 2018	reindeer	5cm / summer 1-h intervals	moisture content (wet-dry mass)	SOM (LOI:475°C, 4h)	C:N, NH$_4$	

834

835 [b] The study reports soil parameters 50yr after the initial disturbance; ca. 15yr earlier vehicle tracks had lower OM and moisture content than undisturbed
836 sites; since then, soil moisture and OM have recovered to pre-disturbance levels.

837 [c] Results not discussed, presented as background information.

1d		biogeochemical processes		Metadata				
Reference	trampling agent	mineralization	soil respiration	bulk density (g/cm3)	soil organic matter %	MAT (°C)	MAP (mm)	Altitude (m asl)
Ayres et al. 2008	human		CO_2 (field)	NA	<5% (<1% organic C)	-18.5	100	NA
Buchkina et al. 1998	vehicle			0.13-0.76	24-47%	-10	325	NA
Bryan 1977	human			NA	2.5-3.5%	0	700	1000
Bölter et al. 2006	reindeer		CO_2 (incubation)	0.94-1.50	5-89%	1.5	450	350
Chapin & Shaver 1981	vehicle		CO_2 (incubation)	ca. 0.1-0.5	ca. 10-95%	NA	NA	75; 250; 655; 300
Falk et al. 2015	muskox		CO_2, CH_4 (field)	NA	NA	-9	260	NA
Forbes 1998	vehicle			NA	NA	NA	NA	NA
Gellatly et al. 1986a	human			NA	NA	-0.5	500	190-220
Gellatly et al. 1986b	human			0.44-1.57	0.4-25.6%	-0.5	500	NA
Gisladottir 2006	human			0.48-0.83	2.8-10%	4.7; 3.2	1450; 1500	280; 60
Greenslade et al. 2012	human			NA	NA	NA	NA	NA
Harper & Kershaw 1997	vehicle			NA	40±16% (6±4% mineral soil)	NA	NA	1400
Herbein & Neal 1990	vehicle	phosphomono- & diesterase[d]		0.09-0.12	79-83%	NA	NA	655
Kevan et al. 1995	vehicle			NA	NA	NA	NA	NA
Krzyszowska 1989	human + vehicle			1.4-1.9	NA	NA	NA	NA
Monz 2002	human			NA	NA	-10	300	NA
Mosbacher et al. 2018	muskox			NA	NA	-9	261	NA
Neal & Herbein 1983	vehicle	sulfatase activity		0.09-0.12	79-83%	NA	NA	655
Niwranski et al 2002	vehicle			NA	NA	-13.3	222	0
Olofsson 2009	simulation	*in situ* incubation (NH_4, NO_3)		NA	NA	-1.4	848	630-720
Racine & Ahlstrand 1991	vehicle			NA	NA	NA	NA	900
Starr et al. 2018	simulation		CO_2 (incubation)	1.4-1.0	36-83%	-2.5	275	210
Sørensen et al. 2009	simulation			NA	10-60%	-1.4	848	630-720
Tejedo et al. 2009	human			0.9-1.3	1.6%	-1.5 - -3	700-1000	NA
Tejedo et al. 2012	human			NA	0.2-3.1%	-1.5 - -3	700-1000	NA
Van der Wal & Brooker 2004	reindeer	laboratory incubation (NH_4, NO_3)[e]		NA	NA	-4.4	200	NA
Van der Wal et al. 2001	reindeer			NA	NA	-4.6	400	NA
Ylänne et al. 2018	reindeer			0.15-0.6 (0.4-1.2 mineral soil)	30-75% (2-8% mineral soil)	NA	NA	500

838

839   [d] The authors identified phosphomonoesterase as the dominant enzyme. Results for wet site were statistically significant; for dry site, effect sizes show a
840   clear reduction in tracks, but no significance at 0.05 level due to high variation. This authors' interpretation of "no effect" is not consistent with recent views
841   on use of statistical significance (). The authors suggest moisture as the most important driver for variation in the enzyme activity.

842

843   [e] Authors linked this with moss layer depth and temperature.

Supplementary Information 2: Results of the literature search

The majority of the observations were from Fennoscandian and Alaskan tundra (Suppl. Fig. S1) and the study locations covered a wide range of environmental contexts. The mean annual temperature ranged from -18.5°C to 4.7°C and precipitation from 100 mm up to 2,000 mm (Suppl. Table S1d). Both permafrost-affected and seasonally thawing systems as well as freely draining and saturated soils with usually high (>20%) organic matter content were included (Suppl. Table S1d). The original papers encompassed a diversity of arctic vegetation types (Walker et al., 2005) including heaths (lichen, moss, *Dryas*; dwarf-shrub), meadows (*Dryas*; forb-graminoid), graminoid-moss mires, tussock tundra, polar (semi)desert and erect shrub tundra. Almost all studies provided vegetation data.

Soil compaction was the most frequently measured parameter with 37 (39, see explanation below) observations (Suppl. Fig. S2). In response to footpaths and vehicles, soil compaction either increased (n = 21) or there was no compaction (neutral, n = 11). However, responses could vary from increases to neutral even within individual studies (Chapin & Shaver, 1981) and, in two cases, soils first compacted and then started to loosen up (Gellatly et al., 1986a; Gellatly, Whalley, Gordon, & Ferguson, 1986b). Ungulate trampling simulation and ungulate presence resulted in no significant compaction (n = 5, Fig. 2), although Ylänne et al. (2018) found that soil tended to be more compacted (i.e. greater bulk density) in heavily reindeer-grazed graminoid tundra in comparison to lightly grazed dwarf shrub tundra. Other soil structural parameters were also reported, namely increased soil horizon loss (n =1) and altered soil aggregation/porosity (Suppl. Table S1a).

Soil mesofauna was reported in footpath, vehicle and ungulate simulation studies and in all cases (n = 11), overall faunal abundance decreased (Suppl. Fig. S2). However, in two cases, responses to trampling varied among and within soil taxa (nematodes, enchytraeids and springtails) (Ayres et al., 2008; Sørensen, Mikola, Kytöviita, & Olofsson, 2009). Footpaths and vehicles could either increase the richness of springtails (Greenslade, Potapov, Russell, D. & Convey, 2012) or decrease the diversity of springtails (Greenslade et al., 2012; Niwranski, Kevan, & Fjellberg, 2002; not shown in Suppl. Fig. S2). There were only three observations of soil microbiota: ungulate trampling simulation reduced fungal abundance (n=1; Sørensen et al., 2009), whereas abundance of bacteria did not change (n=2; Bölter, Möller, & Peth, 2006; Sørensen et al., 2009; Suppl. Fig. S2). Root responses to trampling agents included increases, decreases and no responses (Suppl. Fig. S2); the seven observations were based on rooting depth, *Poa* root profile, belowground net primary production and root biomass, C and N (Suppl. Table S1b).

38

876   We retrieved 58 observations on microclimatic variables, including soil temperature (n

877   = 19), moisture (n = 28) and thaw depth (n = 11; Suppl. Fig. S2). In response to vehicles and footpaths,

878   soil temperature increased or did not change. In addition, simulated ungulate trampling and reindeer

879   presence increased soil temperatures and amplitudes of diurnal temperature fluctuation in freely

880   draining soils (Olofsson, 2009; van der Wal et al., 2001), yet musk ox presence resulted in cooling of

881   waterlogged soils (Falk et al., 2015; Mosbacher, Michelsen, Stelvig, Hjermstad-Sollerud, & Schmidt,

882   2018) (Suppl. Fig. S2). Thaw depth mainly increased in footpaths and vehicle ruts, with two

883   observations of no change. Soil moisture responses were similar among footpaths, vehicle ruts and

884   ungulate presence, and included increases, neutral responses and decreases.

885   Soil organic matter (SOM, including soil organic C, mainly reported as concentrations,

886   Suppl. Table 1c) was reported by 31 observations. Footpaths and vehicle ruts featured mainly neutral

887   (n = 10) or negative (n = 12) effects on SOM, yet there were also increases in footpaths (Suppl. Fig.

888   S2). Simulated ungulate trampling and ungulate presence did not affect SOM (n = 4) in all but one

889   observation where SOM declined. Footpath and vehicle studies often linked reduced SOM with loss

890   of vegetation cover (e.g. Gisladottir, 2006; Kevan, Forbes, Kevan, & Behan-Pelletier, 1995) and

891   Bryan (1977) reported SOM reductions due to trampling-induced horizon loss. Soil nutrient, N and

892   phosphorus (P), responses were mainly positive or neutral (Suppl. Fig. S2). Neutral responses were

893   reported in vehicle ruts and footpaths (n = 9) as well as with simulated ungulate trampling (n = 2). In

894   some vehicle ruts (n = 4) nutrient contents also increased, and Chapin and Shaver (1981) associated

895   higher available P with more compacted soils. Ungulate presence increased soil mineral N, although

896   in these cases, trampling effects were, by design, confounded by fertilization and vegetation shift (van

897   der Wal & Brooker, 2004; Ylänne et al., 2018). In addition, there were 11 observations on soil pH

898   (Suppl. table 1c). We found 9 observations of soil biogeochemical processes, which included soil

899   respiration, net ecosystem CO_2 exchange, N mineralization, methane fluxes and microbial

900   extracellular enzyme activities (Suppl. Table 1c-d). The response to trampling was most often neutral

901   or negative (Suppl. Fig. S2). However, Sørensen et al. (2009) reported that simulated ungulate

902   trampling decreased soil respiration (and soil fungi, see text above) whereas both Olofsson (2009),

903   using simulated trampling, and Van der Wal and Brooker (2004), based on reindeer presence, found

904   that trampling increased soil N mineralization rates, and associated this with the simultaneous decline

905   in mosses.

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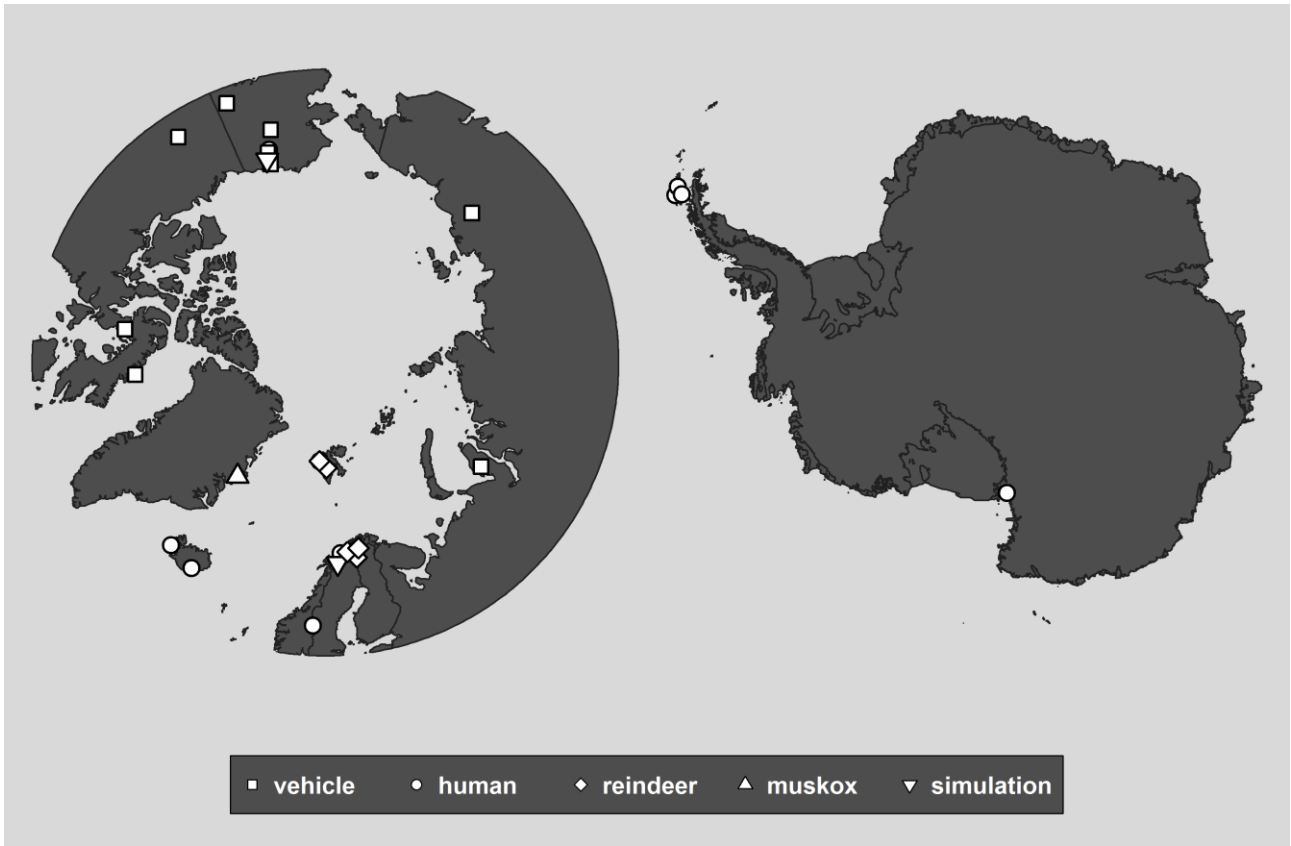
Supplementary figure S1 Map showing the sites of the reviewed studies from Arctic and Antarctic
tundra. Different trampling agents are indicated by symbols. To indicate the spatial coverage of
studies including multiple sites, the map includes 4 sites for Chapin and Shaver (1981), 2 sites for
Gisladottir (2006) and 2 sites for Ylänne et al. (2018). One site in Greenland was used in two studies
using musk ox as trampling agent (Falk et al. 2015; Mosbacher et al. 2018), and one site in northern
Sweden was used in two studies using trampling simulation as trampling agent (Olofsson 2009;
Sørensen et al. 2009).
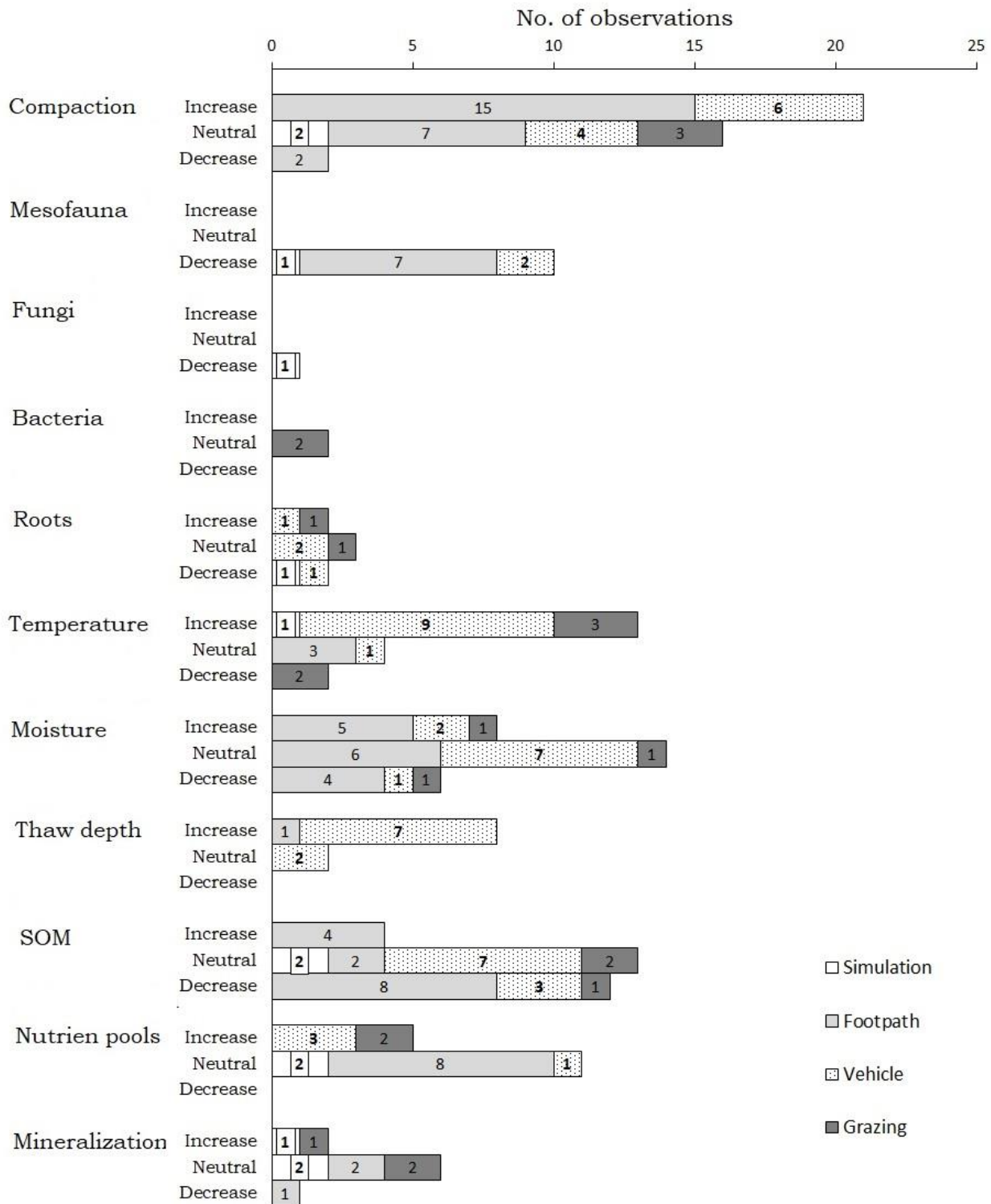
Supplementary figure S2 Summary of the review results, including the number of observations for each soil parameter, qualitative response to trampling (increase, neutral or decrease) and trampling agent. Notably, within a same study site, soil compaction could shift from increase to decrease (soil loosening) as was found in two cases (Gellatly et al., 1986ab).

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