

1 **Cervid exclusion alters boreal forest properties with little cascading impacts on soils**

2 Short title: *Cascading effects of moose exclusion*

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10 **Author contributions:** The study was planned by ALK, GA, EJS, SJW and JDMS. Field work was  
11 conducted by ALK, GA, AMAV, and JDMS. Lab work was conducted by ALK and AMAV. Statistical  
12 analyses were conducted by ALK, with significant input from JDMS. ALK wrote the manuscript with  
13 input from all co-authors.

14

15 **Abstract**

16 Large herbivores are capable of modifying entire ecosystems with a combination of direct (e.g.  
17 browsing/grazing, trampling, defecation) and indirect (e.g. affecting plant species composition that  
18 then alters soil properties) effects. With many ungulate populations increasing across the northern  
19 hemisphere it is important to develop a general theory for how these animals can be expected to  
20 impact their habitats. Here we present the results of an eight-year experimental exclusion of moose  
21 (*Alces alces*) from 15 recent boreal forest clear-cut sites in central Norway. We used standard  
22 univariate techniques to describe the treatment effect on multiple forest and soil properties and  
23 combined this with a multivariate Bayesian network structure learning approach to objectively assess

24 the potential mechanistic pathways for indirect effects on soils and soil fertility. We found that  
25 excluding moose had predictable direct effects, such as increasing the ratio of deciduous to  
26 coniferous tree biomass and the canopy cover and decreasing soil bulk density and temperature.  
27 However, we found no treatment effects on any measures of soil processes or quality  
28 (decomposition, nitrogen availability, C:N ratio, pH, nutrient stocks), and furthermore, we found only  
29 limited evidence that the direct effects had cascading (indirect) effects on soils. These findings  
30 oppose the commonly held belief that moose exclusion will increase soil fertility, but still highlights  
31 the strong ability of moose to directly modify forested ecosystems.

32 **Keywords:** *Alces alces*, Cervid, Boreal forest, Herbivory, Norway, Bayesian Network, nitrogen  
33 availability, tea bag index, carbon stocks

34

## 35 Introduction

36 Increasing cervid populations in many forests throughout northern Europe and America (Prins and  
37 Gordon 2008; Apollonio and others 2010) are expected to intensify their impact on critical ecosystem  
38 dynamics, such as successional patterns and nutrient cycling (Côté and others 2004). The moose (or  
39 Eurasian elk, *Alces alces*; including several sub-species) is the largest of the cervids and it has a similar  
40 and equally wide-ranging distribution as the boreal forest (Telfer 1984). They especially seek out  
41 early successional stands where browse is readily available (Bjørneraas and others 2011). As a  
42 consequence, habitat suitability for moose has increased across its range with the advent of clear-  
43 cutting as the main timber harvesting method (e.g. Axelsson and Östlund 2001), and this probably  
44 facilitated the recent rapid increase in Fennoscandian moose numbers after c. 1970 (Austrheim and  
45 others 2011).

46 Through their selective feeding on preferred (mostly deciduous) tree species (Hörnberg 2001;  
47 Månsson and others 2007), the moose and other large ungulate herbivores function as ecosystem  
48 engineers, shaping the very forests they inhabit (Pastor and Naiman 1992; Edenius and others 2002;

49 Kielland and others 2006; Speed and others 2013). Selective browsing by large ungulates in low-  
50 productivity ecosystems is hypothesised to accelerate forest succession by providing a competitive  
51 advantage to less preferred slow-growing climax species with recalcitrant and long-lived tissues  
52 (Davidson 1993; Bardgett and Wardle 2003; Wardle and others 2004). In the boreal forest, a  
53 herbivore-mediated deterioration in litter quality and quantity caused by an increased dominance of  
54 late successional conifer species (McInnes and others 1992) is associated with a deceleration in  
55 nutrient cycling (Pastor and others 1993; Ritchie and others 1998; Dufresne and others 2009). The  
56 positive effects on nutrient cycling from the input of moose dung and urine is not thought to be  
57 strong enough to cancel out the effect of litter type (Pastor and others 1993). Therefore, based on  
58 data from four c. 39 year old fenced exclosures, Pastor and others (1993) proposed that, in the long  
59 term, selective moose browsing in boreal forests can indirectly decrease soil fertility and forest  
60 productivity by altering the canopy composition.

61       There is growing awareness of the fundamental role soils play in underpinning several ecosystem  
62 services, therefore making soils a vital resource worthy of attention and protection (Blum 2005;  
63 Dominati and others 2010; Adhikari and Hartemink 2016). The impact of herbivores on soils has been  
64 the topic of numerous studies, but generalisations are lacking partly due to variation between sites in  
65 how they respond to herbivory (Wardle and others 2001), difficulties in elucidating the causality  
66 behind the observed herbivore-induced changes, and the presence of both direct and indirect effects  
67 (Wardle and others 2004).

68       With new statistical methods and increased sample sizes, the point about limited generalisations  
69 from herbivore studies have been addressed. Kardol and others (2014) analysed the effects of deer  
70 exclusion on soil properties at 26 sites in New Zealand, and how this had indirect effects on plant  
71 growth. This study had an explicit focus on describing the mechanistic basis behind the indirect  
72 effects and used as the model variables the difference between treatments (exclosure and open  
73 plots) at each site to fully account for the idiosyncrasies of site responses to herbivory (Wardle and  
74 others 2001). Such efforts represent an important step towards generality and a systems-approach

75 to studying ungulate-soil dynamics. Structural analyses aimed at revealing causality have been taken  
76 much further in closely related fields of study and study systems (Myerud and others 2008;  
77 Huffman and others 2009; Veen and others 2010; Laskurain and others 2013). As an example, Beguin  
78 and others (2011) applied both univariate tests and multivariate path analyses to evaluate the  
79 relative direct and indirect effects of deer browsing and soil disturbance on plant communities. This  
80 study found that even though deer browsing affected herbaceous plant richness when analysed  
81 directly as the single response variable, a multivariate path analysis showed that this effect was  
82 mediated by changes in the abundance of browsing tolerant taxa and this in turn was regulated by  
83 the presence of a browsing sensitive species. This study exemplifies how novel insights into rather  
84 complex causal pathways can be obtained from quite simple study designs with the use of structural  
85 analysis, forgoing the need for complex multiple-factorial experiments.

86 In this study from the boreal forest of central Norway, we analyse the effect of eight years of  
87 moose exclusion from 12 to 15 recent clear-cuts on multiple forest and soil properties using both  
88 univariate and multivariate techniques. Our main hypothesis was that moose exclusion would (H1)  
89 cause changes in plant species composition and physical forest properties which will cascade and  
90 further manifest themselves as increased soil fertility, as proposed by Pastor and others (1993).  
91 Based on previous studies we also aimed to test a subset of hypotheses, that moose exclusion will:  
92 (H2) decrease soil bulk density (Gass and Binkley 2011; Kardol and others 2014) and increase organic  
93 soil depth (Ellis and Leroux 2017) due to cessation of trampling; (H3) generally have a larger impact  
94 at productive compared to less productive sites (Mathisen and others 2010; Speed and others 2014),  
95 and; (H4) reduce soil temperatures due to increased shade (canopy cover) (Kielland and Bryant  
96 1998), causing a subsequent decrease in the decomposition rate of standardised litter (Kielland and  
97 others 1997) due to the positive relationship between temperature and decomposition rate (Zhang  
98 and others 2008).

## 99 Methods

### 100 Study design

101 Field work was conducted at 15 sites in recently clear-cut boreal forests in Trøndelag, central Norway  
102 (Figure 1; Table 1). At each site, two 20 × 20 m plots were chosen inside a homogenous area and  
103 randomly assigned to either the *exclosed* or *open* treatment. Fences were erected around the  
104 exclosed plots in 2008, 2-6 years following the clear-cutting, using 208 cm tall wire mesh solidly  
105 anchored by wooden poles, and an additional wire at 250 cm height was strung between the fence  
106 poles (Figure 2). The two plots were a minimum of 20 m apart to reduce any potential edge effects.  
107 The sites were selected to cover both pine (*Pinus sylvestris*) and spruce (*Picea abies*) forests over a  
108 wide productivity range. The sites are not known to have been artificially fertilized at any point, and  
109 we believe it unlikely that this has occurred. Most sites were planted following logging (see Table 1)  
110 and a few large trees were also left standing from before the logging. No soil preparation,  
111 scarification, thinning, or other silvicultural activities were performed, with the exception of the open  
112 plots at three of the sites (nr 9, 10, and 13 in Table 1) which were inadvertently thinned by forest  
113 managers in late 2015. These sites are removed from the analysis of forest structure, decomposition,  
114 soil temperature, and nutrient dynamics, but retained for the analysis of the remaining, less  
115 transient, forest properties (specified in Table 2).

116 Moose (*Alces alces*) densities are relatively high in this region, with metabolic biomass  
117 ranging from 28.92 to 102.11 kg km<sup>-2</sup> (Austrheim and others 2011), or about 0.48 to 1.86 moose km<sup>-2</sup>  
118 (Solberg and others 2012; Erling J. Solberg, *unpubl. data*). Domestic sheep and cattle on summer  
119 pasture, as well as wild red deer (*Cervus elaphus*), are also present in these areas, but at considerably  
120 lower densities. Roe deer (*Capreolus capreolus*) is often numerous, but make up a relatively low  
121 fraction of the total metabolic biomass. Rodents and hares are omnipresent, and unlike larger  
122 herbivores, they could freely enter the exclosures. See Speed and others (2013) for more information  
123 on field locations and herbivore densities.

## 124 **Biomass models and deciduous:coniferous biomass ratio**

125 A dataset containing tree heights and diameter at ground level recorded in permanent subplots since  
126 2009 (see Speed and others (2013) for details) was used as input for locally calibrated species specific  
127 biomass models to estimate above-ground biomass of individual trees for each year of the  
128 experiment. We calculated the ratio of deciduous to coniferous biomass (D:C biomass ratio) from the  
129 estimated standing aboveground tree biomass in 2016. See Extended Methods in the Supplementary  
130 Information for more details.

## 131 **Canopy Cover and Site Productivity Index**

132 Estimates of canopy cover were produced by using the Gap Light Analysis Mobile Application (Tichý  
133 2015). This application produces a modified canopy cover index (CCI) that ranges from 0-100% and  
134 which represent the fraction of a horizontal projection through the canopy which is covered by tree  
135 crowns. Forty images from different locations inside each plot were taken at 50 cm height during  
136 peak foliage in 2016 and were averaged to produce a single estimated value of CCI for each plot. We  
137 then characterised the productivity potential of each site by creating a compound productivity index  
138 consisting of summed standardised values (divided by max value) of the CCI and average annual  
139 biomass increments for the exclosed plots. Including CCI in the compound index was necessary  
140 because initial analyses revealed that, due to sampling error, annual biomass production alone was  
141 insufficient to characterise the sites in terms of productivity potential (see Extended Methods for  
142 more information).

## 143 **Soil temperature, decomposition, and nitrogen availability**

144 Three temperature loggers (HOBO Pendant® waterproof data logger; UA-001-64; Onset Computer  
145 Corporation, MA, USA) in each experimental plot were used to record soil temperature during the  
146 soil experiments in early spring and extended into peak growing season. Their location was 4 m away  
147 from the plot centre toward three of the plot corners (randomly chosen) were they were buried 5 cm  
148 into the soil (from the top of the organic layer). The loggers were programmed to record every 6

149 hours. Mean daily temperatures were averaged to give mean temperature between 15<sup>th</sup> June and  
150 25<sup>th</sup> July (canopies are fully developed in early-mid June) and temperature sums for the duration of  
151 both the decomposition and nitrogen (N) availability experiment (see below).

152 Relative measures of organic matter decomposition were evaluated using the Tea Bag Index  
153 (Keuskamp and others 2013). Pairs of Lipton green tea and Lipton rooibos tea were buried next to  
154 the temperature loggers in the early spring (April-May), a time when soil moisture is consistently high  
155 due to the recent snowmelt and nutrient runoff is probably at high levels (Muller 1978). They were  
156 retrieved after 90 days. The Tea Bag Index produces a decomposition rate  $k$  and a litter stabilisation  
157 factor  $S$  where a high  $S$  implies less complete decomposition.

158 Plant Root Simulating (PRS) probes (Western AG Innovations Inc, Saskatoon, Canada) were  
159 placed in the corners of a 1 × 1 m quadrat centred on the temperature loggers and used to measure  
160 inorganic N (ION) availability ( $\text{NO}_3$ ,  $\text{NH}_4$ , and total). The probes are 15 cm long plastic sticks fitted  
161 with an ion (either cation or anion) exchange resin which absorbs charged molecules (e.g.  $\text{NO}_3^-$  and  
162  $\text{NH}_4^+$ ) in the soil solution in a similar manner to how roots take up these nutrients. Pairs of cation and  
163 anion probes were inserted vertically into the top soil layers at the same time as the tea bags were  
164 deployed and retrieved after 49 to 92 days. Plastic cylinders of 10 cm diameter were driven into the  
165 soil around each probe pair in order to exclude roots which otherwise would compete with the  
166 probes for the same ions. Our measure therefore represents ION availability (rather than surplus),  
167 including any N released from the decomposition of the severed roots. Samples were shipped to  
168 Western AG Innovations Inc (Saskatoon, Canada) where  $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$  was determined  
169 colourimetrically using a flow injection analysis system. In addition, we calculated relative  
170 nitrification as  $\text{NO}_3$  divided by total ION. The three thinned sites were excluded from the analysis of  
171 temperature, decomposition and N availability. See the Extended Methods section for more details.

## 172 Soil core sampling and analysis

173 Soils were sampled from all 15 sites in April-May 2016, at the same time as the deployment of tea  
174 bags and PRS probes. Three subsamples (> 2 meters apart) were randomly chosen around the centre

175 of each experimental plot and later combined into a composite sample. The moss (later discarded)  
176 and litter layer was first removed inside a 10 cm diameter circle. A steel corer with a 2 cm diameter  
177 was used to extract a soil core from the same place as the litter sample was taken. The soil organic  
178 layer was visually separated from the mineral soil, which was collected in three 10 cm increments  
179 from the top down to 30 cm depth. The 20-30 cm fraction was not analysed further due to the  
180 prevalence of shallow soil and hence insufficient samples. The composite samples were analysed for  
181 total carbon (C) and N using a dry combustion method. Bulk density (i.e. soil compaction;  $\text{kg m}^{-3}$ ), C  
182 and N stocks ( $\text{kg m}^{-2}$ ) and concentrations ( $\text{kg kg}^{-1}$ ), were calculated for each soil layer, and pH was  
183 measured using standard procedures (see Extended Methods).

#### 184 **Data analyses**

185 All analyses were performed in R-Studio (v. 0.99.903; R version: 3.3.2 (R Core Team 2016)). Linear  
186 mixed effects models (Kuznetsova and others 2016) were used to look for any effect of herbivore  
187 exclusion, site productivity, and their interaction, on multiple aspects of the soil and soil processes,  
188 and D:C biomass ratio. To avoid circularity, a simplified productivity measure was used when  
189 analysing CCI. A random intercept was fitted for site to account for the paired study design. Model  
190 reduction was performed by using sequential likelihood ratio tests and main effects are reported as  
191 the results of likelihood ratio tests after adding (in-significant terms) or removing (significant terms)  
192 them from the minimum adequate model. Residuals were visually checked for normality and  
193 homoscedacity of variance within all levels of the explanatory variables, and response variables were  
194 transformed (log, square root) if model assumptions were violated. Pearson's correlations (Revelle  
195 2016) were used to look for associations between paired treatment differences in the response  
196 variables and Spearman's *rho* correlations were used to investigate the role of burial length, soil  
197 temperature, and precipitation sums on decomposition and N availability. See Extended Methods for  
198 more details.



## 199 Bayesian Network

200 To further analyse potential causal pathways of the soil responses to herbivore exclusion, we  
201 constructed a Gaussian Bayesian network using the *bnlearn*-package (Nagarajan and others 2013)  
202 with each node representing the treatment effect (exclosure minus open plot) of one variable, and  
203 therefore the arcs represent associations between node responses. Bayesian networks use a  
204 graphical model structure (called a directed acyclic graph) where arcs (or paths, or arrows) link  
205 together nodes representing either discrete, or as in this case, continuous Gaussian variables. Arcs  
206 can be '*selected*' from expert knowledge about the system and the underlying causalities, or '*learned*'  
207 automatically from a search algorithm. The resulting model structure can be helpful for visualising  
208 the studied system, but can also be used to infer and generalise beyond the available data; to guide  
209 and inspire the creation of novel hypotheses; identify knowledge gaps; and in some cases, strong  
210 support for the presence of arcs and combinations of arcs (pathways) can be used to infer about  
211 causality in a system (Nagarajan and others 2013). We used our knowledge about the ecological  
212 system in choosing to constrain the structure learning not to consider certain arcs going from  
213 dynamic soil processes (decomposition, nutrient dynamics, etc.) to more overarching variables  
214 concerning forest structure. Note that arcs were still allowed to go in the other direction. See  
215 Extended Methods for details and further justification. Although such bottom up controls on forest  
216 structure surely exist, we judge that within the temporal scale of this experiment, top-down control  
217 on soil processes dominate. For that reason we also chose to treat soil pH as a site characteristic and  
218 not a response variable, similar as with site productivity. These constrictions on the model allowed us  
219 to designate N stocks and availability as target nodes, which could be affected, through a series of  
220 cascading effects, by forest structure and tree species composition. The remaining model structure  
221 was learned from the local search algorithm tabu with the tabu list set to 10 to keep the algorithm  
222 from getting stuck in a local minimum. Arc strengths were computed as relative frequencies after  
223 bootstrapping the model structure with 10 000 iterations, and the average network was compiled

224 using a threshold for arcs strengths of 0.75. Conditional independence tests were performed for all  
225 serial connections using mutual information for Gaussian variables in the *ci.test*-function.

## 226 Results

### 227 Direct effects of moose exclusion

228 Eight years of moose exclusion significantly reduced soil temperatures and bulk density, and  
229 increased the soil organic depth, and the deciduous:coniferous (D:C) biomass ratio (Figure 3; Table  
230 2). Soil summer temperatures were 0.56°C ( $\pm$  0.1 SE) cooler inside the enclosures compared to open  
231 plots. The depth of the organic layer was 3.96 ( $\pm$  0.39 SE) and 5.07 ( $\pm$  0.40 SE) cm in the open and  
232 enclosed plots, respectively (n=15). The mean D:C biomass ratio was 0.64 ( $\pm$  0.15 SE; median 0.57)  
233 and 3.26 ( $\pm$  1.33 SE; median 1.77) in the open and enclosed plots respectively. There was a  
234 significant interaction effect of the exclusion treatment and site productivity (measured as annual  
235 tree production) on the canopy cover index (CCI). The change in CCI from the open to the enclosed  
236 plot was between -9 and +46% (mean 12.71  $\pm$  4.81 SE) with the largest effect being associated with  
237 more productive sites (Figures 2, S1).

### 238 Decomposition, pH, and total C and N

239 There was no effect of moose exclusion or site productivity on decomposition rate *k*, litter  
240 stabilisation factor *S*, ION availability (NO<sub>3</sub>, NH<sub>4</sub>, total ION), or relative nitrification (Table 2). *S*, but  
241 not *k*, was correlated with temperature and precipitation sums, with warmer and wetter microsite  
242 conditions being associated with more complete decomposition (Table S1). Nitrogen availability was  
243 correlated with burial length so we did not attempt to tease apart the unique contribution from  
244 temperature and precipitation (Table S1).

245 Moose exclusion did not affect the soil C or N stocks, concentrations, or the C:N ratio in the  
246 organic soil layer (Table 2), or the mineral soil (Table S2). Overall (N=30), total soil C and N stocks  
247 were 8.717 ( $\pm$ 0.43 SE) and 0.33 ( $\pm$ 0.02 SE) kg m<sup>-2</sup>, respectively. Soil N and C concentrations decreased  
248 markedly with depth (Figure S2). Soil pH varied between 4.0 and 4.7 and decreased strongly from the

249 litter towards the organic and the start of the mineral soil, before it again increased (Figure S2).  
250 Means of response variables for each browsing treatment are given in Table S3.

### 251 Site productivity and interactions with moose exclusion

252 In the mixed effects models, high site productivity was associated with high litter pH and total N  
253 stocks (including N in the litter and at 10-20 cm depth), as well as reduced C:N ratios of litter and  
254 organic soil (Tables 2, S3). In addition to the interaction effect on the CCI (see “Direct effects of  
255 moose exclusion”) there was also a significant interaction effect of ungulate exclusion and site  
256 productivity on total C and total N at 10-20 cm depth, as well as total N for the full depth (Table S2).  
257 This was due to a stronger positive relationship between productivity and the abovementioned  
258 variables for the open plots as compared to the exclosures (Figure S3).

### 259 Indirect effects of moose exclusion

260 Correlations between treatment effects (exclosed plots – open plots) are given in table 3.  
261 Significantly positive or negative correlations indicate that the variables were changing  
262 simultaneously or opposingly in response to herbivore exclusion, respectively. For example, the  
263 change in  $S$  and  $k$  in response to moose exclusion was positively correlated, indicating that induced  
264 rapid decomposition (high  $k$ ) was associated with less complete decomposition (high  $S$ ), and *vice*  
265 *versa*. Also, increases in canopy cover were correlated with increases in inorganic nitrogen  
266 availability, but changes in the D:C biomass ratio and soil bulk density was not significantly  
267 correlated with changes in any other variable.

268 The Bayesian network identified 6 arcs with strengths above 0.75, two of which were above  
269 0.95. By using the default significance threshold in the model averaging (0.501), the tabu algorithm  
270 identified a total of 44 arcs, so the model presented here can be considered as simplified and  
271 possibly conservative. However, by visually observing the relationships behind the arcs (using  
272 scatterplots) and by comparing with the correlation matrix (Table 3), we believe the default  
273 threshold level was too liberal in the inclusion of arcs. The arc strengths generally corresponded well

274 with the observed correlations between treatment effects in Table 3. The strongest arc was between  
275 site productivity and changes in canopy cover, reflecting the significant interaction effect of moose  
276 exclusion and site productivity. Note, however, that this arc introduces some circularity because  
277 canopy cover is a component of the productivity index. However, the interaction effect between site  
278 productivity and canopy cover was still present when this circularity was removed (Table 2; Figure  
279 S1). There was also a strong arc between changes in organic soil depth and organic soil N, and  
280 subsequently, conditional dependence was found for changes in total organic soil C and organic soil  
281 depth given organic soil N (mutual information (Gaussian) = 12.788,  $df=1$ ,  $P<0.001$ ). Organic soil N  
282 and C stocks was not linked to any other nodes, including the other factors used for calculating the  
283 stocks (bulk density and C and N concentrations).

284 A negative arc suggest that reduced soil temperatures as a result of herbivore exclusion was  
285 associated with increased N concentrations in the organic soil. No arcs were found to connect  
286 changes in inorganic N availability to changes in any of the other variables. Also, no arcs were found  
287 to connect changes in canopy cover to any downstream variables, even though the correlation  
288 analysis (Table 3) indicated a positive association with N availability.

## 289 Discussion

290 In this study we applied a multivariate systems-approach to increase our understanding of the  
291 mechanisms by which large herbivores can impact soils in forested ecosystems. Using a structural  
292 analysis based on a well-replicated, regional-scale herbivore exclosure experiment, we believe we  
293 have addressed some of the key aspects which have prevented generalisations from previous  
294 herbivore exclusion studies. There were strong and predicted effects of moose exclusion on  
295 aboveground forest properties (canopy cover, deciduous:coniferous biomass ratio) and physical soil  
296 properties (bulk density, soil temperature, organic soil depth), but no effect on belowground soil  
297 processes and quality (decomposition, mineralisation, C:N ratio, nutrient stock and availability).  
298 Further, and in disagreement with our main hypothesis H1, we found only limited evidence for

299 indirect effects of moose exclusion on soil fertility (or soil processes) mediated through the effect on  
300 canopy composition. This implies that the impact of moose in early successional forests is mainly  
301 through direct effects related to browsing, trampling, and defecation, and that changes in soil  
302 parameters are scarcer, smaller, or take longer to manifest.

303 Pastor and others (1993) suggested that the effect of long-term moose presence in boreal  
304 forests is to reduce soil fertility by causing a shift in the canopy composition away from palatable  
305 species with high quality litter, towards unpalatable, late-successional species with recalcitrant litter.  
306 This mechanism for reduced soil fertility is also supported by the strong association between  
307 palatability and decomposition rates (Cornelissen and others 1999). The concept of soil fertility is  
308 ambiguous (Patzel and others 2000), but for the context of boreal forest, known to be largely N  
309 limited (Tamm 1991), we define it based on N availability, including organic N as some boreal plant  
310 species are known to directly utilise amino acids (Nasholm and others 1998). Similar exclusion-  
311 induced increases in N availability as that found by Pastor and others (1993) have been reported  
312 from a range of high-latitude studies (Harrison and Bardgett 2004; Gass and Binkley 2011; Kardol and  
313 others 2014), and notably also from regenerating boreal clear-cut sites in Canada (Dufresne and  
314 others 2009). See also Andriuzzi and Wall (2017) for a meta-analysis. However, soils are not expected  
315 to change over short time frames (e.g. Relva and others 2014), and our eight years is considerably  
316 less than the c. 39 years of moose exclusion in Pastor and others (1993). On the other hand, our  
317 study differs by being conducted on recent clear-cut sites where the impact of moose can be more  
318 immediate compared to in mature forests (Tremblay and others 2007; Dufresne and others 2009). In  
319 any case, more time is needed to assess if the initial changes in plant species composition will have a  
320 greater impact on soil processes as the forest matures towards harvest age (60-100 years).

321 The observed increase in the ratio of deciduous to coniferous (D:C) biomass inside the fences  
322 (Figure 3) agrees with the increase in palatable species following moose exclusion found by others  
323 (McInnes and others 1992; Tremblay and others 2007; Hidding and others 2013; Ellis and Leroux  
324 2017). We attribute this to the direct effect of selective browsing of moose on deciduous species

325 (Hörnberg 2001; Månsson and others 2007). This effect of moose browsing is often perceived as  
326 causing an acceleration of the forest succession towards late successional, less palatable 'climax'  
327 species (e.g. Bardgett and Wardle 2003; Wardle and others 2004), but may also represent a shift in  
328 the successional trajectory away from a mixed canopy composition (Hidding and others 2013). A  
329 long time period is needed to assess whether the current tree species composition inside our  
330 exclosures represents a transient stage in succession towards conifer dominance, or if mixed forest  
331 stands can persist as a stable state in the absence of herbivores. No natural boreal forests systems  
332 known to us provide this insight, as large herbivores are so omnipotent around the northern  
333 hemisphere.

334         Even though moose exclusion did not directly increase the stocks or the concentrations of C  
335 or N in the organic soil (or the total soil), the observed increase in the organic soil depth was  
336 associated with increased C and N content in the organic soil layer. We believe this represents a  
337 plausible causal relationship: if soil depth increases, nutrient stocks also increase. Although it is  
338 unlikely to be a direct cause-and-effect relationship, a detectable reduction in soil temperatures  
339 inside the exclosures was associated with increased N concentrations in the organic layer. If this  
340 represents a trend that will continue, we may see a detectable increase in soil C and N with time. We  
341 speculate that increased litter fall from a canopy with a higher representation of deciduous trees  
342 could cause an increase in organic soil depth and subsequently soil C stocks. An essential and yet  
343 unknown aspect of this is whether increasing spruce dominance outside the exclosures can reverse  
344 this trend, as spruce forests have been shown to be very efficient at sequestering C (Vesterdal and  
345 others 2008). This needs to be addressed before understanding the full implications of herbivore  
346 removal on soil C storage. For early successional forest, however, our analysis suggests that changes  
347 in the depth of the organic soil is the major driver for changes in C and N stocks, and that changes in  
348 bulk density and in concentrations of C and N are less important. We may expect short-term  
349 herbivore exclusion not to influence soil C and N stocks as these are generally large pools that change  
350 only over longer time spans of decades or more (Stark and others 2000; Wardle and others 2001;

351 Köster and others 2015), but see Gass and Binkley (2011). Consistent with our study, no change in  
352 soil C stocks was also reported by Wardle and others (2001), who highlight the large variation  
353 between sites and their idiosyncratic response to herbivores.

354 Surprisingly, and in contrast to our second hypothesis H2, the observed and predicted  
355 decrease in soil bulk density with moose exclusion (Gass and Binkley 2011; Kardol and others 2014)  
356 was not correlated to the observed increase in soil organic depth, implying they were not changing  
357 due to the same single external factor, such as trampling. The relationship is probably more complex  
358 than originally assumed, and leaves one to speculate what other variable could explain the changes  
359 in soil physical properties, e.g. trampling and kicking by moose hoofs, litter quality and production,  
360 and pedoturbation.

361 Site productivity is an important moderator of moose impacts (Mathisen and others 2010;  
362 Speed and others 2014). Interaction effects between moose exclusion and site productivity were not  
363 common in our dataset. Most notably, canopy cover increased more inside the exclosures at  
364 productive sites compared to less productive sites (Figures 2, S1), and total N stocks had a stronger  
365 positive relationship with site productivity in the open plot as compared to the exclosures (Figure S3).  
366 However, our productivity gradient was substantial, going from poor pine sites to rich spruce sites  
367 with annual biomass increments inside the exclosures ranging from close to zero to  $\sim 15000 \text{ kg ha}^{-1}$   
368 (Figure EM2), so more, and stronger, interaction effects were expected. Note, however, that the  
369 three thinned sites that were excluded from several of the analyses were all among the six most  
370 productive sites.

371 In initial support of hypothesis 4, moose exclusion lead to increased canopy cover and  
372 reduced summer soil temperatures. Kielland and Bryant (1998) found that excluding moose from  
373 boreal floodplain sites caused soils to become wetter and cooler and attributed this to the observed  
374 decrease in light intensity (indicating increased canopy cover). We tested the association of the  
375 effect of moose exclusion on soil temperature against the effect on canopy cover and surprisingly  
376 failed to come to the same conclusion: the correlation was only marginal, and no arcs between the

377 two variables were identified in the Bayesian network. This may serve to highlight an important  
378 weakness in the statistical power of this study, arising from differences in scale: all variables in the  
379 Bayesian network are means for each plot, but soil temperature (and likely other soil variables as  
380 well, like decomposition and N availability) responds to micro-environmental factors at an even  
381 smaller scale. Still, if canopy cover was the only driver for changes in soil temperatures, we believe  
382 the relationship would appear significant in our model. This therefore raises the question of what  
383 other important drivers exists for herbivore-induced changes in soil temperature. One explanation is  
384 that changes in the field-layer vegetation cover cancels out the effect of the tree canopies. Future  
385 studies are needed to investigate this possibility. Note also that this discussion revolves around  
386 summer temperatures, but that important winter processes (e.g. Sulkava and Huhta 2003; Kielland  
387 and others 2006) are also driven by temperature. In winter, soil temperatures are largely regulated  
388 by snow depth, which could potentially be indirectly affected by chronic herbivory. Our impression  
389 from multiple field rounds in early springtime, however, does not indicate different melt-out times  
390 between open and exclosed treatments.

391         Also contrary to hypothesis 4, we found that decomposition rate  $k$  of standardised litter was  
392 not affected directly, nor indirectly, by moose exclusion. This agrees with Ellis and Leroux (2017), but  
393 is in contrast to Kielland and others (1997) who found a decrease in decomposition rate of  
394 standardised litter (cellulose) inside herbivore exclusion fences. They attributed this to physical  
395 factors, of which reduced soil temperature is perhaps the most important (see Yuste and others  
396 2007). A possible explanation for the lack of treatment effect on decomposition rate in our study is  
397 that changes in  $k$  due to temperature are offset by possibly increased microbial activity inside the  
398 exclosures due to increased litter quality and/or litter quantity (Kuzyakov and others 2000), leading  
399 to no net change. Alternatively, the spatial variation in the soil biotic and abiotic conditions are so  
400 great that our sampling effort was insufficient. The latter is supported by the relatively low intraclass  
401 correlation coefficients for the random variable site (Table 2) which indicate that most of the  
402 variation is at an even smaller spatial scale than site (i.e. between subplots).



403           We found no change in soil C:N ratios, an important soil quality indicator, as a result of  
404 moose exclusion. A low ratio indicates less microbial immobilisation and lower nitrogen limitations of  
405 plant growth, and as predicted, the C:N ratio of the organic soil was negatively correlated to  
406 productivity at our sites. No change in the soil C:N ratio is frequently reported in herbivore exclusion  
407 studies (Wardle and others 2001; Harrison and Bardgett 2004; Stark and others 2010; Gass and  
408 Binkley 2011). Soil C:N might change as a result of litter quality. For example, a reduction in foliar C:N  
409 ratios within a species can occur as a response to browsing (e.g. Kielland and others 1997). Also, litter  
410 C:N ratios can change due to a species compositional change towards deciduous species with lower  
411 C:N ratios compared to coniferous species (Vesterdal and others 2008; Strand and others 2016), but  
412 see Persson and others (2005).

413           To conclude, this study was novel in that it used a Bayesian network approach in addition to  
414 standard univariate techniques to investigate and conceptualise the mechanistic pathways for the  
415 indirect effects of herbivore exclusion on soils, with site-level replication that fully accounts for the  
416 idiosyncratic responses of sites to herbivory reduction. We found that excluding moose for eight  
417 years from recent boreal forest clear-cuts led to strong and predictable effects on multiple forest  
418 properties, including canopy composition, but that these effects did not cascade and manifest  
419 themselves as observable differences in soil properties. We suggest that the direct effects on tree  
420 species composition observed after eight years of moose exclusion will continue to drive a diverging  
421 successional trajectory towards a higher number of mature deciduous trees. Since larger trees  
422 produce higher litter quantities than smaller trees, one can expect the role of species composition in  
423 driving soil microbial processes to increase with time. Therefore, indirect effects of moose on soil  
424 processes should also increase with time, consistent with the findings of Pastor and others (1993).  
425 Still, understanding herbivore impacts during early succession is important due to the large areas of  
426 boreal forest that are of a young age as an effect of past and present forestry (Axelsson and Östlund  
427 2001; Granhus and others 2012) and the ability of large-herbivores to induce alternative successional  
428 trajectories following logging. Finally, we have demonstrated that soil fertility or quality is not

429 strongly affected by browsing in the short-term, but the strong direct effects of herbivore exclusion  
430 found in this study still highlights the ability of large herbivores to modify forested ecosystems.

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440

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598

## 599 **Figures**

600 Figure 1. Map of field site locations in Trøndelag, central Norway. The numbers refer to site numbers  
601 in Table 1.

602



603 Figure 2. Photographs of the fences used to keep ungulate herbivores out of the enclosed  
604 treatments. Picture A is from site 8 (Table 1; second most productive site) taken 16 June 2016  
605 (Photo: Audun Hageskal), and picture B is from a site 7 (second least productive) taken 28 April 2016  
606 (Photo: Anders L. Kolstad). Notice the large difference in deciduous biomass arising from the  
607 cessation of browsing at the productive site (A), and the two large pines left standing inside the fence  
608 (B) as remnants from before the clear-cutting.

609

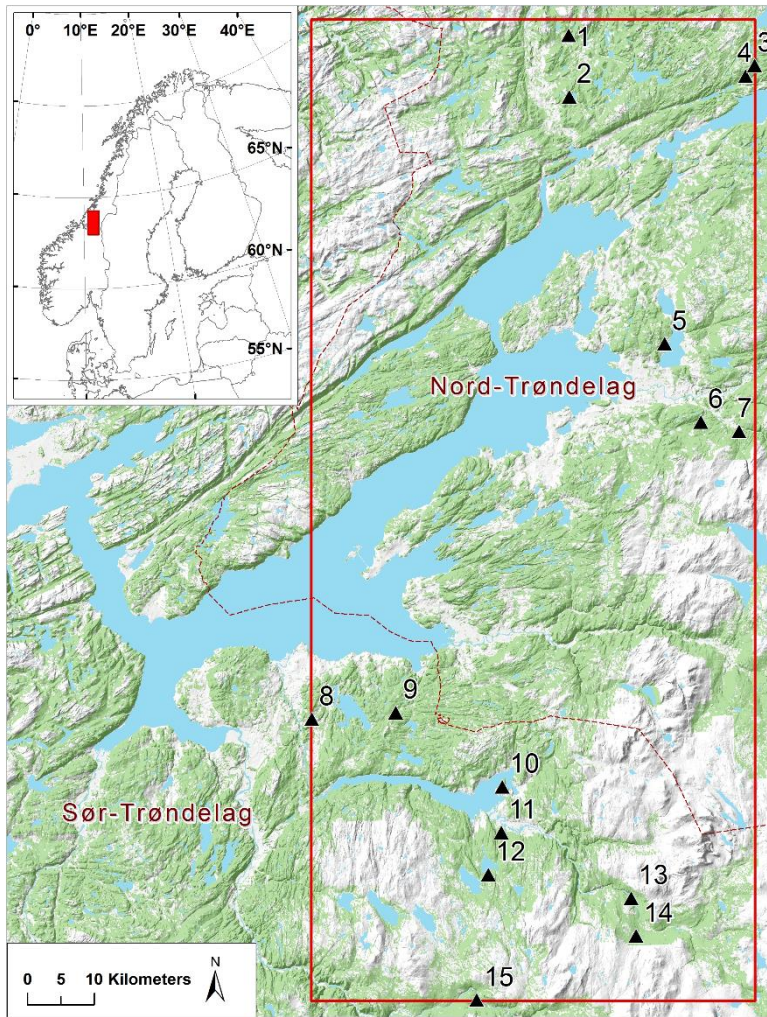
610 Figure 3. Treatment effect (8 years of ungulate exclusion) on selected ecosystem properties at 12-15  
611 boreal forest clear-cut sites. Positive values (above the dashed line) indicate that the measured value  
612 for that property was higher inside the ungulate enclosure compared to outside. Shaded boxes  
613 indicate that the treatment effect was statistically significant. Data points are unique sites and are  
614 plotted as circles. Boxes represent the interquartile ranges (IQR) and are plotted with the median  
615 (solid line) and mean (cross). Whiskers are maximum 1.5 IQR. The two highest values in the box for  
616 D:C biomass ratio come from sites 5 and 7 (Table 1).

617

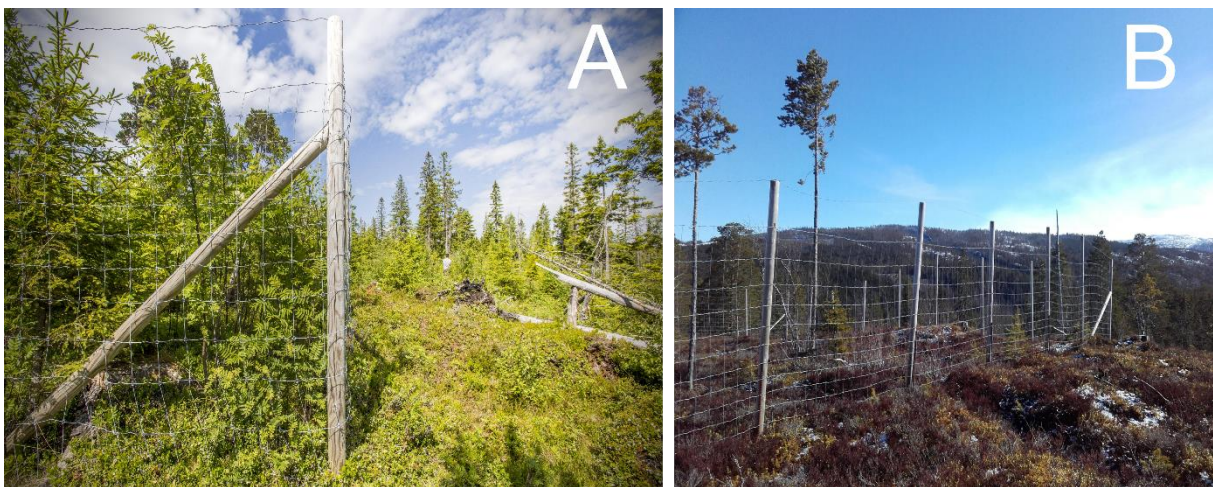
618 Fig. 4. Gaussian Bayesian network where each node is a treatment effect (*enclosure-open plot*;  $n=12$ ),  
619 except for Productivity Index and soil pH (of the organic soil) which are site characterising variables  
620 (same value for both treatments). Shaded nodes indicate a significant effect of moose exclusion in  
621 the direction of the arrow, as inferred from mixed effects models (Table 2). Arcs between nodes  
622 represent either negative (dashed lines) or positive (solid) causal relationships inferred through the  
623 network model. Numbers refers to arcs strengths (relative frequencies of the presence of an arc after  
624 1000 bootstrap iterations). Only arcs with strengths above 0.75 are plotted and arcs with strengths  
625 above 0.9 are thicker than the rest. The box encompasses variables associated with soil processes,  
626 and nodes above the box are related forest properties hypothesised to influence the soil. The lower  
627 part of the soil processes box include total and inorganic N thought to be closely related to soil

628 fertility in boreal forest soils which are generally N limited. Square brackets refer to concentrations. A  
629 number of constraints were put on the model. Notably, nodes inside the Soil Processes Box were not  
630 allowed to affect nodes outside the box (see Extended methods for full list and justification of  
631 constraints).

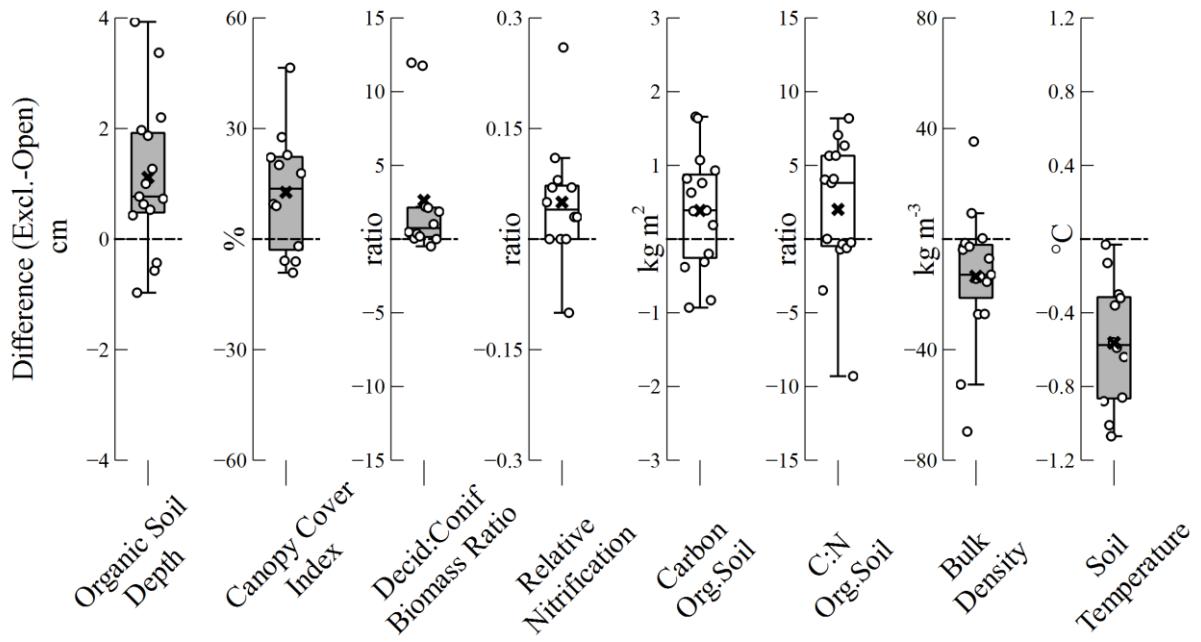
632



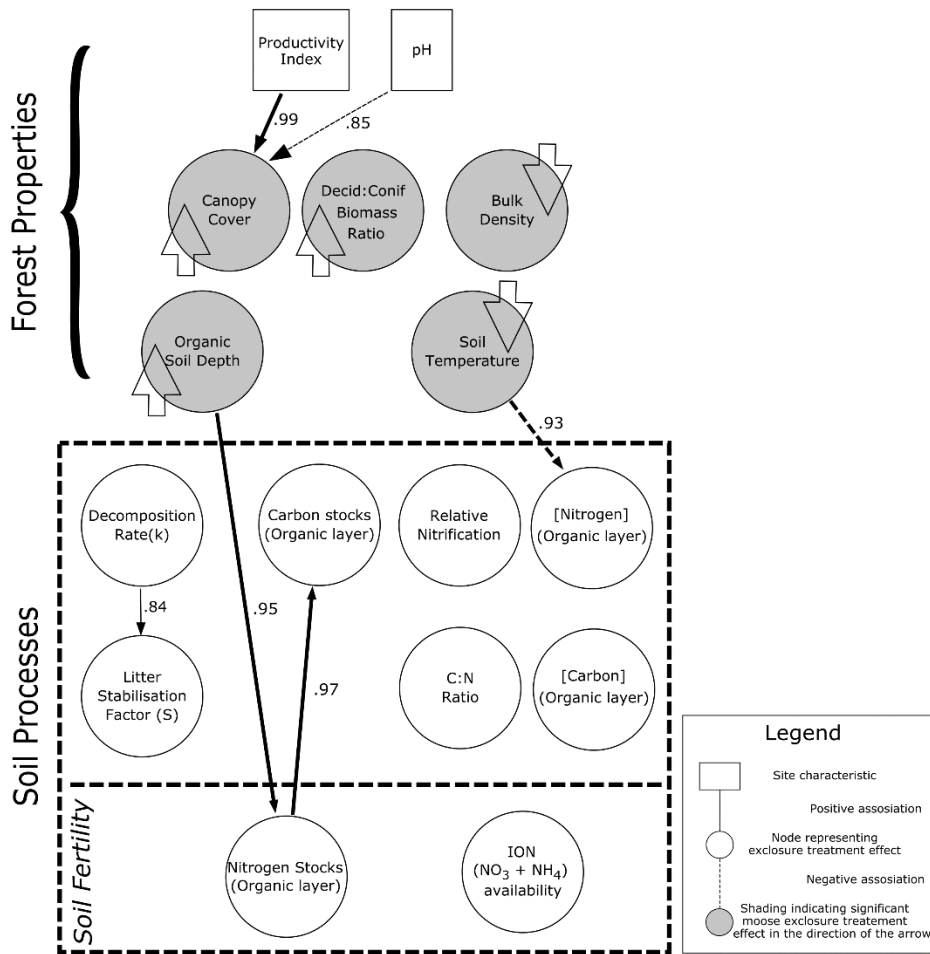
634  
635 Figure 1  
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638 Figure 2



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640 Figure 3  
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643 Figure 4

644 **Tables**

645 Table 1. Characteristics of 15 field sites in Trøndelag, central Norway. Site numbers correspond with  
646 the labels in Figure 1.

647

648 Table 2. Results of linear mixed effects models testing the effect of moose exclusion and site  
649 productivity on 26 ecosystem properties. Main effects are reported as results from likelihood ratio  
650 tests comparing against a minimum adequate model. Significant parameters are in bold ( $\alpha=0.05$ ).  
651 Arrows indicate the direction of change. Square brackets indicate concentrations.

652

653 Table 3. Correlation matrix (Pearson's  $r$ ) of the treatment effects (exclosure-open plot;  $n=12$ ) of  
654 response variables analysed in response to ungulate exclusion. Significant correlations ( $\alpha=0.05$ ) are in  
655 bold. No p-value adjustments are made. Square brackets indicate concentrations.

656

657

658 Table 1.

Site number	Clear-cut (year)	Species planted after clear-cut	Elevation (m a.s.l.)	Productivity Index <sup>b</sup>
1	2004	Spruce	123	1.4
2	2006	Spruce	291	0.7
3	2005	Spruce	252	0.8
4	2004	Spruce	158	0.9
5	2006	Spruce	127	0.4
6	2003	Spruce	202	1.8
7	2005	Pine	229	0.2
8	2002	Spruce and Pine	237	1.9
9 <sup>a</sup>	2002	Spruce and Pine	247	1.4
10 <sup>a</sup>	2004	Spruce	184	1.9
11	2002	None	311	0.5
12	2003	Spruce	379	0.9
13 <sup>a</sup>	2005	Spruce	298	1.3
14	2005	Spruce	429	1.0
15	2005	None	286	~0.0

<sup>a</sup> The control plot was inadvertently thinned in 2015 and so the site is excluded from all analysis except those of soil C and N stocks and concentrations, C:N ratio, and bulk density. <sup>b</sup> More productive sites have a greater productivity index value. See methods for details of the calculation of the productivity index. a.s.l. = above sea level.

659

660

661 Table 2.

		# Obs.	# Sites	Moose Exclusion		Productivity Index	Interaction Effect	ICC
D:C biomass ratio	Log	24	12	$\chi^2_{(1)}=4.9083$ <b>P = 0.0267</b>	↑	$\chi^2_{(1)} = 0.3582$ <i>P = 0.5495</i>		Site: 0.4654
Bulk density <sub>organic</sub>		30	15	$\chi^2_{(1)}=4.1789$ <b>P = 0.0409</b>	↓	$\chi^2_{(1)}=1.3629$ <i>P = 0.2430</i>		Site: 0.9070
Canopy Cover Index		24 <sup>a</sup>	12				$\chi^2_{(1)} = 6.1764$ <b>P = 0.0130<sup>b</sup></b>	Site: 0.2536
Organic soil depth		30	15	$\chi^2_{(1)} = 8.0271$ <b>P = 0.0046</b>	↑	$\chi^2_{(1)} = 0.2425$ <i>P = 0.6224</i>		Site: 0.5966
Soil temp		71	12	$\chi^2_{(1)}=12.547$ <b>P = 0.0004</b>	↓	$\chi^2_{(1)}=2.1967$ <i>P = 0.1383</i>		Site: 0.4285
S		66	12	$\chi^2_{(1)}=0.9481$ <i>P = 0.3302</i>		$\chi^2_{(1)}=3.6761$ <i>P = 0.0552</i>	(↑)	Site: 0.3398
k	Log	66	12	$\chi^2_{(1)}=0.2162$ <i>P = 0.642</i>		$\chi^2_{(1)}=3.1221$ <i>P = 0.0772</i>		Site: 0.1182
NO <sub>3</sub> availability	Log	24 <sup>a</sup>	12	$\chi^2_{(1)}=0.2657$ <i>P = 0.6062</i>		$\chi^2_{(1)}=1.2876$ <i>P = 0.2565</i>		Site: 0.8694
NH <sub>4</sub> availability	Log	72	12	$\chi^2_{(1)}=0.0501$ <i>P = 0.9230</i>		$\chi^2_{(1)}=0.1205$ <i>P = 0.7285</i>		Site: 0.4254
Total ION	Log	72	12	$\chi^2_{(1)}=0.5241$ <i>P = 0.4691</i>		$\chi^2_{(1)}=0.0639$ <i>P = 0.8004</i>		Site: 0.2626
Rel. Nitrification		24 <sup>a</sup>	12	$\chi^2_{(1)}=3.2997$ <i>P = 0.0693</i>	(↑)	$\chi^2_{(1)}=0.6134$ <i>P = 0.4335</i>		Site: 0.9012
C stocks <sub>organic</sub>		30	15	$\chi^2_{(1)}=3.3581$ <i>P = 0.0669</i>	(↑)	$\chi^2_{(1)}=0.8891$ <i>P = 0.3457</i>		Site: 0.2565
N stocks <sub>organic</sub>		30	15	$\chi^2_{(1)}=1.7298$ <i>P = 0.1884</i>		$\chi^2_{(1)}=1.0296$ <i>P = 0.3102</i>		Site: 0.4607
[Nitrogen] <sub>organic</sub>		30	15	$\chi^2_{(1)} = 0.1465$ <i>P = 0.7019</i>		$\chi^2_{(1)}=0.5949$ <i>P = 0.4405</i>		Site: 0.7989
[Carbon] <sub>organic</sub>		30	15	$\chi^2_{(1)}=1.2475$ <i>P = 0.2640</i>		$\chi^2_{(1)}=2.2266$ <i>P = 0.1357</i>		Site: 0.8199
C:N <sub>organic</sub>		30	15	$\chi^2_{(1)}=2.6992$ <i>P = 0.1004</i>		$\chi^2_{(1)}=13.575$ <b>P = 0.0002</b>	↓	Site: 0.4759
pH <sub>organic</sub>		30	15	$\chi^2_{(1)}=0.0170$ <i>P = 0.8964</i>		$\chi^2_{(1)}=1.6974$ <i>P = 0.1926</i>		Site: 0.5410

<sup>a</sup>Variable was averaged to give a single value for each plot, thus normalising the model residuals. <sup>b</sup>A simplified site productivity measure was used to avoid circularity (see Methods). D:C = deciduous : coniferous; S = litter stabilisation factor; k = decomposition rate; ION = inorganic nitrogen; ICC = intraclass correlation coefficient.

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663 Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Productivity Index	1															
2 D:C Biomass Ratio	-0.4	1														
3 Bulk Density	-0.56	0.35	1													
4 Canopy Cover Index	<b>0.71</b>	-0.19	-0.08	1												
5 Organic Soil Depth	-0.19	0.37	0.15	0.04	1											
6 Soil Temperature <sup>a</sup>	-0.41	0.38	0.45	-0.37	0.06	1										
7 Nitrogen Stocks (organic layer)	-0.11	0.21	0.27	0.23	<b>0.83</b>	-0.33	1									
8 Carbon Stocks (organic layer)	-0.12	0.42	0.33	0.3	<b>0.84</b>	-0.19	<b>0.94</b>	1								
9 [Nitrogen] (organic layer)	0.14	-0.20	0.31	0.32	0.23	<b>-0.89</b>	0.54	0.44	1							
10 [Carbon] (organic layer)	0.17	0.05	-0.05	0.44	0.21	<b>-0.64</b>	0.50	<b>0.58</b>	<b>0.74</b>	1						
11 C:N	0.18	0.36	0.11	0.19	-0.08	0.30	-0.15	0.1	-0.32	0.36	1					
12 Relative Nitrification	0.26	-0.24	0.24	0.42	-0.09	-0.22	0.27	0.15	0.08	0	-0.15	1				
13 k	0.1	0.18	0.3	0.15	0.47	0.27	0.38	0.35	-0.23	-0.27	-0.13	0.04	1			
14 S	0.2	-0.03	0.02	-0.05	-0.05	0.45	-0.3	-0.31	-0.56	<b>-0.60</b>	-0.06	-0.26	<b>0.75</b>	1		
15 pH (organic layer)	-0.37	-0.53	-0.07	-0.49	0.07	0.19	-0.11	-0.32	-0.10	-0.52	<b>-0.65</b>	-0.13	0.02	0.18	1	
16 Inorganic Nitrogen availability	0.07	-0.26	0.21	<b>0.61</b>	0.26	-0.27	0.41	0.44	0.49	<b>0.58</b>	0.02	0.03	0.09	-0.17	-0.01	1

<sup>a</sup> Soil temperature is the mean between 15<sup>th</sup> June and 25<sup>th</sup> July. D:C = deciduous : coniferous; S = litter stabilisation factor; k = decomposition rate

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