

RESEARCH ARTICLE

Strong above-ground impacts of a non-native ungulate do not cascade to impact below-ground functioning in a boreal ecosystem

Makayla Swain¹ | Shawn J. Leroux¹  | Robert Buchkowski² 

¹Department of Biology, Memorial University of Newfoundland, St John's, Newfoundland, Canada

²Atlantic Forestry Centre, Fredericton, New Brunswick, Canada

Correspondence

Shawn J. Leroux

Email: sleroux@mun.ca

Funding information

Natural Sciences and Engineering Research Council of Canada Discovery Grant

Handling Editor: Laura Prugh

Abstract

1. Experimental studies across biomes demonstrate that herbivores can have significant effects on ecosystem functioning. Herbivore effects, however, can be highly variable with studies demonstrating positive, neutral or negative relationships between herbivore presence and different components of ecosystems. Mixed effects are especially likely in the soil, where herbivore effects are largely indirect mediated through effects on plants.
2. We conducted a long-term experiment to disentangle the effects of non-native moose in boreal forests on plant communities, nutrient cycling, soil composition and soil organism communities.
3. To explore the effect of moose on soils, we conduct separate analyses on the soil organic and mineral horizons. Our data come from 11 paired exclosure-control plots in eastern and central Newfoundland, Canada that provide insight into 22–25 years of moose herbivory. We fit piecewise structural equations models (SEM) to data for the organic and mineral soil horizons to test different pathways linking moose to above-ground and below-ground functioning.
4. The SEMs revealed that moose exclusion had direct positive impacts on adult tree count and an indirect negative impact on shrub percent cover mediated by adult tree count. We detected no significant impact of moose on soil microbial C:N ratio or net nitrogen mineralization in the organic or mineral soil horizon. Soil temperature and moisture, however, was more than twice as variable in the presence (i.e. control) than absence (i.e. exclosure) of moose. Overall, we observed clear impacts of moose on above-ground forest components with limited indirect effects below-ground. Even after 22–25 years of exclusion, we did not find any evidence of moose impacts on soil microbial C:N ratio and net nitrogen mineralization.
5. Our long-term study and mechanistic path analysis demonstrates that soils can be resilient to ungulate herbivore effects despite evidence of strong effects above-ground. Long-term studies and analyses such as this one are relatively rare yet critical for reconciling some of the context-dependency observed across studies of ungulates effects on ecosystem functions. Such studies may be particularly valuable in ecosystems with short growing seasons such as the boreal forest.

KEYWORDS

herbivory, moose, nitrogen mineralization, nutrient cycling, path analysis, plant-animal interactions, spruce budworm

1 | INTRODUCTION

Large ungulate herbivores have important effects on ecosystems through three common mechanisms: consumption of plant material, trampling of soil and surface vegetation and defecation (Forbes et al., 2019; Tuomi et al., 2021; Figure 1). These mechanisms and others (e.g. carcasses) interact to influence ecosystems processes such as soil nutrient stocks and flows but there remains substantial uncertainty in the strength of large ungulate herbivore effects on ecosystems (see review in Sitters & Andriuzzi, 2019). This is true, even when we account for the important differences between the effects of browsers and grazers (see reviews in Andriuzzi & Wall, 2017; Bernes et al., 2018; Forbes et al., 2019; Sitters & Andriuzzi, 2019; Staver et al., 2021; Wardle et al., 2004).

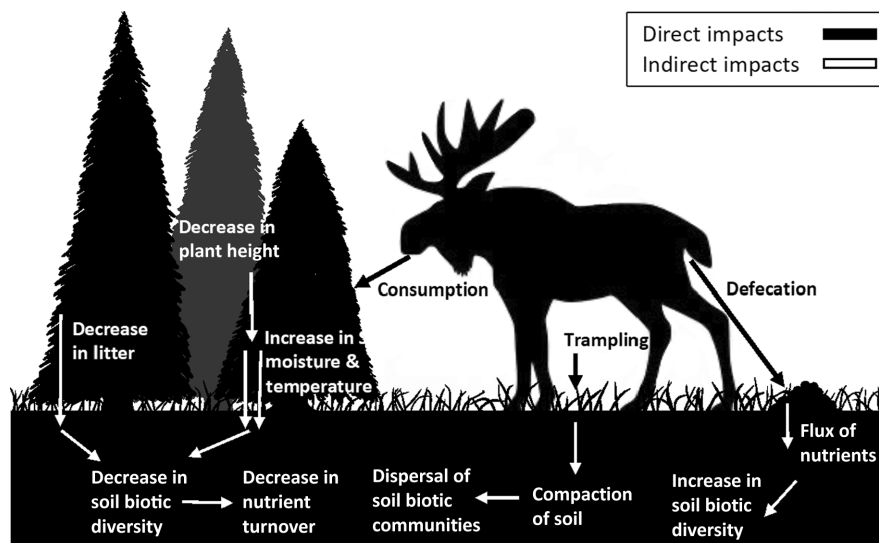
Early syntheses (e.g. Wardle et al., 2004) suggested that ecosystem productivity was the main driver of ungulate effects on ecosystem nutrient cycling with positive (i.e. accelerated cycling) effects expected in productive ecosystems dominated by grazers, such as grasslands, and negative (i.e. decelerating) effects in unproductive ecosystems dominated by browsers, such as boreal forests. More recent syntheses (e.g. Sitters & Andriuzzi, 2019), however, expand on this simple framework and synthesize evidence for how plant traits and specific ungulate mechanisms (e.g. trampling vs. browsing) may yield positive or negative effects of ungulates in productive or unproductive ecosystems. Even within one ecosystem—for example, the boreal forest—where primary productivity may be less variable than when comparing across ecosystems, disparate studies have demonstrated strong negative (e.g. Pastor et al., 1993) or none to weak (e.g. Kolstad et al., 2018) effects of moose on nutrient cycling. Consequently, factors other than primary productivity must be impacting herbivore effects on ecosystems (Sitters & Andriuzzi, 2019).

The reasons for these contrasting results are not well understood but critical for forecasting ecosystem functioning under global changes.

Cervids are a useful group of organisms to study the ecosystem effects of large herbivores, because many species have well-documented ecosystem effects across their range (see reviews in Bernes et al., 2018; Côté et al., 2014; Leroux et al., 2020; Pastor et al., 2006). Many studies have observed that cervids such as moose (*Alces alces*) and whitetail deer (*Odocoileus virginianus*) can shift plant species composition in forests to plants with low-quality foliage and litter (i.e. high C:N ratio; Côté et al., 2014; De Vriendt et al., 2021; Hidding et al., 2013; Pastor et al., 1988; Rotter & Rebertus, 2015) by browsing more palatable, high-quality forage (i.e. low C:N ratio). These changes in the plant community, along with direct trampling and defecation on the soil surface were thought to decrease soil C and N concentrations (Pastor et al., 1993). However, recent research on moose has observed no effect of moose on soil N availability and soil C:N ratio (Ellis & Leroux, 2017; Kolstad et al., 2018). Measuring the effect of cervids on soil N mineralization and microbial communities may help explain longer-term changes in forest productivity and site quality.

Experimental studies of other large browsers and grazers across biomes show considerable disagreement in the strength of these animal's effect on soil ecosystem functioning (e.g. Ibanez-Alvarez et al., 2022 and see reviews in Andriuzzi & Wall, 2017; Daskin & Pringle, 2016; Forbes et al., 2019). Soil sampling methods in ungulate enclosure experiments (see Appendix S1: Table A.1 for overview of common approaches) are highly variable, with some studies focusing on specific horizons (e.g. Pastor et al., 1993: organic horizon; Peschel et al., 2015: mineral horizon) but most focusing on a set depth ranging from 10 cm (e.g. Cline et al., 2017) to 40 cm (e.g. Liu et al., 2015). Kolstad et al. (2018) is one of the few examples that analyse ungulate (i.e. moose) effects on the organic and mineral horizons. The set

FIGURE 1 Conceptual diagram depicting how the three main direct impacts by a browser can have far-reaching indirect impacts. Predicted direct impacts of a large ungulate browser are shown in black and indirect impacts are shown in white.



depth approach adopted by most is very likely to sample across horizons in most ecosystems. We surmise that this variability in soil sampling methods across studies may be one reason for the observed variation (in both magnitude and direction) of large herbivore effects on soil N availability, C:N ratio and elemental cycling.

Soil is not homogeneous, but instead it is made up of horizons each with different properties and links to above-ground processes (Fierer et al., 2003; Quideau et al., 2001). The uppermost soil horizon is mainly an organic horizon and is most heavily impacted by recent above-ground conditions and plant communities (Bhattarai et al., 2015; Pastor et al., 1993; Vanhala et al., 2008). The second horizon and those below are typically mineral horizons and are less impacted by above-ground conditions in the short term. Organic and mineral horizons have very different properties. For example, in boreal podzols, the organic horizon typically has a higher percent carbon content (>17% total C) and has faster C and N mineralization rates than the mineral horizon (Laganière et al., 2015; Liu et al., 2015). We expect mineralization rate, nutrient content and microbial community composition in the organic soil horizon to be more responsive to moose than these properties in the mineral soil horizon (Pastor et al., 1993).

We used a long-term (22–25 years) experiment on the Island of Newfoundland, Canada with 11 paired moose enclosure (i.e. fenced) and control plots to measure the ecosystem influences of moose browsing. We use structural equation models to uncover the potential direct and indirect mechanisms linking moose to soil ecosystem functioning. Specifically, we predicted that areas where moose are excluded will: (i) have taller and more abundant tree communities and lower shrub cover (Bernes et al., 2018; De Vriendt et al., 2021; Ellis & Leroux, 2017), (ii) have a lower soil temperature and soil moisture (Cline et al., 2017; Frank et al., 2011; Kolstad et al., 2018),

(iii) higher microbial biomass C:N ratio (Cline et al., 2017; Peschel et al., 2015) and (iv) higher net N mineralization rates (Frank, 2008; see Appendix S1: Figure A.1 for a conceptual diagram of predictions and Table A.2). We partition our soil analysis into two soil horizons; organic and mineral soil horizons. We expect that (v) moose impacts on the organic horizon will be stronger than on the mineral horizon.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted this study in the central-east coast maritime boreal forests of Newfoundland with nine sites in Terra Nova National Park (TNNP), and two sites east of TNNP (i.e. Bunyan's Cove and Fox Marsh; Figure 2; see Appendix S1: Section S1 for more details on site selection). Sites with paired enclosure and control plots were established in TNNP in 1998 and in Bunyan's Cove and Fox Marsh in 1995. The sites have four different disturbance histories; no recent disturbance ($n=2$), spruce budworm outbreak in 1970–80s ($n=2$), spruce budworm outbreak in 1990s ($n=5$) and clear-cut in the 1990s ($n=2$). Enclosures measure 35 m × 35 m in TNNP and Bunyan's Cove and 15 m × 15 m in Fox Marsh. Enclosures are tall enough (~3 m) to exclude all large animals, with the lower portion open to allow small animals (e.g. snowshoe hare [*Lepus americanus*]) to access the area. Control (i.e. unfenced) plots were located within ~10–25 m of their paired enclosure and had the same dimensions. We established four 4 m × 4 m sub-plots in each enclosure and control at least 5 m or 1 m inside the enclosure fencing for the 35 m × 35 m and 15 m × 15 m enclosures, respectively (Appendix S1: Figure A.2). Moose densities



FIGURE 2 Locations of the 11 paired enclosure/control plots used in our study. Located in the eastern portion of Newfoundland, Canada, nine are in Terra Nova National Park (green polygon), one in Clarenville and one in Fox Marsh. Shapes represent the disturbance categories for each site and abbreviations are: PC, Platters Cove; BE, Blue Hill East; HW, Blue Hill West; OT, Outport Trail; BC, Bunyan's Cove; HC, Blue Hill Center; MN, Minchin's; HB, Halls Beach; OH, Ocher Hill; BB, Bread Cove; and FM, Fox Marsh. Due to close proximity, individual dots for Blue Hill West and Blue Hill East as well as Outport Trail and Minchin's sites overlap at this resolution.

around our sites likely peaked in the mid-1990s and have declined since. Current densities vary between 0.2 and 1 individual/km² at our sites. We sampled from July 20th to September 2nd 2020 with standardized time intervals between sampling and lab processing for each site (see Appendix S1: Tables A.3–A.5 for timing of sample collection and lab processing, and additional sampling details).

2.2 | Plant community

To test prediction (i) we surveyed each sub-plot to identify trees, shrubs and ground cover between July 20th and August 2nd. We identified and counted all the trees in each sub-plot and measured the height of all saplings less than 3 m. We classified palatable species based on previous studies of moose herbivory in Newfoundland (see Ellis & Leroux, 2017 and references therein). We identified all shrubs to species and then measured the percent cover of shrubs for the whole sub-plot. Finally, in a 1 m × 1 m quadrat in each corner of the sub-plot ($n=4$), we measured percent ground cover of grass, moss and rock.

2.3 | Soil temperature and moisture

To test the soil temperature and moisture portion of prediction (ii) we placed 1 m Environment Teros 11 temperature/water content probe linked to 1 m Environment ZL6 data logger in each of our exclosure and control plots (except Ocher Hill and Bread Cove due to cost restrictions, $n=9$ data loggers and $n=18$ probes) between July 20 and August 2. At each plot, we placed the probes in an area with a plant community that was representative of the whole plot. Probes collected soil temperature (°C) and soil water content (m³/m³) data every 6 h for approximately 1 month (see Appendix S1: Table A.3). We also collected soil gravimetric moisture at the sub-plot level by drying wet prepared core samples to constant mass at 60°C (~48 h; see below).

2.4 | Soil core collection

For predictions (ii)–(v), we collected two soil cores at all four corners of each sub-plot ($n=8$ soil cores per sub-plot (total=176 soil cores); Appendix S1: Figure A.2) between July 20 and August 2. We took a 6.4 cm diameter soil core to either 25 cm deep or until we hit rock. At each corner, the primary core was collected to be taken back to the lab. We extracted and placed the secondary core in a Ziploc bag, buried it in the depression from which it was taken, and left it to incubate for ~30 days in situ before returning to collect it (see Appendix S1: Table A.3 for details on timing).

In the field, we separated the primary cores into the organic horizon and the mineral horizon, and placed each horizon in separate sealed bags (four bags per soil horizon, per sub-plot). We visually identified organic and mineral horizons by colour, composition and

lines of horizon break (Soil Classification Working Group, 1998). In the lab, we passed each separated soil sample sequentially through two sieves (no. 5 (4 mm) and no. 10 (2 mm)) to remove large particulate organic matter and fine roots. We bulked the sub-plot samples by horizon, to create one homogenized sample of organic soil and one of mineral soil for every sub-plot ($n=4$ cores, combined to $n=1$ sample per horizon, per sub-plot; see Appendix S1: Figure A.3 for a schematic of soil core processing).

2.4.1 | Microbial biomass C:N ratio

To test the soil microbial component of prediction (iii) we used standard protocols for chloroform fumigation (see Appendix S1: Section S2 for full description of method). We sent the extracts to the Laboratoire de chimie organique et inorganique of the Ministère des Forêts, Québec. A Shimadzu TOC-V CPN Total Organic Analyzer equipped with a TNM-1 Total Nitrogen unit was used to analyse samples for total extractable carbon (TC) and total extractable nitrogen (TN). Standards for this analyser is 3 mg/L N (as NO₃⁻) in HCl 0.05% from a multi-element commercial standard (AccuSPEC, SCP Science). Results were given in units of mg/L and were converted to mg/g soil ((mg/L * L K₂SO₄)/g soil) and then divided by a standard to account for typically extraction error (C: 0.45 [Beck et al., 1997] and N: 0.54 [Brookes et al., 1985]). To find the C and N attributed to microbial biomass we subtracted before and after concentrations for each sample.

2.4.2 | Net nitrogen mineralization

To test prediction (iv) we compared dissolved inorganic nitrogen (DIN) content for each horizon of the primary cores to those of the secondary cores (incubated in situ and retrieved between August 19th and September 2nd). We processed the secondary cores with the same sieving and homogenizing methods as the primary cores, described above. We sent 20–40 g of each horizon from both primary cores and incubated secondary cores to the Agriculture & Food Laboratory at the University of Guelph, where Ammonium (NH₄-N) and Nitrate (NO₃-N) concentrations were determined; each soil sample was extracted with 2 M KCL, and extracts were analysed using a Seal AQ2 discrete analyser. We used the following equation to calculate the amount of nitrogen mineralized over a ~30-day field incubation period: $N_{\text{Net N Mineralized}} = [(Nitrate_{\text{After}} + Ammonium_{\text{After}}) - (Nitrate_{\text{Before}} + Ammonium_{\text{Before}})] / \text{Days Incubated}$ (Robertson et al., 1999).

2.5 | Statistical analysis

We fit separate structural equation models (SEMs) to the organic horizon and mineral horizon data to evaluate the effects of moose exclosure (a categorical variable; presence/absence) on plant

community and soil properties (Lefcheck, 2016). We did not fit SEMs to all our data but rather to the subset of key *a priori* pathways that capture the main effects while not resulting in overfit models. Our experimental design does not isolate different mechanisms for moose effects on the ecosystem but rather allows us to investigate net effects of moose over more than two decades. Given previous research in this system did not show significant direct effects of moose on some soil properties (e.g. soil C:N ratio, Ellis & Leroux, 2017), we built SEMs to consider moose indirect effects on soils via changes in the plant communities and so do not include direct links between moose and soil variables. That said, given the piecewise SEMs we fit (see below for details) are evaluated for conditional independence among nodes (i.e. Shipley's test of directed separation) our analytical framework would identify important direct or indirect paths not specified *a priori*. Consequently, this analytical framework is well suited to identify both direct and indirect relationships between moose and boreal forests and soils.

The SEMs were created using one generalized linear mixed model (GLMM) with a Poisson error structure and a logit link with total adult tree count as response, and four linear mixed models with height of palatable saplings, shrub percent cover, soil microbial C:N ratio and soil net N mineralization as response variables. The maximum number of predictor variables per GLMM is four. This SEM structure allows us to test predictions i, iii, iv and v regarding the effects of moose on plant communities, microbial C:N ratio and soil nitrogen mineralization in the organic and mineral horizon.

We included two co-variables in our SEMs. Specifically, we included soil gravimetric moisture, and percent plant material in the organic soil horizon (i.e. residual after sieving) as co-variables in the understorey plant models (i.e. height of palatable saplings and shrub percent cover) and microbial C:N ratio model. We did not test explicitly for effects of moose on soil total percent extractable C and N as previous work in this system has done so and found no relationship (see Ellis & Leroux, 2017).

We included disturbance as a secondary predictor variable because recent evidence in boreal (see review in Leroux et al., 2020) and other ecosystems (e.g. temperate forest; Nuttle et al., 2013) demonstrates that large ungulate effects can be mediated by insect or fire disturbance history. Empirical evidence in our study system (e.g. Charron & Hermanutz, 2017; Leroux et al., 2021) suggests that canopy opening size created by insect disturbance is a good measure of disturbance effects. Consequently, we model initial disturbance as a categorical variable with three levels: open, partial and closed. This metric of disturbance represents plant community at the start of the experiment. The plant community data we collected in 2020 allow us to test how the ecosystem has changed over time with a focus on moose effects via the experimental enclosure-control design.

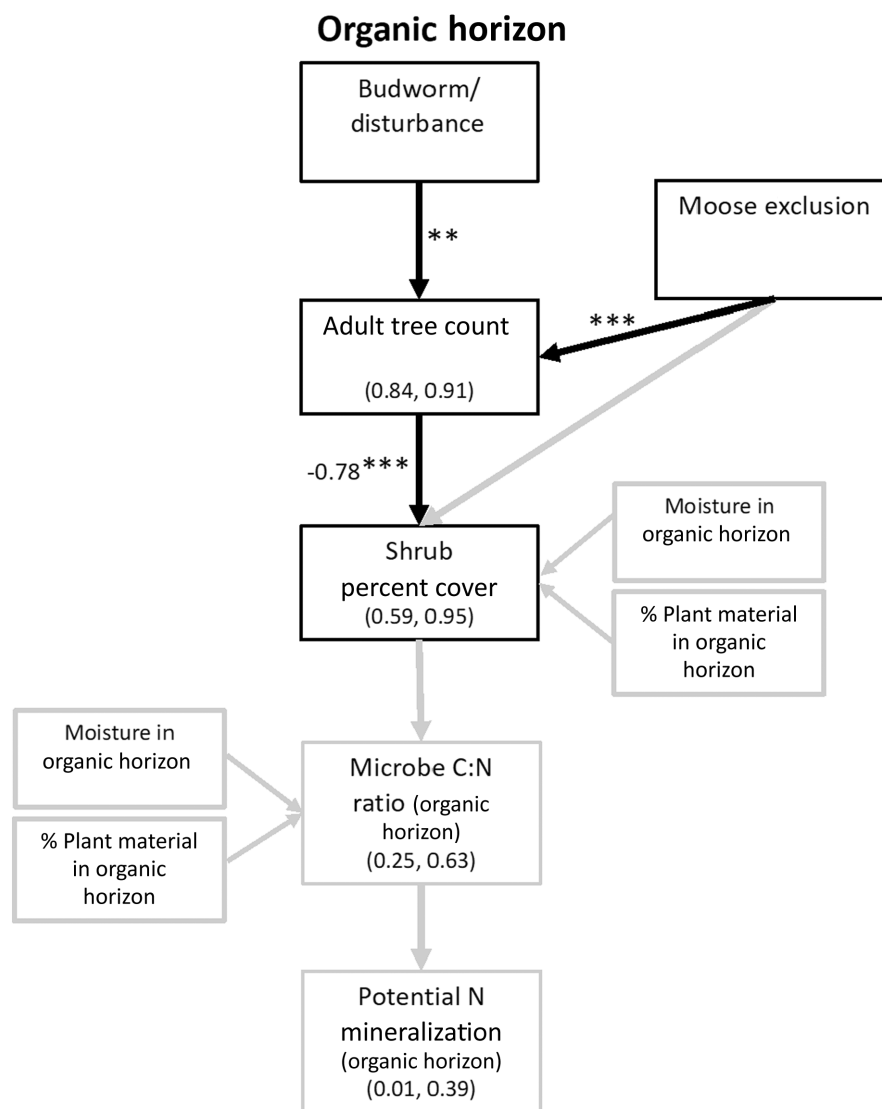
We took the sum of adult tree count across all sub-plots per plot to derive total adult tree count per plot. We took the average of sub-plot estimates for each other variable to get a mean value per plot. We treated adult tree count differently from the other data as we want to retained an integer (i.e. count) value for this metric. Sites are classified as a random intercept in each model to account for the

paired design between enclosure and control plots at each site. The above-ground variables are consistent in our two SEMs. The main difference between the two SEMs is the below-ground data—one SEM is fit to soil microbial C:N ratio, net soil N mineralization and soil moisture for the organic soil horizon, and the other to data from the mineral soil horizon. In addition, we removed data for 13 organic horizons and 16 mineral horizon sub-plots that were impacted by animals (e.g. rodent digging up soil bag) or where chemical analysis was not successful. Because of these removals, there were different subplots used in the SEMs for the organic and mineral horizons and the estimated coefficients for above-ground components varied slightly. We used R v.4.2.3 (R Core Team, 2020) to complete analyses along with the packages *lme4* (Bates et al., 2021) for mixed models, and *psem* (Lefcheck, 2016) for SEMs.

The models for height of palatable saplings did not converge and therefore, we removed this variable from the SEM analysis and simply report means (\pm SD) of observed patterns. We evaluated conditional independence among nodes in our SEMs with Shipley's test of directed separation (i.e. d-sep test) to ensure that there are no missing relationships without paths in our SEMs. This test showed that the SEMs did not meet the assumption of conditional independence with two missing relationships for the organic soil horizon and three for the mineral soil horizon model. One path that appeared highly related was moose exclusion on total adult tree count. We added this path to both SEMs as it captures a key ecological relationship. Specifically, after 22–25 years of moose exclusion, we might expect a direct impact of moose on adult trees to be emerging (Gosse et al., 2011; McLaren et al., 2009). Comparing the Fisher C value against the chi-squared distribution showed that the addition of this pathway allowed both SEM models to pass the Fisher C threshold (p -value > 0.05). However, the d-sep test showed that the mineral soil horizon SEM were still missing two relationships. Consequently, we added paths between total adult tree count and mineral soil moisture and mineral soil net N mineralization and mineral soil moisture to the mineral soil horizon SEM as correlated errors (Lefcheck, 2016). Note that our model did not identify any significant direct paths between moose and soil components in either horizon. We conducted visual assessment of the residual plots for each model included in the SEM and we report the marginal and conditional R^2 and standardized coefficient estimates for each model (Figure 3 and Table 1 for organic horizon, Appendix S1: Figure A.4 and Table A.6 for mineral horizon).

We fit additional linear mixed models to test predictions related to moose effects on soil temperature and water content (predictions ii)—two key variables of soil condition that were not included as response variables in our SEMs to avoid overfitting these models. Specifically, we fit two linear mixed models with summer soil temperature and water content over 1 month as response variables and moose exclusion as the explanatory variable. Sites were classified as a random intercept in each model to account for the paired enclosure and control design at each site. We conducted visual assessment of the residual plots and computed marginal and conditional R^2 for each linear mixed model. All data and R code are available online in Swain et al. (2023).

FIGURE 3 Results of a piecewise structural equation model examining the impact of disturbance and moose exclusion on above- and below-ground components of maritime boreal forest on the organic soil horizon. Black arrows and boxes denote statistically significant relationships (see Table 1), and grey arrows and boxes denote non-significant relationships. Numbers on black arrows are the standardized coefficient estimates with *** <0.001, ** <0.01, and * <0.05. Red boxes show covariates with coefficients that had a significant relationship with a main dependent variable in the model. Values at the bottom of each main box are the marginal and conditional R^2 for each model response variable. Variables included as correlated variables are not shown in the figure—see Table 1 for full model results.



3 | RESULTS

3.1 | Structural equation model results

The SEMs for the organic soil horizon and mineral soil horizon provided a good fit to the data (organic horizon: Fisher's $C = 21.21_{df=24}$, $p = 0.63$; mineral horizon: Fisher's $C = 22.28_{df=20}$, $p = 0.33$). There were three statistically significant ($p < 0.05$) pathways for the organic and mineral soil horizon, each (Figure 3, Table 1, Appendix S1: Figure A.4 and Table A.6).

We found strong direct relationships between budworm disturbance and total adult tree count in the organic horizon model, as well as between moose exclusion and total adult tree count in the organic and mineral horizon models (e.g. Figures 3 and 4). The height of palatable sapling models did not converge but we observed saplings, on average, ~21 cm taller in the exclosures compared to the controls (mean palatable sapling height in exclosures (SD) and controls was 84.57 cm (38.37) and 63.03 cm (29.78), respectively). Sites with open and partially open canopies from disturbance on average had more adult trees than closed canopy sites (Table 1, Appendix S1: Table A.6; mean number adult trees

per sub-plot in open: 16 (SD=13.3), partial: 14 (13.2), closed: 6 (2.5)). There were also more adult trees in moose exclosures compared to control plots where moose were present (Table 1, Appendix S1: Table A.6; mean number adult trees in exclosure: 22 (SD=11.7), control: 5 (3.9)). Total adult tree count had a negative effect on shrub percent cover in the organic horizon SEM ($p < 0.001$). Above-ground coefficients for the organic horizon and mineral horizon SEMs varied slightly due to differences in the final number of samples (see Section 2 for details); however, the relationships were mostly consistent between horizons.

There were two significant relationships that were not consistent between the organic and mineral soil horizon SEMs (Figure 3, Appendix S1: Figure A.4). For the organic horizon, there was a negative relationship between disturbance and total adult tree count but this effect was not significant in the mineral soil horizon SEM ($p = 0.05$). Also for the organic horizon, there was a negative relationship between total adult tree count and shrub percent cover but this negative relationship was not significant in the mineral soil horizon SEM ($p = 0.06$). Finally, neither SEMs revealed any direct or indirect effects of moose on soil microbial C:N ratio or net N mineralization rates (Table 1, Appendix S1: Table A.6).

TABLE 1 Piecewise structural equation model results for the organic soil horizon. Results of the piecewise structural equation model examining the direct and indirect impact of disturbance and moose exclusion on above-ground and below-ground function in maritime boreal forests. Disturbance is a categorical variable measured as canopy openness (i.e. open, partial, closed) created by budworm or forest harvesting. Moose exclusion is categorical variable with categories enclosure and control. For the categorical variables, we provide *p*-values for the full variable and estimates (+ SE) for each level compared to the reference category (i.e. Budworm disturbance reference is 'closed' and Moose exclusion reference is 'control'). Site was included as a random intercept in each model. Standardized Estimate, standardized coefficient estimate; Raw Estimate, non-standardized coefficient estimate; SE, standard error of coefficient estimate; and *p*, *p*-value with statistical significance shown as *** <0.001, ** <0.01 and * <0.05.

Response	Predictor	Standardized estimate	Raw estimate	SE	<i>p</i>
Adult tree count	Budworm disturbance				0.004**
	Budworm disturbance=Open		1.003	0.310	
	Budworm disturbance=partial		0.885	0.304	
	Moose exclusion ^a				<0.001***
	Moose exclusion=enclosure		1.540	0.154	
Shrub percent coverage	Moose exclusion				0.90
	Moose exclusion=enclosure		0.005	0.041	
	Adult tree count	-0.777	-0.012	0.002	<0.001***
	Moisture of organic horizon	-0.324	-0.001	0.001	0.153
	Percent plant material in	-0.370	-0.01	0.005	0.075
	Organic horizon				
Microbial C:N ratio in organic horizon	Shrub percent coverage	0.005	0.024	1.046	0.984
	Moisture of organic horizon	-0.253	-0.003	0.004	0.386
	Percent plant material in	-0.403	-0.055	0.039	0.227
	Organic horizon				
Net N mineralization in organic horizon	Microbial C:N ratio in organic horizon	0.121	0.240	0.444	0.628

^aIncluded as paths a posteriori (see Section 2 for details).

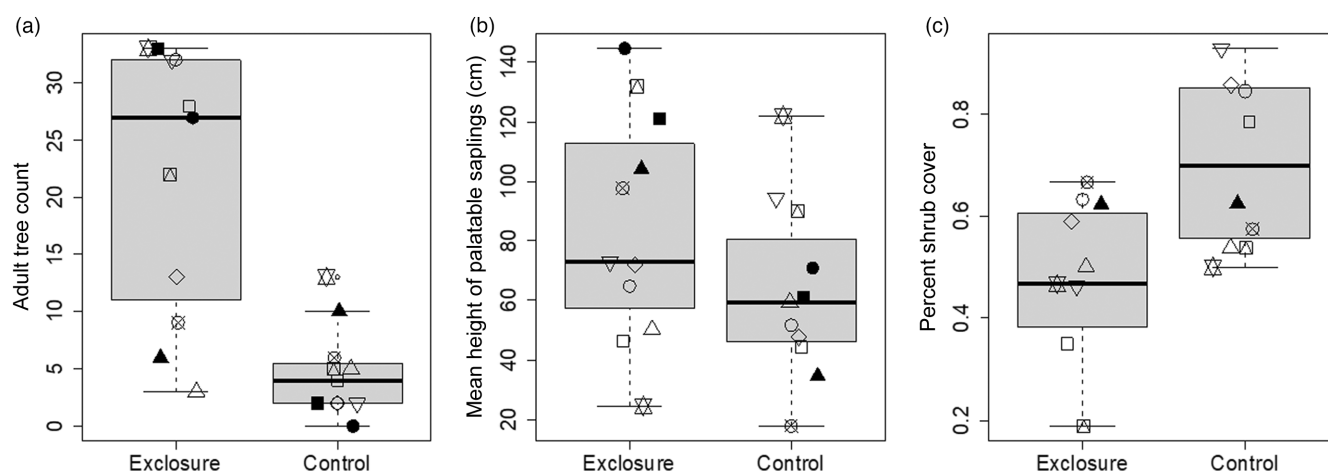


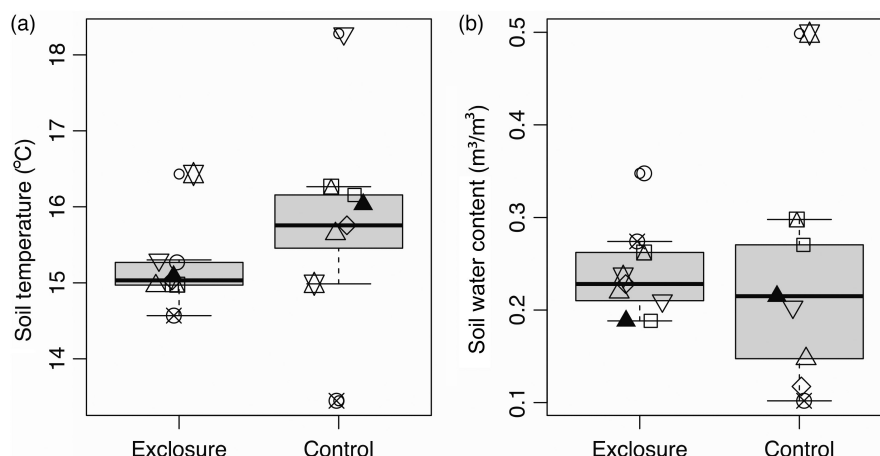
FIGURE 4 (a) Adult tree count, (b) mean height of palatable saplings, (c) percent shrub cover in 11 paired enclosure and control sites in Newfoundland, Canada. Symbols are defined as follows: ○ PC, Platters Cove; □ BE, Blue Hill East; ◇ HW, Blue Hill West; △ OT, Outport Trail; ▽ BC, Bunyan's Cove; ✕ HC, Blue Hill Center; ▲ MN, Minchin's; ■ HB, Halls Beach; ● OH, Ocher Hill; ■ BB, Bread Cove; and ◻ FM, Fox Marsh.

3.2 | Linear mixed models of moose impact on soil temperature and water content

We fit two linear mixed models to evaluate our predictions that went beyond our SEM (Figure 5, Appendix S1: Table A.7). We found very

little evidence of moose impacts on mean soil temperature (marginal $R^2=0.09$, conditional $R^2=0.16$) but we observed higher variability in soil temperature in controls (mean=15.8°C, SD=1.3°C) relative to enclosures (mean=15.2°C, SD=0.52°C). The soil water content model did not converge and we observed similar mean soil

FIGURE 5 (a) Soil temperature ($^{\circ}\text{C}$) over 1 month, (b) soil water content (volume of water (m^3)/volume of soil(m^3)) over 1 month in nine paired enclosure and control sites in Newfoundland, Canada. See caption in Figure 4 for symbol definitions.



water content but higher variability in soil water content in controls (mean= 0.23 m^3 of water/ m^3 of soil, $\text{SD}=0.12 \text{ m}^3/\text{m}^3$) relative to enclosures (mean= $0.24 \text{ m}^3/\text{m}^3$, $\text{SD}=0.05 \text{ m}^3/\text{m}^3$, Figure 5, Appendix S1: Table A.7).

4 | DISCUSSION

Classic studies of large ungulate systems (see review in Wardle et al., 2004) suggest the prevalence of cascading indirect impacts of large ungulates on ecosystem function (Pastor et al., 1988, 1993). Recent work has called into question the generality of these earlier findings (Ellis & Leroux, 2017; Ibanez-Alvarez et al., 2022; Kolstad et al., 2018) and has attempted to explain the disparate effects of ungulates on ecosystem properties (Andriuzzi & Wall, 2017; Daskin & Pringle, 2016; Sitters & Andriuzzi, 2019; Staver et al., 2021). In our 22–25 year experiment we measured above-ground and below-ground effects of moose on two soil horizons. We found that moose have a significant impact on above-ground plant communities but limited to no effect on soil properties. Data from this long-term experiment suggests that soil functioning in our boreal forest system may be resilient to large ungulate impacts.

The effects of ungulate foraging, trampling and defecating are first observed above-ground (Tuomi et al., 2021). This explains why we see strong and consistent above-ground effects of moose across boreal study systems (Isle Royale: Pastor et al., 1993, Sweden: Persson et al., 2005, Newfoundland: Ellis & Leroux, 2017, Norway: Kolstad et al., 2018, Quebec: De Vriendt et al., 2021). Moose prefer foraging on nitrogen-rich shoots from trees and shrubs, making it harder for these highly palatable species to grow to canopy-level heights. As expected, our data demonstrate that moose exclusion has a positive impact on the total abundance of adult trees and negative indirect impact on understorey plant cover (Figures 2 and 3). This is likely because trees, proliferating in the absence of moose, shade out shrubs and compete for resources (De Vriendt et al., 2021; Kneeshaw & Bergeron, 1999; Sadanandan Nambiar & Sands, 1993). The effect of moose exclusion on count of adult trees was not seen in shorter-term studies in boreal Canada (Ellis & Leroux, 2017; Gosse

et al., 2011; Leroux et al., 2021) but appears to emerge on longer time scales here, for example 20+ years of exclusion. Finally, we found that areas with higher disturbance (open and partial) had more adult trees. Increases in adult tree count can be attributed to the opening of canopy by disturbance, allowing for more sapling trees to grow and reach adult height before significant thinning has occurred (Gosse et al., 2011; McLaren et al., 2009). This likely reflects a demographic rate asymmetry in trees where most trees tend to recruit faster than they thin (e.g. Sterner et al., 1986). Therefore, large ungulate herbivory interacts with disturbance history to shape plant communities (De Vriendt et al., 2021; Leroux et al., 2021; Nuttle et al., 2013).

Our SEM analysis did not identify any significant direct paths between moose and soil components in either horizon, suggesting, as previous work has in this system (Ellis & Leroux, 2017) and others (Kolstad et al., 2018), that there is no evidence for direct effects of moose on soil characteristics or functions. We expected, however, that the changes in above-ground plant communities caused by moose should indirectly alter soil properties related to nutrient cycling, such as net nitrogen mineralization and microbial C:N ratio (Bardgett & Wardle, 2010; Pastor et al., 2006; Sitters & Andriuzzi, 2019; Wardle et al., 2004). Any changes in soil properties could indicate a strong legacy of plant community change through altered relationships between plants and soil. Counter to expectations, our SEM for both the organic and mineral soil horizon did not show any evidence for an indirect effect of moose on soil microbial C:N ratio or potential N mineralization (Figure 3, Tables 1, Appendix S1: Figure A.4 and Table A.6). We also did not observe a statistically significant difference in soil temperature in the presence or absence of moose but soil temperature and water content were more than twice as variable in the presence of moose (Figure 4). In boreal ecosystems, microbial C:N and fungi:bacteria ratios are usually positively related (Sterner & Elser, 2002). A lower microbial C:N ratio would suggest a higher bacterial community, which is often positively correlated with N mineralization and turnover (Högberg et al., 2007). Our results are similar to findings of weak indirect effects of moose on soil N availability and nutrient stocks in Kolstad et al. (2018)'s shorter term experiment ($n=8$ years). Consequently,

indirect cascading impacts by moose are not evident after 22–25 years in our study system. This result is counter to many other studies of large ungulate effects on soils (see review in Appendix S1: Table A.1). However, there is large variability in the soil core depth and consequently horizons sampled across studies of ungulate–ecosystem interactions. For example some studies take soil cores—with or without removing the organic horizon—to a maximum depth of 10 cm (e.g. Cline et al., 2017; Frank, 2008) or 30 cm (e.g. Ellis & Leroux, 2017; Liu et al., 2015), whereas others explicitly focus on the A1 and O2 horizons (e.g. Pastor et al., 1993). Kolstad et al. (2018) is one of the few cases we have found that analysed both organic and mineral horizons to a maximum of 30 cm depth separately. In their Norway boreal forest system, Kolstad et al. (2018) observed no significant effects of moose across soil horizons which is consistent with our findings of only weak to no indirect effect of moose across soil horizons (Figure 3). We recommend explicit documentation and investigation of the impacts of soil sampling depth, and standardized approaches to soil sampling in future work on large ungulate–soil functioning.

Moose density at our sites is low (0.2–1 ind/km²) and similar to densities reported in Norway (0.5–1.9 ind/km²; Kolstad et al., 2018)—two study areas reporting weak effects of moose on boreal soils. In contrast moose densities reported on Isle Royale are relatively high (1.5–4.6 ind/km²; Pastor et al., 1993) and authors show strong effects of moose on soils in this system. Brandner et al. (1990) found that moose suppression of balsam fir height and recruitment on Isle Royale increased with moose density. Studies in Newfoundland (current study), Norway (Kolstad et al., 2018) and Isle Royale (Pastor et al., 1993) all report large effects of moose on above-ground plant communities (height, biomass) but perhaps strong effects on soils only emerge under sustained high moose densities. An additional factor that may explain weaker effects of moose in our maritime boreal system is the shorter and cooler growing season relative to other boreal regions (Ellis & Leroux, 2017).

The exclosures used in our study were established 22–25 years before we collected our data which is longer in duration than many (Ellis & Leroux, 2017; Gass & Binkley, 2011; Kolstad et al., 2019) but not all (Cline et al., 2017; Pastor et al., 1993) exclosure experiments in similar ungulate ecosystem studies. However, moose were established in Newfoundland around 100 years before the exclosures were built (Pimlott, 1953) and became abundant in and around our study area in the 1980s (McLaren et al., 2004). The history of disturbance and large ungulate herbivory prior to exclosures being erected is rarely reported in large ungulate–ecosystem studies (Leroux et al., 2021). Site legacy, however, could be critical to predicting large ungulate effects on ecosystems (Leroux et al., 2020; Nuttle et al., 2013). Soils, particularly mineral horizons, are slow to form as they are very dependent on many environmental factors such as climate, soil invertebrate communities and topography (Jenny, 1941). As a result, the soils within moose exclosures in this system may yet contain a legacy of moose indirect effects from the decades between their introduction and the exclosure construction.

Ecology has a long history of large herbivore exclosure–control experiments. Such experiments, however, are usually not designed to decipher different mechanisms or direct and indirect effects of herbivores on ecosystems, but rather the net effect. When applied to data from such designs, path analyses, as we have shown here, can be useful to test for direct and indirect effects of large herbivores on ecosystems. A detailed understanding of the direct and indirect mechanisms linking large herbivores to soil functioning may be critical to predict how the loss or expansion of large herbivores may impact different ecosystems. We see two promising and complementary avenues to develop this mechanistic understanding; one based on increased precision in sampling and the other based on increased breadth of sampling. First, future work should attempt to better isolate the different effects of herbivores in their design. For example, sampling could be done on and off ungulate trails to study trampling impacts on ecosystems (see review in Tuomi et al., 2021). In the end, we value the classic herbivore exclosure–control design but also call for alternate designs to move this field forwards. Second, large herbivore–ecosystem studies must move beyond single study areas and embrace integration across distributed networks of experiments (Borer et al., 2014; Forbes et al., 2019; Leroux et al., 2020). Substantial variation in large herbivore effects on soil functioning may be driven by species, environment, or experimental design. A distributed network of large herbivore exclosure experiments could be arrayed along gradients of large herbivore species, species abundance, and/or primary productivity thereby enabling researchers to explicitly test the relative importance of these different contexts on large herbivore effects. To start, these networks could be an accumulation of existing experiments. For example, Petersen et al. (2023) assembled data from 100 paired moose exclosure–control plots across five countries and a large primary productivity gradient to demonstrate consistent responses of forest structure to moose exclusion. Conducting a similar analysis of soil responses across exclosure experiments would let us make more general conclusions below-ground. A recent comprehensive review by Pringle et al. (2023) also provides additional approaches to developing a better mechanistic understanding of the impacts of large herbivores on terrestrial ecosystems.

Moose are not native to the island of Newfoundland and have become an agent of change in the boreal forest ecosystem there since their introduction over 100 years ago. At least so far, we find that the most significant effects of moose presence on the boreal forests of Newfoundland remain above-ground. This suggests that below-ground dynamics may be relatively stable in the face of significant above-ground impacts of this large herbivore.

AUTHOR CONTRIBUTIONS

Makayla Swain, Shawn J. Leroux and Robert Buchkowski conceived of the project and analyses, interpreted results, and wrote and revised the manuscript. Makayla Swain collected data, Makayla Swain and Shawn J. Leroux conducted the analyses with input from Robert Buchkowski.

ACKNOWLEDGEMENTS

The authors thank the many partners for the support and assistance since the inception of this project over 20 years ago. In particular, The authors thank R. Wissink (formerly of TNNP) for developing the idea of measuring the impact of moose back in 1996. The authors thank B. McLaren (Lakehead University) and L. Hermanutz (Memorial University) for their part in designing and supporting the early years of this project. The authors are grateful to J. Feltham, R. Power, J. Gosse, L. Siegwart Collier and K. Tulk (formerly of Parks Canada), and S. Avery (formerly of NL Provincial Forestry Dept.) for ongoing monitoring. The authors thank J. Bosch for field assistance and C. Brown, S. Ziegler, E. Forbes, A. Meyer and anonymous reviewers for constructive feedback on earlier versions of the paper. Funding for this study was provided by a Natural Sciences and Engineering Research Council of Canada Discovery Grant to S.J.L.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to report.

DATA AVAILABILITY STATEMENT

All data and R code used in this paper are available on figshare: <https://doi.org/10.6084/m9.figshare.22788860.v1> (Swain et al., 2023).

ORCID

Shawn J. Leroux  <https://orcid.org/0000-0001-9580-0294>

Robert Buchkowski  <https://orcid.org/0000-0001-6381-8609>

REFERENCES

- Andriuzzi, W. S., & Wall, D. H. (2017). Responses of belowground communities to large aboveground herbivores: Meta-analysis reveals biome-dependent patterns and critical research gaps. *Global Change Biology*, 23, 3857–3868.
- Bardgett, R. D., & Wardle, D. A. (2010). *Aboveground-belowground linkages: Biotic interactions, ecosystem processes, and global change*. Oxford Series in Ecology and Evolution. Oxford University Press.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., Baueur, A., & Krivitsky, P. N. (2021). lme4: Linear mixed-effects models using "Eigen" and S4 (version 1.1–27.1). <https://CRAN.R-project.org/package=lme4>
- Beck, T., Joergensen, R. G., Kandeler, E., Makenschin, F., Nuss, E., Oberholzer, H. R., & Scheu, S. (1997). An inter-laboratory comparison of ten different ways of measuring soil microbial biomass C. *Soil Biology and Biochemistry*, 29, 1023–1032.
- Bernes, C., Macura, B., Jonsson, B. G., Junninen, K., Müller, J., Sandström, J., Löhmus, A., & Macdonald, E. (2018). Manipulating ungulate herbivory in temperate and boreal forests: Effects on vegetation and invertebrates. A systematic review. *Environmental Evidence*, 7, 13.
- Bhattarai, A., Bhattarai, B., & Pandey, S. (2015). Variation of soil microbial population in different soil horizons. *Journal of Microbiology and Experimentation*, 2, 75–78.
- Borer, E. T., Harpole, W. S., Adler, P. B., Lind, E. M., Orrock, J. L., Seabloom, E. W., & Smith, M. D. (2014). Finding generality in ecology: A model for globally distributed experiments. *Methods in Ecology and Evolution*, 5, 65–73.
- Brandner, T. A., Peterson, R. O., & Risenhoover, K. L. (1990). Balsam fir on Isle Royale: Effects of moose herbivory and population density. *Ecology*, 71, 155–164.
- Brookes, P. C., Landman, A., Pruden, G., & Jenkinson, D. S. (1985). Chloroform fumigation and the release of soil nitrogen: A rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biology and Biochemistry*, 17, 837–842.
- Charron, L., & Hermanutz, L. (2017). Simplicity is key: Restoration protocols for nonregenerating forests degraded by overabundant herbivores. *Restoration Ecology*, 25, 432–441.
- Cline, L. C., Zak, D. R., Upchurch, R. A., Freedman, Z. B., & Peschel, A. R. (2017). Soil microbial communities and elk foraging intensity: Implications for soil biogeochemical cycling in the sagebrush steppe. *Ecology Letters*, 20, 202–211.
- Côté, S. D., Beguin, J., de Bellefeuille, S., Champagne, E., Thiffault, N., & Tremblay, J. (2014). Structuring effects of deer in boreal forest ecosystems. *Advances in Ecology*, 2014, 917834.
- Daskin, J. H., & Pringle, R. M. (2016). Does primary productivity modulate the indirect effects of large herbivores? A global meta-analysis. *Journal of Animal Ecology*, 85, 857–868.
- De Vriendt, L., Lavoie, S., Barrette, M., & Tremblay, J.-P. (2021). From delayed succession to alternative successional trajectory: How different moose browsing pressures contribute to forest dynamics following clear-cutting. *Journal of Vegetation Science*, 32, e12945.
- Ellis, N. M., & Leroux, S. J. (2017). Moose directly slow plant regeneration but have limited indirect effects on soil stoichiometry and litter decomposition rates in disturbed maritime boreal forests. *Functional Ecology*, 31, 790–801.
- Fierer, N., Schimel, J. P., & Holden, P. A. (2003). Variations in microbial community composition through two soil depth profiles. *Soil Biology and Biochemistry*, 35, 167–176.
- Forbes, E. S., Cushman, J. H., Burkepile, D. E., Young, T. P., Klope, M., & Young, H. S. (2019). Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. *Functional Ecology*, 33, 1597–1610.
- Frank, D. A. (2008). Ungulate and topographic control of nitrogen: Phosphorus stoichiometry in a temperate grassland; soils, plants and mineralization rates. *Oikos*, 117, 591–601.
- Frank, D. A., Depriest, T., Mclauchlan, K., & Risch, A. C. (2011). Topographic and ungulate regulation of soil C turnover in a temperate grassland ecosystem. *Global Change Biology*, 17, 495–504.
- Gass, T. M., & Binkley, D. (2011). Soil nutrient losses in an altered ecosystem are associated with native ungulate grazing. *Journal of Applied Ecology*, 48, 952–960.
- Gosse, J., Hermanutz, L., McLaren, B., & Deering, P. (2011). Degradation of boreal forests by nonnative herbivores in Newfoundland's national parks: Recommendations for ecosystem restoration. *Natural Areas Journal*, 31, 331–339.
- Hidding, B., Tremblay, J.-P., & Côté, S. D. (2013). A large herbivore triggers alternative successional trajectories in the boreal forest. *Ecology*, 94, 2852–2860.
- Högberg, M. N., Chen, Y., & Högberg, P. (2007). Gross nitrogen mineralisation and fungi-to-bacteria ratios are negatively correlated in boreal forests. *Biology and Fertility of Soils*, 44, 363–366.
- Ibanez-Alvarez, M., Baraza, E., Serrano, E., Romero-Munar, A., Cardona, C., Bartolome, J., & Krumins, J. A. (2022). Ungulates alter plant cover without consistent effect on soil ecosystem functioning. *Agriculture, Ecosystems and Environment*, 326, 107796.
- Jenny, H. (1941). *Factors of soil formation: A system of quantitative pedology*. McGrawHill Book Company, INC.
- Kneeshaw, D. D., & Bergeron, Y. (1999). Spatial and temporal patterns of seedling and sapling recruitment within canopy gaps caused by spruce budworm. *Écoscience*, 6, 214–222.
- Kolstad, A. L., Austrheim, G., Graae, B. J., Solberg, E. J., Strimbeck, G. R., & Speed, J. D. M. (2019). Moose effects on soil temperatures, tree canopies, and understory vegetation: A path analysis. *Ecosphere*, 10, e02966.
- Kolstad, A. L., Austrheim, G., Solberg, E. J., Venete, A. M. A., Woodin, S. J., & Speed, J. D. M. (2018). Cervid exclusion alters boreal forest

- properties with little cascading impacts on soils. *Ecosystems*, 21, 1027–1041.
- Laganière, J., Podrebarac, F., Billings, S. A., Edwards, K. A., & Ziegler, S. E. (2015). A warmer climate reduces the bioreactivity of isolated boreal forest soil horizons without increasing the temperature sensitivity of respiratory CO₂ loss. *Soil Biology and Biochemistry*, 84, 177–188.
- Lefcheck, J. S. (2016). PiecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7, 573–579.
- Leroux, S. J., Charron, L., Hermanutz, L., & Feltham, J. (2021). Cumulative effects of spruce budworm and moose herbivory on boreal forest ecosystems. *Functional Ecology*, 35, 1448–1459.
- Leroux, S. J., Wiersma, Y. F., & Vander Wal, E. (2020). Herbivore impacts on carbon cycling in boreal forests. *Trends in Ecology & Evolution*, 35, 1001–1010.
- Liu, N., Kan, H. M., Yang, G. W., & Zhang, Y. J. (2015). Changes in plant, soil, and microbes in a typical steppe from simulated grazing: Explaining potential change in soil C. *Ecological Monographs*, 85, 269–286.
- McLaren, B. E., Roberts, B. A., Djan-Chékar, N., & Lewis, K. P. (2004). Effects of overabundant moose on the newfoundland landscape. *Alces*, 40, 45–59.
- McLaren, B. E., Taylor, S., & Luke, S. H. (2009). How moose select forested habitat in Gros Morne National Park, Newfoundland. *Alces*, 45, 125–135.
- Nuttle, T., Royo, A. A., Adams, M. B., & Carson, W. P. (2013). Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecological Monographs*, 83, 3–17.
- Pastor, J., Cohen, Y., & Hobbs, N. T. (2006). The roles of large herbivores in ecosystem nutrient cycles. In K. Danell, R. Bergstrom, P. Duncan, & J. Pastor (Eds.), *Large herbivore ecology, ecosystem dynamics, and conservation* (pp. 289–325). Cambridge University Press.
- Pastor, J., Dewey, B., Naiman, R. J., McInnes, P. F., & Cohen, Y. (1993). Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology*, 74, 467–480.
- Pastor, J., Naiman, R. J., Dewey, B., & McInnes, P. (1988). Moose, microbes, and the boreal forest. *Bioscience*, 38, 770–777.
- Persson, I.-L., Pastor, J., Danell, K., & Bergstrom, R. (2005). Impact of moose population density on the production and composition of litter in boreal forests. *Oikos*, 108, 297–306.
- Peschel, A. R., Zak, D. R., Cline, L. C., & Freedman, Z. (2015). Elk, sagebrush, and saprotrophs: Indirect top-down control on microbial community composition and function. *Ecology*, 96, 2383–2393.
- Petersen, T. K., Kolstad, A. L., Kouki, J., Leroux, S. J., Potvin, L. R., Tremblay, J.-P., Wallgren, M., Widemo, F., Cromsigt, J. P. G. M., Courtois, C., Austrheim, G., Gosse, J., den Herder, M., Hermanutz, L., & Speed, J. D. M. (2023). Airborne laser scanning reveals uniform responses of forest structure to moose (*Alces alces*) across the boreal forest biome. *Journal of Ecology*, 111, 1396–1410. <https://doi.org/10.1111/1365-2745.14093>
- Pimlott, D. (1953). *Newfoundland moose*. North American Wildlife Conference: Transactions.
- Pringle, R. M., Abraham, J. O., Anderson, T. M., Coverdale, T. C., Davies, A. B., Dutton, C. L., Gaylard, A., Goheen, J. R., Holdo, R. M., Hutchinson, M. C., Kimuyu, D. M., Long, R. A., Subalusky, A. L., & Veldhuis, M. P. (2023). Impacts of large herbivores on terrestrial ecosystems. *Current Biology*, 33, R584–R610.
- Quideau, S., Chadwick, O., Benesi, A., Graham, R. C., & Anderson, M. A. (2001). A direct link between forest vegetation type and soil organic matter composition. *Geoderma*, 104, 41–60.
- R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing Retrieved from <https://www.R-project.org/>
- Robertson, G. P., Coleman, D. C., Bledsoe, C. S., & Sollins, P. (1999). *Standard soil methods for long-term ecological research*. Oxford University Press.
- Rotter, M., & Rebertus, A. (2015). Plant community development of Isle Royale's moose-spruce savannas. *Botany*, 93, 75–90.
- Sadanandan Nambiar, E. K., & Sands, R. (1993). Competition for water and nutrients in forests. *Canadian Journal of Forest Research*, 23, 1955–1968.
- Sitters, J., & Andriuzzi, W. S. (2019). Impacts of browsing and grazing ungulates on soil biota and nutrient dynamics. In I. J. Gordon & H. H. T. Prins (Eds.), *The ecology of browsing and grazing II. Ecological studies (analysis and synthesis)* (Vol. 239). Springer Cham.
- Soil Classification Working Group. (1998). *The Canadian system of soil classification* (3rd ed.). Agriculture and Agri-Food Canada Publication 1646.
- Staver, A. C., Abraham, J. O., Hempson, G. P., Karp, A. T., & Faith, J. T. (2021). The past, present, and future of herbivore impacts on savanna vegetation. *Journal of Ecology*, 109, 2804–2822.
- Sterner, R. W., & Elser, J. J. (2002). *Ecological stoichiometry: The biology of elements from molecules to biosphere*. Princeton University Press.
- Sterner, R. W., Ribic, C. A., & Schatz, G. E. (1986). Testing for life historical changes in spatial patterns of four tropical tree species. *Journal of Ecology*, 74, 621–633.
- Swain, M., Leroux, S., & Buchkowski, R. (2023). Data from: Strong aboveground impacts of a non-native ungulate do not cascade to impact belowground functioning in a boreal ecosystem. *Figshare Digital Repository* <https://doi.org/10.6084/m9.figshare.22788860.v1>
- Tuomi, M., Väisänen, M., Yläne, H., Brearley, F. Q., Barrio, I. C., Bräthen, K. A., Eischeid, I., Forbes, B. C., Jónsdóttir, I. S., Kolstad, A. L., Macek, P., Bon, M. P., Speed, J. D. M., Stark, S., Svavarsdóttir, K., Thórsson, J., & Guillermo Bueno, C. (2021). Stomping in silence: Conceptualizing trampling effects on soils in polar tundra. *Functional Ecology*, 35, 306–317.
- Vanhala, P., Karhu, K., Tuomi, M., Björklöf, K., Fritze, H., & Liski, J. (2008). Temperature sensitivity of soil organic matter decomposition in southern and northern areas of the boreal forest zone. *Soil Biology and Biochemistry*, 40, 1758–1764.
- Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, 304, 1629–1633.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Table A.1. Table summarizing soil core methods across diverse ungulate exclosure experiments.

Table A.2. Literature summary of evidence in support (or not) for each concept that shows diverse qualitative effects (+: Positive, -: Negative, O: None) of ungulate herbivores on soil ecosystems.

Table A.3. Dates of initial and secondary visit for each site.

Table A.4. Dates soil processing and time sensitive lab procedures were completed for each site.

Table A.5. Data collected from each method and the level at which they were collected for each site.

Table A.6. Piecewise structural equation model results for the mineral soil horizon.

Table A.7. Linear mixed model results for direct impact of moose exclusion on soil temperature.

Figure A.1. Conceptual diagram showing predicted effects of disturbance and moose exclusion on components of maritime boreal forests aboveground and belowground.

Figure A.2. Exclosures in TNNP and Bunyan's Cover are 35 m × 35 m (n = 9) and the exclosure in Fox Marsh is 15 m × 15 m.

Figure A.3. Conceptual diagram outlining our methods for soil core collection and processing.

Figure A.4. Results of a piecewise structural equation model examining the impact of disturbance and moose exclusion on above and belowground components of maritime boreal forest on the mineral soil horizon.

How to cite this article: Swain, M., Leroux, S. J., & Buchkowski, R. (2023). Strong above-ground impacts of a non-native ungulate do not cascade to impact below-ground functioning in a boreal ecosystem. *Journal of Animal Ecology*, 92, 2016–2027. <https://doi.org/10.1111/1365-2656.13993>