# Deer slow down litter decomposition by reducing litter quality in a temperate forest

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## Abstract

In temperate forest ecosystems, the role of deer in litter decomposition, a key nutrient cycling process, remains debated. Deer may modify the decomposition process by affecting plant cover and thus modifying litter abundance. They can also alter litter quality through differential browsing and affect decomposer ability by changing soil abiotic properties and the nature of decomposer communities. We used two litterbag experiments in a quasi-experimental situation resulting from the introduction of Sitka black-tailed deer *Odocoileus odocoileus sitkensis* on forested islands of Haida Gwaii (Canada). We investigated the effects of deer on decomposition through their impacts on litter quality and on decomposer ability. After one year, the effect of deer on litter quality resulted in a lower rate of mass loss in litter from litterbags. This mass loss mainly reflected a 21 and 38 % lower rate of carbon (C) and nitrogen (N) loss, respectively. Presence of deer resulted in lower decomposer ability for the rate of carbon loss, but not for nitrogen loss. The level of C loss after one year was 5% higher for litter decomposing on an island without deer. But the change in the rate of carbon loss explained by the effect of deer on decomposer ability was outweighed by the effect deer had on litter quality. Additional effects of deer on the decomposition process through feces deposition were significant but minor. These results question the role the large increase in deer populations observed in temperate forests at continental scales may play in broad scale patterns of C and N cycling.

## Introduction

*Deer and the functioning of temperate forests*

Until recently, the role of large herbivores in nutrient cycling processes has been relatively neglected (Tanentzap & Coomes, 2012). In temperate forests from Europe and Eastern North America, dominated by coniferous or by broadleaved trees, this may be partly because ungulates, essentially deer, became largely missing as a result of hunting and/or loss of favorable land cover (McShea, Underwood, & Rappole, 1997; Apollonio, Andersen, & Putman, 2010). The extirpation of their natural predators, followed in the second part of the 20$^{th}$ century, on both continents, by changes in hunting regulations and in land-uses, such as increased planting of winter crops by agriculture or, in some areas, farm abandonment and reversion to forests (see e.g. Côté, Rooney, Tremblay, Dussault, & Waller, 2004; Fuller & Gill, 2001; Milner et al., 2006) resulted in a dramatic rebound in deer populations that brought them back to the forefront of ecological thinking (Terborgh & Estes, 2013). The initial emphasis of research was on the consequences of deer recovery on forest vegetation, beginning with impacts on tree regeneration and growth (Gill, 1992), and, more recently, on aboveground understory community functioning (Horsley, Stout, & DeCalesta, 2003; Royo, Collins, Adams, Kirschbaum, & Carson, 2010), including cascading effects on different segments of the trophic network [invertebrates, birds (e.g. Chollet & Martin, 2013; Foster, Barton, & Lindenmayer, 2014)].

While our grasp of deer effects on forest aboveground communities has dramatically improved, their repercussions on belowground patterns and processes are still insufficiently understood (Bardgett & Wardle, 2003; Hobbie & Villéger, 2015). These belowground effects will be partly mediated by the effects deer have on litter decomposition and its pivotal role at the interface between aboveground primary production and belowground processes (Chapin, Matson, & Vitousek, 2011). In temperate forest ecosystems, contrary to grasslands or boreal forest, there are still only a few studies on how large herbivores affect litter decomposition.

*Deer and litter decomposition*

Deer may modify belowground processes by affecting two of the main parameters that control decomposition: litter quality and decomposer ability (Prescott, 2010). Through plant removal, combined with selective foraging, deer modify plant community composition, plant stoichiometry, as well as the relative contribution of canopy and understory vegetation to litter composition (Côté et al., 2004). These changes in litter quantity and quality will affect decomposition processes and nutrient cycling (Bardgett & Wardle, 2003) .

Deer are also susceptible to modify belowground processes through the alteration of decomposer ability. This alteration can result from changes in edaphic properties such as increased soil temperature and salinity that follow exposure of bare soil after vegetation removal by browsing, or from soil compaction caused by trampling and its effects on soil water and oxygen content (Schrama et al., 2013). Deer also release dung and urine, a source of organic matter more easily decomposable than recalcitrant plant litter, and a source of inorganic nitrogen for soil decomposers that enhances their development (Sitters et al., 2017). These effects may affect the structure and functioning of decomposer communities [soil fauna (Andriuzzi & Wall, 2017) and microorganisms (Cline, Zak, Upchurch, Freedman, & Peschel, 2017; Eldridge et al., 2017)] with effects on the rate of litter decomposition (Handa et al., 2014).

Recent evidence indicate that decomposition occurs more rapidly when litter is placed under the plant species from which it originated (Gholz, Wedin, Smitherman, Harmon, & Parton, 2000; Ayres et al., 2009; Austin, Vivanco, González-Arzac, & Pérez, 2014). This “home-field advantage” (HFA) is attributed to decomposer specialization. Home-field advantage may compensate the aforementioned potential changes in decomposition caused by deer. But studies explicitly testing this hypothesis are scarce, and provided contrasting results (see Olofsson & Oksanen, 2002; Penner & Frank, 2018).

There is recognition of the multiplicity of pathways through which deer may affect litter decomposition (see Bardgett & Wardle 2003 for a conceptual model), but our knowledge is mainly

based on the independent study of each pathway, which led to apparent contradictions in results. To better identify the mechanisms behind the effect of deer on litter decomposition we designed a study that combined approaches able to disentangle the relative effects of these different pathways on the process.

*A quasi-experimental context*

This study is part of a long term effort to use the introduction of Sitka black-tailed deer *Odocoileus odocoileus sitkensis* at the end of the 19th century to the Haida Gwaii archipelago (British Columbia, Canada, Golumbia, Bland, Morre, & Bartier, 2008) as an unplanned experiment on trophic interactions. Native to the coastal forests of British Columbia, Sitka black-tailed deer colonized most, but not all, islands, resulting in a quasi-experimental situation with, side by side, islands colonized by deer, and a limited number of small isolated islands never colonized. All these islands are forested. The occurrence of reference islands without deer made it possible to demonstrate that, on islands where deer were present, independent of island size, deer herbivory was the main factor structuring plant, invertebrate and songbird communities, overwhelming other biotic or abiotic factors (i.e. island area, soil and micro-habitat diversity (Table S1 in Supporting Information) and Chollet, Baltzinger, Saout, & Martin, 2013; Gaston, Stockton, & Smith, 2006; Martin & Baltzinger, 2002; Martin, Stockton, Allombert, & Gaston, 2010). Recurrent experimental culls on some islands allowed to document the potential for recovery of the aboveground vegetation and songbirds (Chollet et al., 2016). As a result, islands can be segregated today into three categories of browsing histories and their associated vegetation patterns. Islands without deer, which are characterized by a diverse and lush understory vegetation dominated by broad leaved shrubs and ferns, producing a diverse and abundant litter. Islands where deer have been present for over 70 years, which are characterized by an open understory dominated by bryophytes where litter is dominated by conifer leaves (Martin et al., 2010; Stockton, Allombert, Gaston, & Martin, 2005). Finally, islands where deer have also been present for over 70 years but that have been subjected to recurrent deer culls over the past two

decades. Their understory is characterized by an intermediate cover of vegetation (Chollet et al., 2016).

We used this extensive aboveground knowledge to design litterbag experiments based on these three browsing treatments, deer absent (no browsing, our reference), deer culled (intermediate browsing), and deer present (severe browsing), to analyze how the prolonged presence of abundant deer affected litter decomposition.

First, we assessed the effect of deer presence on litter decomposition at the scale of an island through a reciprocal litterbag translocation experiment involving litter representative of the three browsing treatments: “no”, intermediate” and “severe” browsing. The objective was to discriminate between the effects deer have on litter decomposition rate, either through their impact on litter quality or through their effect on decomposer ability (including effects on soil properties and on decomposer community composition), and this by explicitly including an assessment of home-field advantage by using the approach proposed by Keiser, Keiser, Strickland, & Bradford (2014). This approach allows to assess home-field advantage through the quantification of its role in decomposition rate relative to the role of litter quality per se (i.e. irrespective of the decomposition environment), and relative to the role of decomposer ability per se (i.e. irrespective of litter quality).

Second, we assessed how the deposition of high quality litter in the form of feces, affected the rate of litter decomposition at a narrow local scale by adding deer feces in a set of litterbags.

We predicted 1) that decomposition of litter collected from the deer-free island would be faster than decomposition of the litter collected from islands with deer (the effect of litter quality change); 2) that, in absence of home-field advantage, decomposition rates on the islands with deer would be higher than on the islands without deer due to an increase in decomposer ability in microbial communities in response to more recalcitrant litter (effect of change in decomposer ability); 3) that, presence of deer excrement would locally speed up the decomposition of plant litter; 4) that, the decomposition pattern observed on the islands where deer were culled should fall in between those observed on the islands with and without deer.

## Material and Method

*Study sites and plot selection*

Haida Gwaii is characterized by a humid temperate-oceanic climate, with mean annual temperature of 8.5°C and precipitation that varies greatly from 1,350 mm on the east coast, where this study took place, to 7,000 mm on the west coast (Banner et al., 2014). The archipelago is covered by temperate rainforests dominated, at low elevation, by western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and Sitka spruce (*Picea sitchensis*). The selected study sites belonged all to the Coastal Western Hemlock Wet Hypermaritime subzone [Biogeoclimatic Ecosystem Classification, code CWHwh1, (British Columbia Ministry of Forests, Lands, and Natural Resource Operations, 2010)] which covers 49% the archipelago, and ranges from sea-level to 350m in elevation (Banner et al., 2014). The bedrock geology of the selected study sites was volcanic and sedimentary, together with intrusions of granitic rock (Sutherland Brown, 1968). The soil type was organic and classified into the Folisol order (Soil Classification Working Group / Groupe de travail sur la classification des sols, 1998).

We selected three islands in Laskeek Bay (52°53'12"N, 131°35'20"W, Fig. S1 in Supporting Information). We chose sampling and experimental sites with similar parent material, and that were representative of the patterns of deer impacts we documented at the scale of the archipelago (Chollet, Bergman, Gaston, & Martin, 2015; Martin et al., 2010) (see Table S1 in in Supporting Information for a synthesis of previous studies). The three islands were Low Island, 9.6 ha, that had never been colonized by deer, Louise Island, 25,000 ha, that has had deer for over 70 years (Vila, Torre, Guibal, & Martin, 2004) and had a current deer density estimated at 30 deer / km², and Reef Island, 249 ha, that had also been colonized by deer more than 70 years ago, but its deer population had been regularly culled between 1997 and 2010. At the time of study Reef Island had a deer population density estimated at about 15 deer / km² and a partially recovered understory vegetation (Chollet et al., 2016). Low, Reef and Louise Islands were therefore representative of three distinct deer herbivory treatments: absence of current or past browsing, intermediate browsing pressure,

176 and severe browsing pressure, respectively. Our emphasis on selecting sites similar in parent material
177 and similar in forest types prevented us to control also for island size. To take this into account we
178 selected all sampling plots in the coastal area on the three islands. On each island we established
179 fifteen 10 m x 10 m forest interior plots, leading to a total of 45 plots. Adjacent plots were separated
180 by at least 100 m.

181 *Above and belowground characteristics in relation to deer presence*

182 In each plot we sampled the vegetation by estimating the percent cover of vascular plants and
183 bryophytes using the Londo scale (Londo, 1976). We measured soil bulk density at the surface of the
184 soil with five replicate measures per plot. For this, we collected soil with a 5.4 cm depth x 4.1 cm
185 diameter (71.29 cm3) copper core hammered into the soil using a mallet. We took care to not change
186 the structure of the soil while sampling. We removed any coarse woody debris from core samples
187 and subtracted their volume from the volume of the core. We then dried soil at 105°C for 24h to
188 obtain a value for bulk density expressed as g of dried soil per $cm^3$ of fresh soil.
189 We used data on soil pH, C:N and organic horizon depth collected in the course of a sister study in
190 plots located in the same area on these same islands (Maillard et al. unpublished data). This data was
191 collected from five plots on Low Island, five plots on Louise Island and six plots on Reef Island. We
192 sampled soil within these plots with a 2.5 cm diameter x 30 cm depth core collecting approximately
193 100 cores per plot. They were mixed and sieved with a 5 mm sieve to ensure homogenization as
194 recommended for soil with high content of organic matter (Haynes & Swift, 1990). We measured soil
195 pH in a 0.01 M CaCl2 solution using a 1:10 ratio (air dried soil: solution). We determined Soil C:N ratio
196 from 3 mg of freeze-dried and ground soil using an Elementar Vario El Cube Analyzer. In each plot we
197 measured the depth of the soil's organic horizon from a soil pit dug within the plot.

198 *Experimental design and protocol*

199 We measured litter decomposition rates using the litterbag method. We made 15 cm * 15 cm bags
200 using polypropylene mesh with two different mesh sizes. We used the litterbags with a 0.2 mm mesh

201 size to target the decomposition solely due to soil microfauna and microorganisms. We used
202 litterbags with a 3.7 x 4.45 mm mesh size to assess the additional effect of mesofauna and
203 macrofauna on litter decomposition.
204 To obtain our litter samples, we collected summer senescent leaves from plant species with a
205 percent cover on the plots greater than 5 %. In total, we sampled 18, 20 and 17 plants species
206 respectively on the island with no browsing, on the island with an intermediate level of browsing,
207 and on the island with a severe level of browsing (Table S2 in in Supporting Information). We dried
208 these litter samples at 30°C for a week before using them.
209 We developed two complementary experiments in order to study the various mechanisms by which
210 deer could affect the decomposition process.
211 *Experiment 1* - To investigate litter decomposition rate in relation to the three browsing treatments
212 we produced, for each plot, three identical litterbags for each of the two mesh-sizes. Each of these
213 six litterbags contained, in the same proportion as in the plot, plant material from all plant species
214 covering more than 5 % of the plot area. We fixed the total mass of litter per litterbag at 4 g. Hence,
215 the mass of litter from each plant species in a given litterbag was calculated according to its relative
216 abundance in the plot. For each mesh size we placed one of the three litterbags on the plot the litter
217 came from ("home"), and placed the two remaining bags on one plot on each of the two remaining
218 islands ("away"). This translocation allowed us to independently test for the relative effects of home-
219 field advantage, of decomposer ability (soil properties and decomposer community composition),
220 and of litter quality on litter decomposition (Fig. S1).
221 *Experiment 2* - To investigate the influence of deer feces on litter decomposition rate within a
222 litterbag we used a standardized litter. We chose litter from one of the dominant tree species on all
223 islands, *P. sitchensis*. To avoid any biases from potential inter-treatment differences in spruce litter
224 quality, we used, for this set of litterbags, a mix of *P. sitchensis* litter collected from all three islands.
225 In order to standardize feces quality we collected fresh deer feces from another island with deer, also
226 situated in Laskeek Bay (East Limestone, 48 ha). We used this material to place on each of the 45

plots one fine-mesh litterbag containing 2 g of deer feces and 2 g of the standardized litter and two fine-mesh litterbags containing controls, one filled only with 5 g of deer feces and one filled only with 2 g of *P. sitchensis* litter. We repeated this with coarse-mesh litterbags.

Thus, to implement these two experiments, we placed a total of 12 litterbags on each plot including 6 fine-mesh litterbags [3 for experiment 1 (1 home and 2 away) and 3 for experiment 2 (1 feces only + 1 *P. sitchensis* only + 1 with feces and *P. sitchensis*)] and a similar set of 6 litterbags for the coarse-mesh litterbags. As a result we had a total of 540 litterbags (12 bags * 45 plots) for the full design. All litter bags were identified and numbered with aluminum tags and placed randomly on the surface of the forest floor on each plot. We used U pins at each corner of the bag to hold them in place. We placed litterbags on the three islands in July 2017, and collected them one year later in July 2018. The remoteness of the islands and associated logistics prevented designing an experiment with a partial collection of litterbags during the year to better assess the kinetics of decomposition. After collection (all but 35 bags were retrieved) we dried the litterbag contents at 70°C for 48h prior to weighing the contents and then performing chemical analyses.

*Mass, Carbon and Nitrogen loss in litterbags*

To assess litter mass loss over a year in each litterbags we subtracted the final mass of the bag's content from its initial mass. To assess C and N loss over a year, we calculated C and N contents of samples with an Elementar Vario El Cube Analyzer (Elementar, Langenselbold, Germany) using 3.5 mg of ground material. We first calculated the initial C and N contents of dried litter using eight individuals of each plant species (vascular and bryophytes) from each island/browsing treatment. Based on these values, and on the relative proportion of each litter in the bags, we calculated the initial C and N content for each litterbag. We also measured initial C and N contents of eight deer pellet groups that were previously dried at 70°C for 48h.

At the end of the experiment we finely ground the dried litter from the fine-mesh litterbags only, to remain within our budget limitations, and measured C and N content. We calculated carbon and nitrogen loss by subtracting the amount of carbon and nitrogen remaining in litter after one year of

253 decomposition from the initial estimates based on our calculations of initial C and N content of the
254 litter material.

255 *Statistical analysis*

256 In order to evaluate the effect of deer herbivory on plant community composition we used a
257 Correspondence Analysis on our data of plant species cover per plot, and performed a between class
258 analysis (Dray & Dufour, 2007). We evaluated the significance of the class effect with a permutation
259 test. To assess the initial litter C:N ratios at each plot we calculated the Community Weighted Mean
260 (CWM) of this initial litter C:N ratio using the formula $CWM_i = \sum_1^j (C_j \times p_j) / \sum_1^j (N_j \times p_j)$
261 where $i$ represents the plot, $j$ the plant species on this plot, $C_j$ and $N_j$ the C and N content of the
262 corresponding litter, and $p_j$ the relative abundance of the corresponding plant species on the plot.
263 We used one way ANOVA with permutation tests to compare litter CWM C:N ratio, soil bulk density,
264 soil pH, soil C:N ratio and organic horizon depth among the three islands. We used the multiple
265 comparison post-hoc test with the function *kruskalmc* from the package pgirmess.
266 To assess differences in the rate of litter mass loss and of C and N loss in both experiments, we
267 calculated the percent differences among treatments in litter mass loss and in C and N loss relative to
268 the no browsing treatment using the formula:
269 $100 - (x_{browsing} \times 100)/x_{no\ browsing}$
270 Where $x_{browsing}$ is the litter, C, or N mass loss in litterbags from either the intermediate or the
271 severe browsing treatment, and $x_{no\ browsing}$ the litter, C, or N mass loss in litterbags from the no
272 browsing treatment.
273 *Analyses of decomposition experiment 1* - We used a two way ANOVA to compare litter mass loss,
274 carbon loss and nitrogen loss from litter after one year among the three origins of litter (from island
275 with no, intermediate or severe deer browsing) and among treatment categories (island with no,
276 intermediate or severe deer browsing).

To disentangle the relative importance of the two main ways deer may modify C and N decomposition, namely litter quality and decomposer ability, we used the Decomposer Ability Regression Test proposed by Keiser et al. (2014) using SAS 9.4 (SAS Institute, Cary, NC). This method statistically discriminates among effects of litter quality (here defined as how rapidly a litter is decomposed regardless of decomposition site), ability [i.e. how rapidly a litter is decomposed at one site regardless of litter quality (includes the effect of soil abiotic conditions and the ability of the decomposer communities)] and home-field advantage [i.e. the acceleration of litter decomposition when litter is placed in the site it comes from (home) and where it can potentially benefit from a local specialization of the decomposer community]. The regression model defines the rate of decomposition of observation i ($Y_i$) by three parameters: litter quality ($Litter_l$), soil ability ($Soil_s$), and HFA ($Home_h$) which are dummy variables that equal 1 or 0, respectively, depending on the presence or absence of the litter mixture, soil community and home combination (in observation i). The parameters to be estimated are $\beta_l$, $\gamma_s$ and $\eta_h$ (Keiser et al., 2014). The average decomposition across all data (i) in a dataset, after controlling for litter, soil and home combinations, is represented by the intercept ($\alpha$), and the error term is defined by $\varepsilon$. The $\beta_l$ and $\gamma_s$ are restricted to prevent collinearity.

$$Y_i = \propto + \sum_{l=1}^{N} \beta_l Litter_{l_i} + \sum_{s=1}^{M} \gamma_s Soil_{s_i} + \sum_{H=1}^{K} \eta_h Home_{h_i} + \varepsilon_i$$

Compared to the classically used Structural Equation Modeling (SEM), the Decomposer Ability Regression Test offers the additional possibility to explicitly test home-field advantage and maximizes the information extracted from the litter transplant experiment (Keiser et al., 2014).

To explore the reasons for differences in litter quality caused by deer we performed linear models between C or N loss and litter CWM C:N ratio.

*Analyses of decomposition experiment 2 (feces manipulation)* - We used a two way ANOVA to compare mass loss, C loss, and N loss of *Picea sitchensis*, feces and the combination of both.

300 For all analyses in which homoscedasticity and normality of the distribution of the residues were not
301 respected, we used ANOVA with permutation tests instead of classical ANOVA (lmPerm package,
302 (Wheeler, 2010).

303 We used the R 3.4.1 environment (R Core Team, 2017) for all statistical analyses (except Decomposer
304 Ability Regression Test).

## 305 Results

306 *Deer modify aboveground and belowground characteristics*

307 The first axis of the Correspondence Analysis significantly discriminated the plant species
308 composition and abundance in the plots according to the intensity of deer browsing (Fig. 1A, Monte-
309 Carlo permutation test: $p<0.001$). In the absence of deer, vegetation cover was higher and there was
310 greater shrub diversity (Table S2 in Supporting Information). The vegetation from plots with severe
311 deer browsing was characterized by a high cover and diversity of bryophytes (Fig. 1A). Plots under
312 intermediate deer browsing showed intermediate plant species diversity and cover. We found no
313 significant difference in the initial C:N ratio of the plant litter among deer browsing treatments (Fig.
314 1B, p-value = 0.2). Soil bulk density was significantly higher on plots from islands with deer (Fig. 1C, p-
315 value < 0.001). Soil pH decreased significantly with increasing deer browsing pressure (Fig. 1D and F,
316 p-value = 0.037 and 0.005 respectively, however statistical power was not sufficient to discriminate
317 which treatment is different in the post-hoc test). Soil C:N was not significantly different among
318 treatments (Fig. 1E, p-value = 0.32). Depth of the organic horizon measured in the plots decreased by
319 44 % with increasing browsing intensity.

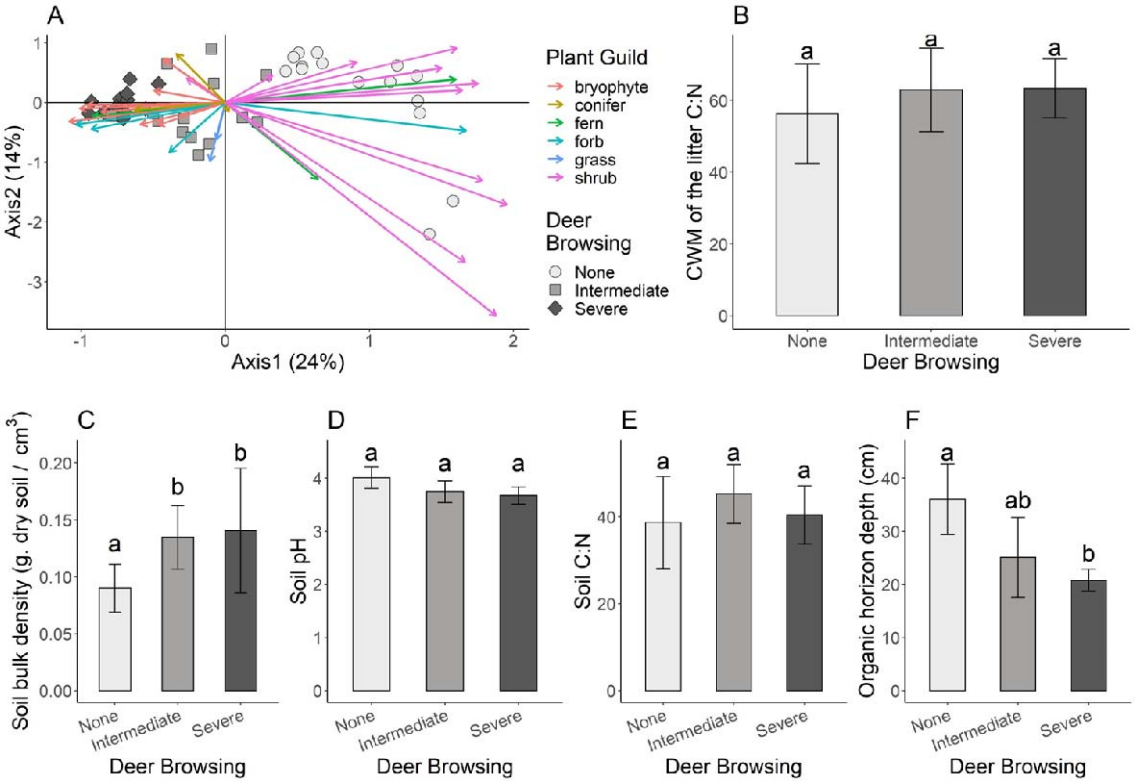



**Figure 1**. Effect of deer herbivory on aboveground (A, B) and belowground (C to F) parameters. Shades of dots and barplots represent the deer browsing treatment with: light grey = no browsing (deer absent), grey = intermediate (deer present for over 70 years but exposed to significant culls between 1997 and 2010) and dark grey = severe browsing (deer present for over 70 years and not exposed to hunting). Small letters on each barplot indicate differences tested by non-parametric post-hoc test. Panel A - Correspondence Analysis on the vegetation data collected at each plot. Dots, squares and lozenges represent the coordinates of the plots from the islands with no browsing, intermediate browsing and severe browsing, respectively. Arrows indicate the species contributions to axes (one arrow per species). Plant species are classified according to their functional group ; Panel B – Community Weighted Mean (CWM) of C:N ratio of the plant community; Panel C- Soil bulk density; Panel D - Soil pH; Panel E- Soil C:N ratio; Panel F - Organic horizon depth.

*Litter mass loss in experiment 1*

Litter mass loss was highest in litterbags with litter from the island with no deer and lowest in litterbags with litter from the island with severe browsing pressure. In fine-mesh litterbags average litter mass loss was 55% in litter from the islands without deer, 43% for litter from islands with intermediate browsing pressure and 34% in litter from islands with severe browsing pressure (Fig. S2A in Supporting Information). This pattern hold whatever the island category litterbags were placed on (Fig. S2A). Variation due to the context in which a given category of litter was placed had

340 only little influence, there was no significant effect of home-field advantage (Figs. S2A and S2B).
341 Decomposers were not more efficient in decomposing litter when it originated from their own
342 environment rather than from other sites. Mass loss was significantly affected by the place of
343 decomposition (Table S3, F = 113.36, p-value = 0.05). This pattern was due to a significantly better
344 ability of the micro-fauna and microorganisms from plots on the island without deer to decompose
345 litter (Figs S2A and S2C, p-value = 0.0045). Litter quality, understood here as the rate of
346 decomposition independent of decomposer ability and home-field advantage [calculated using the
347 method developed by Keiser et al., (2014)], was the main driver of carbon loss (Fig.S2D). Litter mixes
348 originating from the island with no deer had the best quality index (highest loss after one year, first
349 three bars on Fig. S2A), followed by the litter mixes originating from the island with intermediate
350 deer browsing and then by litter mixes originating from the island with severe deer browsing (Figs.
351 S2A and S2D).
352 In coarse-mesh litterbags the overall patterns of decomposition was similar to those from fine-mesh
353 litterbags (compare Figs. S2A to S2D and Figs. S2E to S2H in Supporting Information), although
354 variability among plots within sites was greater (Figs. S2A and S2E). As a result, mass loss in litter
355 mixes originating from islands with intermediate and severe deer browsing were respectively 25%
356 and 39% lower than in litter mixes originating from the plots on the island without deer (p-value <
357 0.001) (Fig. S2C). There was no evidence for home-field advantage in large mesh litter bags (Fig. S2F).
358 Place of decomposition significantly affected litter mass loss (Figure S3, F = 4.54, p-value = 0.01). The
359 ability of the micro-fauna and microorganisms to decompose litter was significantly lower for litter
360 placed in plots exposed to severe browsing (Fig. S2G, p-value = 0.009). As observed for fine-mesh
361 litterbags, litter quality had a significant effect on litter decomposition in coarse-mesh bags (Fig. S2H,
362 p-value < 0.001).
363
364 *Carbon and Nitrogen loss in fine-mesh litterbags in experiment 1*

365 The loss of carbon in the litterbags after one year was highest for litter representative of the
366 vegetation on islands without deer and lowest for litter representative of the vegetation on islands
367 with the most severe browsing pressure (Fig. 2A, F = 108.78, p-value = < 0.001) a pattern consistent
368 with the pattern of litter mass loss. When compared to the carbon loss observed in litter originating
369 from the island with no deer, carbon loss after one year was 12% lower in litter collected from the
370 island with intermediate browsing, and 30% lower in litter collected from the island with severe
371 browsing, this independently of the incubating (i.e. island) context (Fig. 2A). Home-field advantage
372 was not significant (Fig. 2B), indicating that decomposers were not more efficient in decomposing
373 litter carbon when it originated from their own environment rather than from other sites. The ability
374 of the micro-fauna and microorganisms to decompose carbon was significantly higher for litter
375 placed in plots without deer than in plots on islands with deer (Fig. 2C, p-value = 0.008). Indeed,
376 carbon loss after one year was 5% lower in litterbags incubated in plots on the island with severe
377 deer browsing than carbon loss observed in plots from the island without deer. Litter quality,
378 understood here as the rate of decomposition independent of decomposer ability and home-field
379 advantage [calculated using the method developed by Keiser et al., (2014)], was the main driver of
380 carbon loss. Litter mixes originating from the island with no deer had the best quality index (highest
381 loss after one year), followed by the litter mixes originating from the island with intermediate deer
382 browsing and then by litter mixes originating from the island with severe deer browsing (Figs 2A and
383 2D).
384 Litter mixes from the island without deer had significantly higher nitrogen loss than litter mixes from
385 islands with deer (Fig. 2E). However, unlike C loss, nitrogen loss was lower for litter mixes originating
386 from the island with intermediate deer browsing than that originating from the island with severe
387 deer browsing (45% and 30% respectively, Fig. 2E, F = 17.53, p-value < 0.001). We detected no home-
388 field advantage for N loss (Fig. 2E). In addition, none of the decomposer communities were better at
389 decomposing and releasing nitrogen (Fig. 2F). Similarly than for carbon, litter quality (sensu Keiser et
390 al. 2014) was the main driver of nitrogen loss in litter bags. However, conversely to carbon, the

lowest rate of N loss after one year was observed in litter from the island with intermediate browsing pressure (Figs 2E and 2H).

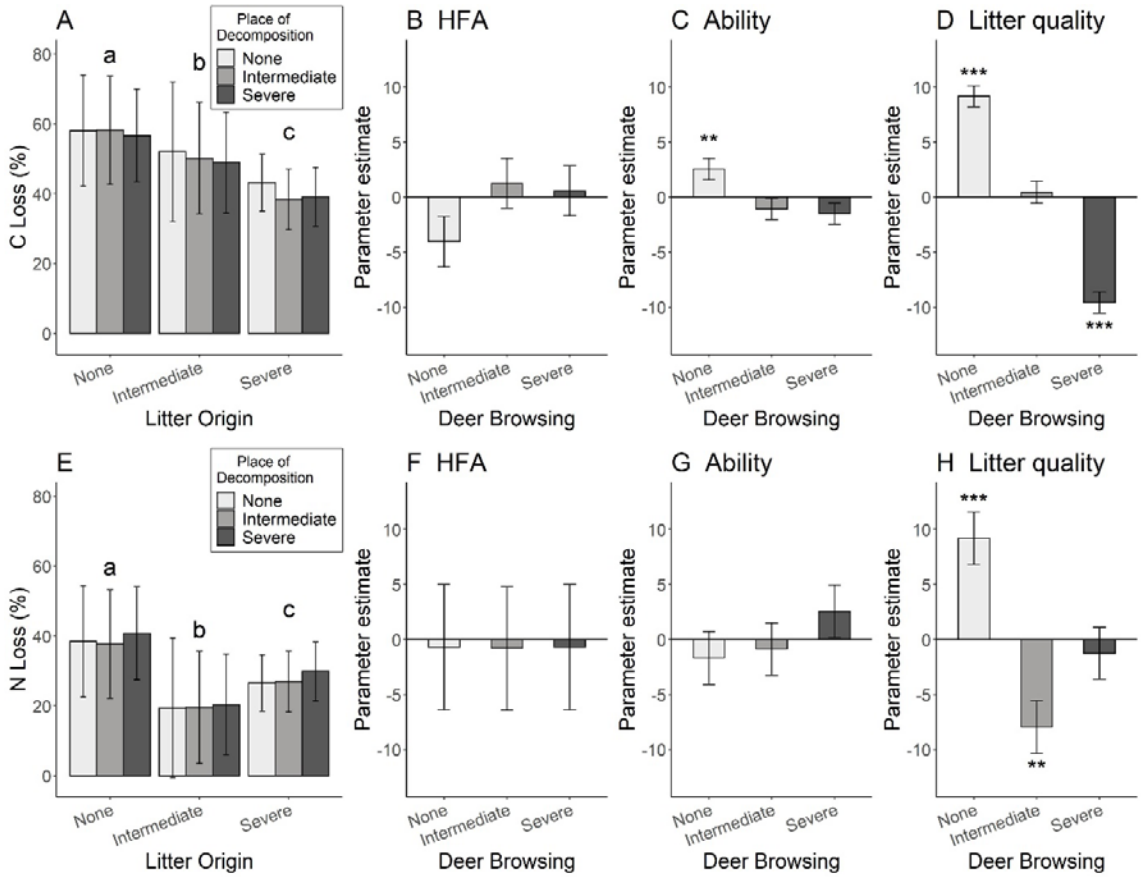
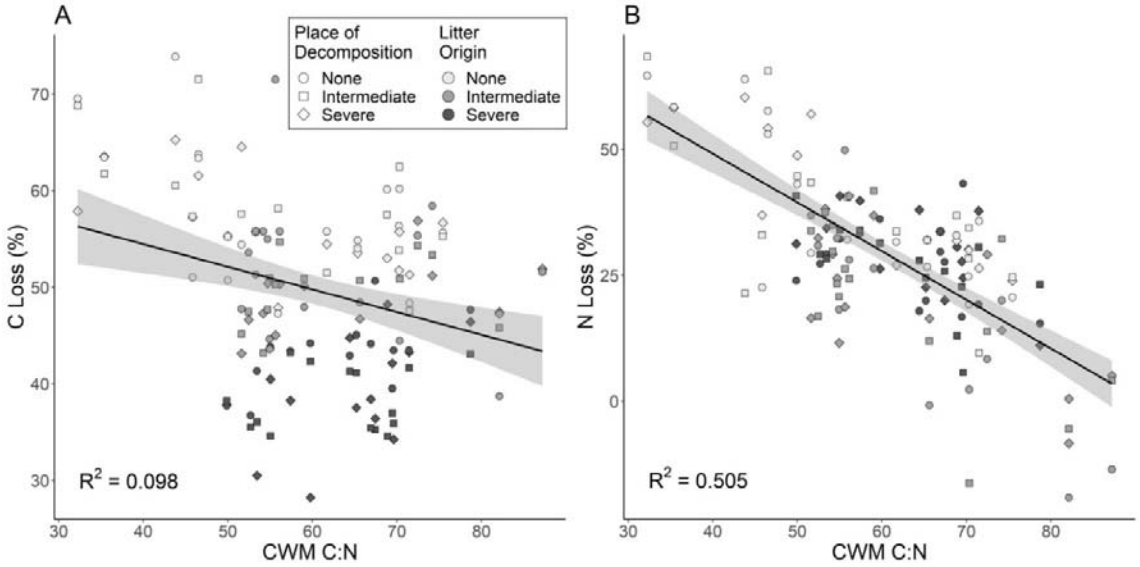



**Figure 2.** Decomposition rate of the plant community litter among deer browsing categories for carbon (top) and nitrogen (bottom) in fine-mesh litterbags in the translocation experiment. Shades of barplots represent the deer browsing intensity with: light grey = no browsing (deer absent), grey = intermediate (deer present for over 70 years but deer density reduced by culls between 1997 and 2010) and dark grey = severe browsing (deer present for over 70 years but not exposed to hunting, highest deer density). Asterisks indicate estimates significantly different from zero with *<0.05, ** <0.01, ***<0.001. Fine letters in each bar plots indicate differences tested by post-hoc test. Panel A and Panel E represent carbon and nitrogen loss after one year among treatments respectively with bars grouped according to litter origin and shades corresponding to the category of deer browsing of the location where the litter bags were placed. Panel B-D and F-H represent the parameter estimates (± SE) calculated using the Decomposer Ability Regression Test proposed by Keiser et al. (2014).

Carbon and nitrogen loss in litterbags after one year were significantly and negatively related to the initial C:N ratio Community Weighted Mean (CWM) of the litter (Fig. 3). For litter carbon loss, the initial litter C:N CWM explained only 10% of its variation (Table S2). Conversely, litter nitrogen loss

410 was strongly linked to the initial litter C:N CWM, which explained 50% of its variability (Table S4 in

411 Supporting Information).




412

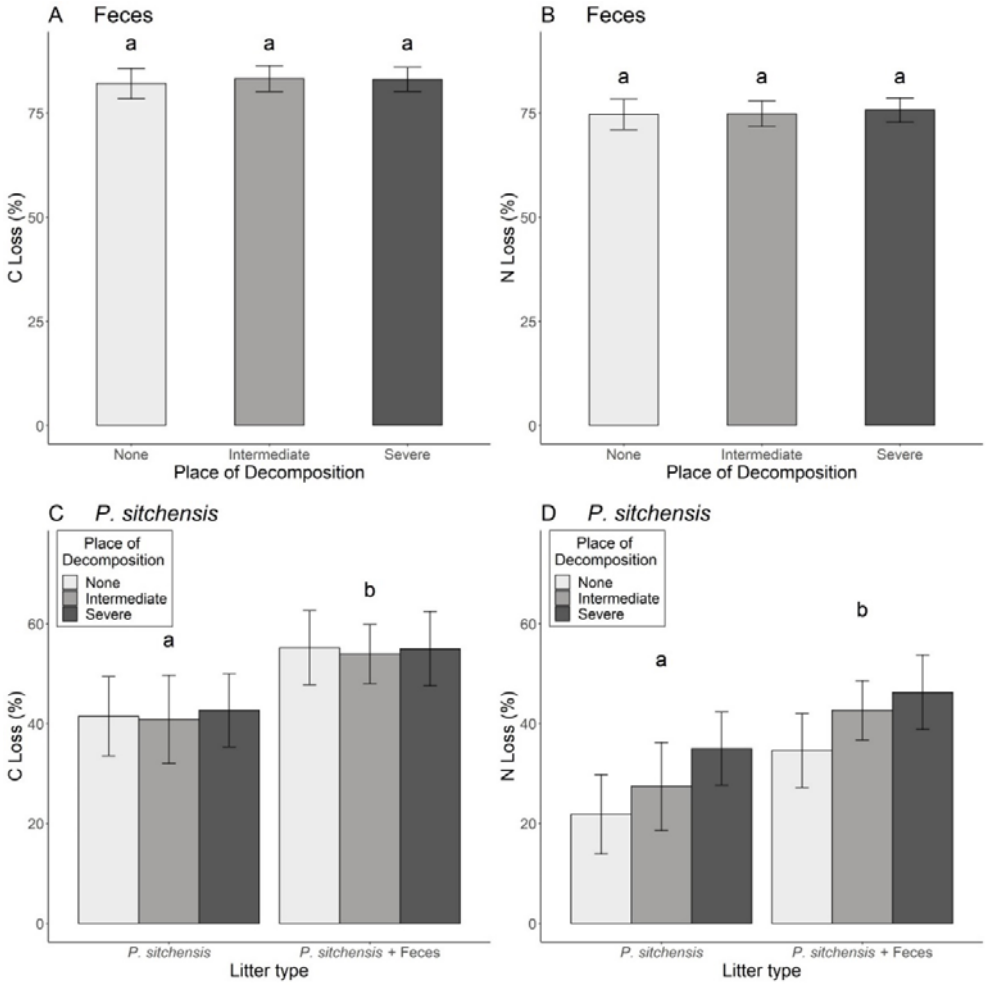
413 **Figure 3.** Linear regression of carbon (left) and nitrogen (right) loss variation with plant C:N
414 Community Weighted Mean. Shades of dots represent the deer browsing intensity on the island
415 where the litter came from, with: light grey = no browsing (deer absent), grey = intermediate (deer
416 present for over 70 years but culled, lower deer density) and dark grey = severe browsing (deer
417 present for over 70 years but not exposed to hunting, highest deer density). The shape of the
418 symbols refer to the browsing category of the island where we placed the litterbags. Details on
419 regressions models are given in Table S2.

420

421 *Feces decomposition in experiment 2*

422 In fine-mesh litterbags place of decomposition had no effect on feces mass loss (Fig. S3A). In coarse-
423 mesh litterbags mass loss from feces after one year was 15% higher on islands with deer than on
424 islands without deer (Fig. S3B, p-value < 0.001). The addition of feces enhanced the mass loss in *P.*
425 *sitchensis* litter by 29% in fine-mesh (p-value = <0.001, Fig. S3C) and by 20% in coarse-mesh litterbags
426 (p-value = 0.047, Fig. S3D), on island with intermediate or no browsing (Fig. S3D). There were no
427 differences among treatments in carbon and nitrogen loss from feces after one year (F = 1.386, p-
428 value = 0.26 and F = 0.416, p-value = 0.66 respectively, Figs. 4A and B). Feces addition significantly
429 increased the C and N loss in *P. sitchensis* litter after one year, by 31% for carbon and 47% for
430 nitrogen (F = 175.62, p-value < 0.001 and F = 66.39, p-value < 0.001 respectively, Fig. 4C and D). The
431 ability of the decomposer community (i.e. decomposition place) had no effect on carbon loss (F =

432 0.752 and p-value = 0.47, Fig. 4C). However, for nitrogen loss in *P. sitchensis* litter after one year, the
433 presence of deer feces significantly improved the decomposition ability of the decomposer
434 community in the plots from the islands with deer (F = 20.10, p-value < 0.001, Fig. 4D).




435

436 **Figure 4.** Carbon and nitrogen loss in feces in relation to browsing treatment (top) and effect of
437 feces addition on carbon and nitrogen loss in *Picea sitchensis* litter (bottom) in fine-mesh litterbags.
438 Shades of barplots refer to the deer browsing category of the place of decomposition with: light grey
439 = no browsing (deer absent), grey = intermediate (deer present for over 70 years but not exposed to
440 hunting, highest deer density) and dark grey = severe deer browsing (deer present for over 70 years
441 but not exposed to hunting, highest deer density). Panel A – Carbon loss in feces; Panel B – Nitrogen
442 loss in feces; Panel C – Carbon loss in *P. sitchensis* litter with and without the addition of feces; Panel
443 D – Nitrogen loss in *P. sitchensis* litter with and without the addition of feces. Small letters above
444 each barplots indicate differences tested by post-hoc test.

445

446

## Discussion

*Deer slow down decomposition through modification of the understory plant communities*

To our knowledge, our study is among the few studies on the effect of large forest herbivores on decomposition processes that have attempted to dissociate the relative effect of changes in plant community composition (community litter quality) from the effects of changes in abiotic soil properties and decomposer community (decomposer ability, Andriuzzi & Wall, 2017). Previous research focused on decomposer ability and, when integrating litter quality, considered only the plant specific responses to herbivory (i.e. changes in plant chemical composition associated to browsing), but neglected the change in plant species composition and relative abundance. In our study, we demonstrated that herbivores change the overall quality of litter reaching the forest floor, and that this is the overriding factor governing litter decomposition, rather than soil properties, composition of the soil decomposer community, or home-field advantage (Fig. 2). This difference in overall litter quality was not exclusively attributed to a modification of the litter C:N CWM (Figs. 1B & 3). This suggests that other parameters of litter quality not measured in our study, such as lignin or anti-herbivore compounds, were also implied in overall litter quality decline in presence of deer. Thereafter we refer to the term 'litter quality' as a composite variable calculated as proposed by Keiser et al. (2014), and representing the rate of decomposition independent of decomposer ability and home-field advantage. The major shift in litter quality caused by deer browsing resulted, after one year, in an overall reduction in litter mass loss in presence of deer. This translated after one year into a 25% lower carbon and a 27% lower nitrogen loss in litter from the island with severe browsing compared to C and N losses in litter from the island with no browsing (Figs. 2A and 2E). This strong control of litter quality on C, and especially on N loss, contrasts with the previous assumption that vegetation changes may affect nitrogen and phosphorus dynamics less than the dynamics of carbon (Bryant, Chapin, & Klein, 1983; Wardle, Bonner, & Barker, 2002).

471 The prevailing importance of change in litter quality that resulted from deer herbivory on
472 decomposition in the temperate forests we studied is in agreement with the microcosm study of
473 Harrison & Bardgett (2003) who showed that decomposition of birch (*Betula pubescens*) litter,
474 originating from inside deer exclosures (unbrowsed) in the Scottish Highlands decomposed faster
475 than litter from outside of the exclosures (browsed), irrespective of the origin of the soil (inside or
476 outside of exclosures). Conversely, Olofsson & Oksanen (2002), in a field translocation experiment
477 assessing the decomposition of four plant species dominating the vegetation of lightly and heavily
478 grazed tundra demonstrated a positive effect of reindeer herbivory on decomposition rate.
479 The dramatic change in litter quality found in our study is the result of an alteration in the understory
480 plant community (Figs. 1A, 2D and 2H). Intense and prolonged deer browsing dramatically changed
481 the understory plant composition and cover, resulting in an up to 90% reduction in understory shrub
482 cover (Table S1 Fig. 1A), and in a shift in litter quality. We interpret this change in litter quality on
483 islands with as the main cause for the dramatic reduction in litter decomposed after one year (Figs
484 S2D and S2H and Figs. 2D and 2H). These modifications not only confirm the severe impact of deer on
485 the understory vegetation of Haida Gwaii (Chollet, Baltzinger, Ostermann, Saint-André, & Martin,
486 2013; Martin et al., 2010) but are consistent with results in other temperate forests (Côté et al.,
487 2004; Boulanger et al., 2018).
488 We found that the reduction in litter quality, and the associated modifications in the decomposition
489 pattern, were partly driven by the variation in the litter CWM C:N ratio (Fig. 3) although we found no
490 overall difference in litter CWM C:N ratio among islands (Fig. 1B). The decline in litter quality affected
491 carbon and nitrogen cycles differently. For carbon, litter quality decreased as deer browsing intensity
492 increased (Fig. 2D). For nitrogen, litter quality was poorer in the intermediate deer browsing than on
493 the island with severe browsing (Fig. 2H). The decline in litter C loss could be explained by the shift
494 from an understory dominated by more decomposable species (shrubs) towards an understory of
495 less decomposable species (conifers and bryophytes) as the level of deer browsing intensity
496 increased. Conifers and bryophytes are known to have slow decomposition rates due to low N

content and high concentrations of structural carbohydrates and aromatic compounds (Cornwell et al., 2008; Turetsky, Crow, Evans, Vitt, & Wieder, 2008). The presence of these secondary compounds may largely explain the lower decomposition of the litter from islands with deer and thus the slight effect of CWM of litter C:N (≈10% of variation explained, Fig. 3). The contrasting result we obtained for N loss from litter after one year suggests that the vegetation shift caused by deer had different consequences for nitrogen mineralization. Although there was no overall significant difference in CWM litter C:N ratio among deer herbivory treatments, the intermediate treatment had the highest values of C:N (Fig. 3), which explains the lowest N loss values observed in this treatment (≈50% of the variation is explained by CWM litter C:N).

*Deer also modify decomposer ability*

Although the change in litter quality (sensu Keiser et al. 2014) caused by deer herbivory was identified as the main driver of the decomposition process, several other changes in the soil decomposer communities affected nutrient cycling. Decomposers from the island without deer had a greater ability to decompose the carbon present in litter, but not nitrogen (Figs. 2C and 2G). The contrast between C and N decomposition among islands when using fine–mesh litterbags, and the similarity in C and N decomposition when using coarse -mesh litterbags (Fig. S2), suggests that the observed decomposition patterns are more likely explained by biotic differences in soils (i.e. differences in decomposer community) than by the effect of abiotic modifications such as higher soil compaction (Fig. 1C). A possible explanation for the observed contrasts in litter decomposition may be a switch in the bacterial:fungal ratio in presence of deer. In fact the disappearance of base-rich shrubs and their replacement by species with high concentrations of phenolic compounds (e.g. bryophytes) as a result of deer browsing may have increased the dominance of fungi which require less calcium and magnesium for growth (Prescott, 2010). This change in decomposer community structure would favor the formation of a mor humus, in which up to 30% of the litter mass is converted to humus rather than decomposing (Prescott, 2010). In addition the dramatic reduction in

523 shrub cover may have reduced the root exudate which stimulate bacterial activity (Ekberg,
524 Buchmann, & Gleixner, 2007). Contrary to carbon, the ability of decomposers to decompose nitrogen
525 in litter did not vary among islands with different patterns of deer herbivory (Fig. 2G). This may be
526 explained by the selection of microorganisms better able to exploit N in environments where this
527 element is the most limiting ("nitrogen mining hypothesis", Craine, Morrow, & Fierer, 2007)
528 compensating for the switch in bacterial:fungal ratio. This hypothesis is supported by our control
529 experiment, where we used a standardized quality of litter *(Picea sitchensis*), and found a greater
530 ability of decomposers to decompose N in litter samples incubated on sites with deer (Fig. 4D).
531 Interestingly, we also found that the inclusion of the soil macro and mesofauna (hereafter fauna) in
532 litter decomposition via the use of coarse-mesh litterbags affected litter mass loss (Fig. S2E).
533 Specifically, we found that litter decomposition was reduced on the island with the highest deer
534 density, suggesting a negative effect of high deer density on the faunal decomposer communities.
535 Previous studies documented negative effects of large herbivores on the abundance and diversity of
536 the soil fauna (see review by Andriuzzi & Wall (2017)), but the consequences on litter decomposition
537 were not studied. This negative effect could be due to a reduction in both the abundance and the
538 activity of the soil fauna through several mechanisms. Directly, through soil trampling by deer which
539 might reduce soil fauna habitat through soil physical compaction and its reduction of soil pore size
540 (Beylich, Oberholzer, Schrader, Höper, & Wilke, 2010). In addition, the reduction of litter quality by
541 deer might be responsible for an indirect slowing down of soil faunal abundance and activity for
542 which litter quality is known to be a controlling factor (García-Palacios, Maestre, Kattge, & Wall,
543 2013; Hendriksen, 1990). As most previous studies on the effects of large herbivores on
544 decomposition focused mainly on the role of microbes, we feel more attention needs to be paid to
545 the role of the soil fauna in order to better understand ecosystem nutrient cycling.
546 Soil fauna also plays an important role in the decomposition of feces, with evidence of home-field
547 advantage (HFA). Indeed deer feces decomposition in our study was more rapid on islands with deer
548 (home) than on the island without (away), but only when including the effects of fauna (coarse-mesh

549 bags, Fig. S3B). We infer that deer have a positive effect on macrofauna decomposing dung. Such a
550 positive effect of large herbivores on this specialized fauna has been recently demonstrated in Japan
551 where Iida, Soga, & Koike (2018) found a positive relationship between the populations of dung
552 beetles and deer density. In our study, we demonstrated that, litter fauna, but not microorganisms,
553 were selected for decomposition of a particular litter type. This is an important result as most of the
554 literature on HFA only considered microorganisms, and this suggests a potential underestimation of
555 fauna on HFA.
556 A large proportion of what we know on the effect of high quality litter deposition (dung and urine) by
557 large herbivores on nutrient cycling comes from the study of domestic animals and/or grassland
558 ecosystems (McNaughton, Banyikwa, & McNaughton, 1997; Frank & Groffman, 1998; Christenson,
559 Mitchell, Groffman, & Lovett, 2010). We demonstrate that in the temperate forests we studied dung
560 decomposed faster, and released a larger proportion of nitrogen, than observed for plant litter. Also,
561 the addition of feces, whatever the mesh size, increased the rate of *Picea sitchensis* decomposition,
562 increasing C loss by 31% and N loss by 47% (Fig. 4C and 4D). This may be explained by the presence of
563 labile nutrients in dung, which enhance the development of microbial communities, increasing rates
564 of nutrient cycling (Bardgett, Keiller, Cook, & Gilburn, 1998). However, despite these results, we
565 found that high quality litter deposition did not affect overall decomposer ability (no higher
566 decomposer ability on islands with deer dung/urine, Fig. 2C and 2G). This contradicts recent studies
567 which demonstrated that feces deposition enhanced plant productivity and soil nutrient availability
568 (Barthelemy, Stark, & Olofsson, 2015; Wang et al., 2018). The explanation for the lack of effect in the
569 forests we studied likely rests with the patchy distribution of solitary deer, in contrast to herding
570 species like reindeer or livestock, and thus reflects the patchy, and limited, amounts of dung
571 deposited locally, amounts that appear not to be sufficient to influence the nutrient cycling at the
572 ecosystem level (Pastor, Naiman, Dewey, & McInnes, 1988).
573
574

## Conclusion

Our results show that in temperate forests abundant deer can play an important role in ecosystem functioning, modifying aboveground, as well as belowground, characteristics, and reducing nutrient cycling. In the last few decades, the awareness and knowledge of the effects of overabundant dee on aboveground communities has been growing worldwide (Côté et al., 2004; Takatsuki, 2009). Our study suggests that these aboveground changes are probably at the root of major modifications in nutrient cycling in temperate forest ecosystems. In addition, it has to be emphasized that our results are likely an underestimation of effects as we did not take into account the dramatic effect deer have on the quantity of litter reaching the forest floor. For example, in Western Europe the current 10 million roe deer *Capreolus capreolus*, in addition to the increasing populations of other ungulates, represent a standing biomass estimated at 0.75 billion kg that consumes ≈20 million tons of green vegetation each year (Apollonio et al., 2010). Consequently, there is critical need to expand our results to other temperate forests to assess the overall consequences increasing deer populations have on broad scale nitrogen cycling in soils (Hobbie & Villéger, 2015) and their potential influence on global carbon storage (Tanentzap & Coomes, 2012).

## Statement of authorship

SC conceived the ideas and designed the methodology in close interaction with MM; SC, MM, JS and J-LM collected the data; MM and SC analyzed the data; SC and MM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## 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*(9), 3857–3868. doi: 10.1111/gcb.13675

Apollonio, M., Andersen, R., & Putman, R. (2010). *European Ungulates and Their Management in the 21st Century*. Cambridge University Press.

Austin, A. T., Vivanco, L., González-Arzac, A., & Pérez, L. I. (2014). There's no place like home? An exploration of the mechanisms behind plant litter–decomposer affinity in terrestrial ecosystems. *New Phytologist*, *204*(2), 307–314. doi: 10.1111/nph.12959

Ayres, E., Steltzer, H., Simmons, B. L., Simpson, R. T., Steinweg, J. M., Wallenstein, M. D., … Wall, D. H. (2009). Home-field advantage accelerates leaf litter decomposition in forests. *Soil Biology and Biochemistry*, *41*(3), 606–610. doi: 10.1016/j.soilbio.2008.12.022

Banner, A., MacKenzie, W. H., Pojar, J., MacKinnon, A., Saunders, S. C., & Klassen, H. (2014). *A Field Guide to Ecosystem Classification and Identification for Haida Gwaii* (Prov. B.C., Victoria, B.C. Land Manag. Handb. 68.).

Bardgett, R. D., Keiller, S., Cook, R., & Gilburn, A. S. (1998). Dynamic interactions between soil animals and microorganisms in upland grassland soils amended with sheep dung: a microcosm experiment. *Soil Biology and Biochemistry*, *30*(4), 531–539. doi: 10.1016/S0038-0717(97)00146-6

Bardgett, R. D., & Wardle, D. A. (2003). Herbivore-Mediated Linkages Between Aboveground and Belowground Communities. *Ecology*, *84*(9), 2258–2268. doi: 10.1890/02-0274

Barthelemy, H., Stark, S., & Olofsson, J. (2015). Strong Responses of Subarctic Plant Communities to Long-Term Reindeer Feces Manipulation. *Ecosystems*, *18*(5), 740–751. doi: 10.1007/s10021-015-9856-y

Beylich, A., Oberholzer, H.-R., Schrader, S., Höper, H., & Wilke, B.-M. (2010). Evaluation of soil compaction effects on soil biota and soil biological processes in soils. *Soil and Tillage Research*, *109*(2), 133–143. doi: 10.1016/j.still.2010.05.010

Boulanger, V., Dupouey, J.-L., Archaux, F., Badeau, V., Baltzinger, C., Chevalier, R., … Ulrich, E. (2018). Ungulates increase forest plant species richness to the benefit of non-forest specialists. *Global Change Biology*, *24*(2), e485–e495. doi: 10.1111/gcb.13899

British Columbia Ministry of Forests, Lands, and Natural Resource Operations. (2010). *Biogeoclimatic Ecosystem Classification Codes and Names*. Forest Analysis and Inventory Branch, Victoria, B.C.

Bryant, J. P., Chapin, F. S., & Klein, D. R. (1983). Carbon/Nutrient Balance of Boreal Plants in Relation to Vertebrate Herbivory. *Oikos*, *40*(3), 357–368. doi: 10.2307/3544308

Chapin, F. S. I., Matson, P. A., & Vitousek, P. (2011). *Principles of Terrestrial Ecosystem Ecology* (2nd ed.). Retrieved from https://www-springer-com.passerelle.univ-rennes1.fr/us/book/9781441995032

Chollet, S., Baltzinger, C., Ostermann, L., Saint-André, F., & Martin, J.-L. (2013). Importance for forest plant communities of refuges protecting from deer browsing. *Forest Ecology and Management*, *289*, 470–477. doi: 10.1016/j.foreco.2012.10.043

Chollet, S., Baltzinger, C., Saout, S. L., & Martin, J.-L. (2013). A better world for bryophytes? A rare and overlooked case of positive community-wide effects of browsing by overabundant deer. *Écoscience*, *20*(4), 352–360. doi: 10.2980/20-4-3627

Chollet, S., Bergman, C., Gaston, A. J., & Martin, J.-L. (2015). Long-term consequences of invasive deer on songbird communities: Going from bad to worse? *Biological Invasions*, *17*(2), 777–790. doi: 10.1007/s10530-014-0768-0

Chollet, S., & Martin, J.-L. (2013). Declining woodland birds in North America: should we blame Bambi? *Diversity and Distributions*, *19*(4), 481–483. doi: 10.1111/ddi.12003

Chollet, S., Padié, S., Stockton, S., Allombert, S., Gaston, A. J., & Martin, J.-L. (2016). Positive plant and bird diversity response to experimental deer population reduction after decades of uncontrolled browsing. *Diversity and Distributions*, *22*(3), 274–287. doi: 10.1111/ddi.12393

Christenson, L. M., Mitchell, M. J., Groffman, P. M., & Lovett, G. M. (2010). Winter climate change implications for decomposition in northeastern forests: comparisons of sugar maple litter with herbivore fecal inputs. *Global Change Biology*, *16*(9), 2589–2601. doi: 10.1111/j.1365-2486.2009.02115.x

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*(2), 202–211. doi: 10.1111/ele.12722

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., … Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, *11*(10), 1065–1071. doi: 10.1111/j.1461-0248.2008.01219.x

Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., & Waller, D. M. (2004). Ecological Impacts of Deer Overabundance. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 113–147. doi: 10.1146/annurev.ecolsys.35.021103.105725

Craine, J. M., Morrow, C., & Fierer, N. (2007). Microbial Nitrogen Limitation Increases Decomposition. *Ecology*, *88*(8), 2105–2113. doi: 10.1890/06-1847.1

Dray, S., & Dufour, A.-B. (2007). The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of Statistical Software*, *22*(1), 1–20. doi: 10.18637/jss.v022.i04

Ekberg, A., Buchmann, N., & Gleixner, G. (2007). Rhizospheric influence on soil respiration and decomposition in a temperate Norway spruce stand. *Soil Biology and Biochemistry*, *39*(8), 2103–2110. doi: 10.1016/j.soilbio.2007.03.024

Eldridge, D. J., Delgado-Baquerizo, M., Travers, S. K., Val, J., Oliver, I., Hamonts, K., & Singh, B. K. (2017). Competition drives the response of soil microbial diversity to increased grazing by vertebrate herbivores. *Ecology*, *98*(7), 1922–1931. doi: 10.1002/ecy.1879

Foster, C. N., Barton, P. S., & Lindenmayer, D. B. (2014). Effects of large native herbivores on other animals. *Journal of Applied Ecology*, *51*(4), 929–938. doi: 10.1111/1365-2664.12268

Frank, D. A., & Groffman, P. M. (1998). Ungulate Vs. Landscape Control of Soil C and N Processes in Grasslands of Yellowstone National Park. *Ecology*, *79*(7), 2229–2241. doi: 10.1890/0012-9658(1998)079[2229:UVLCOS]2.0.CO;2

Fuller, R. J., & Gill, R. M. A. (2001). Ecological impacts of increasing numbers of deer in British woodland. *Forestry*, *74*(3), 193–199. doi: 10.1093/forestry/74.3.193

García-Palacios, P., Maestre, F. T., Kattge, J., & Wall, D. H. (2013). Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecology Letters*, *16*(8), 1045–1053. doi: 10.1111/ele.12137

Gaston, A. J., Stockton, S. A., & Smith, J. L. (2006). Species-area relationships and the impact of deer-browse in the complex phytogeography of the Haida Gwaii archipelago (Queen Charlotte Islands), British Columbia. *Écoscience*, *13*(4), 511–522. doi: 10.2980/1195-6860(2006)13[511:SRATIO]2.0.CO;2

Gholz, H. L., Wedin, D. A., Smitherman, S. M., Harmon, M. E., & Parton, W. J. (2000). Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology*, *6*(7), 751–765. doi: 10.1046/j.1365-2486.2000.00349.x

Gill, R. M. A. (1992). A Review of Damage by Mammals in North Temperate Forests: 3. Impact on Trees and Forests. *Forestry: An International Journal of Forest Research*, *65*(4), 363–388. doi: 10.1093/forestry/65.4.363-a

Golumbia, T., Bland, L., Morre, K., & Bartier, P. (2008). History and current status of introduced species on Haida Gwaii. In *Lessons from the islands: introduced species and what they tell us*

*about how ecosystems work* (Canadian Wildlife Service, Environment Canada, Vols. 1–Queen Charlotte City, pp. 8–31). Ottawa: Gaston AJ, Golumbia TE, Martin JL, Sharpe ST.

Handa, I. T., Aerts, R., Berendse, F., Berg, M. P., Bruder, A., Butenschoen, O., … Hättenschwiler, S. (2014). Consequences of biodiversity loss for litter decomposition across biomes. *Nature*, *509*(7499), 218–221. doi: 10.1038/nature13247

Harrison, K. A., & Bardgett, R. D. (2003). How browsing by red deer impacts on litter decomposition in a native regenerating woodland in the Highlands of Scotland. *Biology and Fertility of Soils*, *38*(6), 393–399. doi: 10.1007/s00374-003-0667-5

Haynes, R. J., & Swift, R. S. (1990). Stability of soil aggregates in relation to organic constituents and soil water content. *Journal of Soil Science*, *41*(1), 73–83. doi: 10.1111/j.1365-2389.1990.tb00046.x

Hendriksen, N. B. (1990). Leaf litter selection by detritivore and geophagous earthworms. *Biology and Fertility of Soils*, *10*(1), 17–21. doi: 10.1007/BF00336119

Hobbie, S. E., & Villéger, S. (2015). Interactive effects of plants, decomposers, herbivores, and predators on nutrient cycling. In *Trophic ecology: Bottom-up and top-down interactions across aquatic and terrestrial systems* (Cambridge University Press). Cambridge: Torrance C. Hanley; Kimberley J. La Pierre.

Horsley, S. B., Stout, S. L., & DeCalesta, D. S. (2003). White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications*.

Iida, T., Soga, M., & Koike, S. (2018). Large herbivores affect forest ecosystem functions by altering the structure of dung beetle communities. *Acta Oecologica*, *88*, 65–70. doi: 10.1016/j.actao.2018.03.003

Keiser, A. D., Keiser, D. A., Strickland, M. S., & Bradford, M. A. (2014). Disentangling the mechanisms underlying functional differences among decomposer communities. *Journal of Ecology*, *102*(3), 603–609. doi: 10.1111/1365-2745.12220

Londo, G. (1976). The decimal scale for releves of permanent quadrats. *Vegetatio*, *33*(1), 61–64. doi: 10.1007/BF00055300

Martin, J.-L., & Baltzinger, C. (2002). Interaction among deer browsing, hunting, and tree regeneration. *Canadian Journal of Forest Research*, *32*(7), 1254–1264. doi: 10.1139/x02-043

Martin, J.-L., Stockton, S. A., Allombert, S., & Gaston, A. J. (2010). Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: lessons from a deer introduction. *Biological Invasions*, *12*(2), 353–371. doi: 10.1007/s10530-009-9628-8

McNaughton, S. J., Banyikwa, F. F., & McNaughton, M. M. (1997). Promotion of the Cycling of Diet-Enhancing Nutrients by African Grazers. *Science*, *278*(5344), 1798–1800. doi: 10.1126/science.278.5344.1798

McShea, W., Underwood, H., & Rappole, J. (1997). *The Science of Overabundance: Deer Ecology and Population Management* (DC: Smithson. Inst. Press.). Washington.

Milner, J. M., Bonenfant, C., Mysterud, A., Gaillard, J.-M., Csanyi, S., & Stenseth, N. C. (2006). Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *Journal of Applied Ecology*, *43*(4), 721–734. doi: 10.1111/j.1365-2664.2006.01183.x

Olofsson, J., & Oksanen, L. (2002). Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment. *Oikos*, *96*(3), 507–515. doi: 10.1034/j.1600-0706.2002.960312.x

Pastor, J., Naiman, R. J., Dewey, B., & McInnes, P. (1988). Moose, Microbes, and the Boreal Forest. *BioScience*, *38*(11), 770–777. doi: 10.2307/1310786

Penner, J. F., & Frank, D. A. (2018). Litter Decomposition in Yellowstone Grasslands: The Roles of Large Herbivores, Litter Quality, and Climate. *Ecosystems*. doi: 10.1007/s10021-018-0310-9

Prescott, C. E. (2010). Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry*, *101*(1), 133–149. doi: 10.1007/s10533-010-9439-0

R Core Team. (2017). *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria*. Retrieved from https://www.R-project.org/

Royo, A. A., Collins, R., Adams, M. B., Kirschbaum, C., & Carson, W. P. (2010). Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology*. doi: 10.1890/08-1680.1

Schrama, M., Heijning, P., Bakker, J. P., van Wijnen, H. J., Berg, M. P., & Olff, H. (2013). Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. *Oecologia*, *172*(1), 231–243. doi: 10.1007/s00442-012-2484-8

Sitters, J., Bakker, E. S., Veldhuis, M. P., Veen, G. F., Olde Venterink, H., & Vanni, M. J. (2017). The Stoichiometry of Nutrient Release by Terrestrial Herbivores and Its Ecosystem Consequences. *Frontiers in Earth Science*, *5*. doi: 10.3389/feart.2017.00032

Soil Classification Working Group / Groupe de travail sur la classification des sols. (1998). *Canadian System of Soil Classification, 3rd Ed.* Retrieved from https://www.nrcresearchpress.com/doi/book/10.1139/9780660174044

Stockton, S. A., Allombert, S., Gaston, A. J., & Martin, J.-L. (2005). A natural experiment on the effects of high deer densities on the native flora of coastal temperate rain forests. *Biological Conservation*, *126*(1), 118–128. doi: 10.1016/j.biocon.2005.06.006

Sutherland Brown, A. (1968). *Geology of the Queen Charlotte Islands, British Columbia* (B.C. Ministry of Energy, Mines and Petroleum Resources Bulletin 54).

Takatsuki, S. (2009). Effects of sika deer on vegetation in Japan: A review. *Biological Conservation*, *142*(9), 1922–1929. doi: 10.1016/j.biocon.2009.02.011

Tanentzap, A. J., & Coomes, D. A. (2012). Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter? *Biological Reviews*, *87*(1), 72–94. doi: 10.1111/j.1469-185X.2011.00185.x

Terborgh, J., & Estes, J. A. (2013). *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*. Island Press.

Turetsky, M. R., Crow, S. E., Evans, R. J., Vitt, D. H., & Wieder, R. K. (2008). Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. *Journal of Ecology*, *96*(6), 1297–1305. doi: 10.1111/j.1365-2745.2008.01438.x

Vila, B., Torre, F., Guibal, F., & Martin, J.-L. (2004). Can we reconstruct browsing history and how far back? Lessons from Vaccinium parvifolium Smith in Rees. *Forest Ecology and Management*, *201*(2), 171–185. doi: 10.1016/j.foreco.2004.06.026

Wang, J., Wang, D., Li, C., Seastedt, T. R., Liang, C., Wang, L., … Li, Y. (2018). Feces nitrogen release induced by different large herbivores in a dry grassland. *Ecological Applications*, *28*(1), 201–211. doi: 10.1002/eap.1640

Wardle, D. A., Bonner, K. I., & Barker, G. M. (2002). Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology*, *16*(5), 585–595. doi: 10.1046/j.1365-2435.2002.00659.x

Wheeler, B. (2010). *Package "lmPerm."*

## Supporting Information

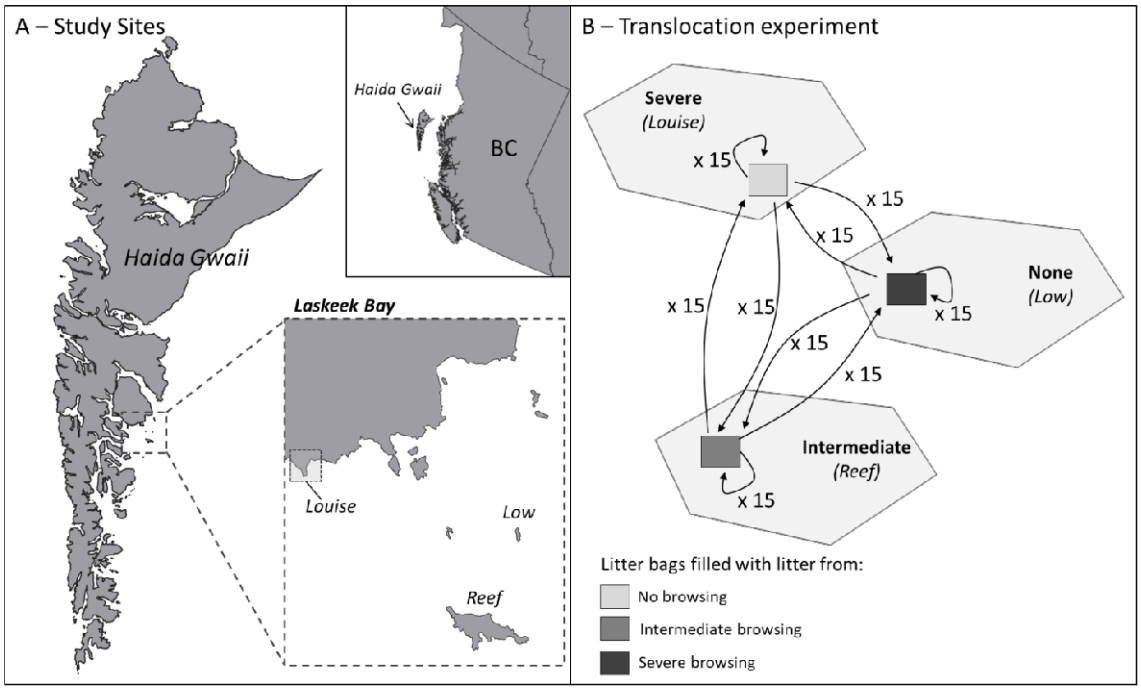


**Figure S1.** Study area and experimental design. A – Map of the study sites, B – Translocation pattern in the experiment 1. None = no deer browsing, intermediate browsing = deer present for over 70 years but exposed to significant culls between 1997 and 2010, severe browsing = deer present for over 70 years but not exposed to culls nor hunting

**Table S1.** Table synthesizing previously published results on the effect of deer on aboveground ecology of Haida Gwaii on islands covering the entire range of island sizes present in the archipelago

| Reference | Method/protocol | Main results |
|---|---|---|
| **Martin et al 1995,** Oikos | Songbird and vegetation sampling, 65 islands ranging from 1 to >300,000 ha | Except for the smallest most remote islands never colonized by deer, deer presence is the key factor explaining plant and animal distribution and community structure |
| **Engelstoft 1995,** Master's thesis | Vegetation sampling on Graham (6,361 km²) and Moresby Islands (3,399 km²) | Deer have dramatically reduced the understory vegetation and keep the sparse understory from recovering. Deer will also have profound affects on the overstory by eliminating recruitment of Western Redcedar |
| **Martin & Baltzinger 2002**, Can. J. For. Res. | Graham (6,361 km²) and Moresby Islands (3,399 km²): in different contexts of deer hunting pressure | Regeneration of western redcedar (*Thuja plicata*) is drastically reduced in presence of deer |
| **Allombert et al. 2005**, Conservation Biology | Six small islands of Laskeek Bay with different browsing histories (no deer vs deer present) | Insect abundance in the vegetation decreased eightfold and species density sixfold on islands with deer |
| **Stockton et al. 2005**, Biological Conservation | Seven small islands of Laskeek Bay with different browsing histories (no deer vs deer present) | Vegetation cover exceeded 80% in the lower vegetation layers on islands without deer and was less than 10% on the islands with deer |
| **Gaston et al. 2006**, Ecoscience | Ten islands of Laskeek Bay with different browsing histories (no deer vs deer present) ranging from 4.5 to 395 ha | Reversal of the normal species number-island area relationship as a result of deer browsing. Conclude that deer are a major factor structuring the island plant communities |
| **Stroh et al. 2008**, Forest Ecology & Management | Graham (6,361 km²): deer exclosure | Protected seedlings survived better, were higher, presented more leafed shoots, and had less stems than unprotected individuals |
| **Chollet et al. 2015**, Biological Invasions | 57 islands ranging from 1 to 425 ha with different browsing histories | Deer are the main factor explaining the abundance of understory vegetation and understory songbirds on the islands except for the few small isolated islands never colonized by deer. |

**Table S2**. List of plant species recorded in the three browsing treatments. All species had a percent cover higher than 5 % in at least one plot. Mean shannon index (Sh.) and richness (Rich.) are given for each plant guild. Mean percent covers are given for each species.

| No browsing | Intermediate browsing | Severe browsing |
|---|---|---|
| **Bryophyte (Sh. = 0, Rich. = 0.13)** | **Bryophyte (Sh. = 0.47, Rich. = 2.07)** | **Bryophyte (Sh. = 0.73, Rich. = 2.93)** |
| *Kindbergia oregana* | *Kindbergia oregana* | *Dicranum scoparium* |
| *Polystichum munitum* | *Marchantia sp* | *Hyloconium spendens* |
| | *Plagiomnium undulatum* | *Kindbergia oregana* |
| **Conifer (Sh. = 0.42, Rich. = 1.73)** | *Polystichum munitum* | *Plagiomnium undulatum* |
| *Picea sitchensis* | *Porella navicularis* | *Rhizomnium glabrescens* |
| *Thuja plicata* | *Rhizomnium glabrescens* | *Rhytidiadelphus loreus* |
| *Tsuga heterophylla* | *Rhytidiadelphus loreus* | *Scapania bolanderi* |
| | *Scapania bolanderi* | |
| **Fern (Sh. = 0.17, Rich. = 1.00)** | | **Conifer (Sh. = 0.73, Rich. = 2.4)** |
| *Pteridium aquilinum* | **Conifer (Sh. = 0.60, Rich. = 2.07)** | *Picea sitchensis* |
| | *Picea sitchensis* | *Thuja plicata* |
| **Forb (Sh. = 0, Rich. = 0.47)** | *Thuja plicata* | *Tsuga heterophylla* |
| *Maianthemum dilatatum* | *Tsuga heterophylla* | |
| | | **Fern (Sh. = 0, Rich. = 0.07)** |
| **Grass (Sh. = 0, Rich. = 0)** | **Fern (Sh. = 0, Rich. = 0.47)** | *Blechnum spicant* |
| - | *Blechnum spicant* | |
| | | **Forb (Sh. = 0, Rich. = 0.07)** |
| **Shrub (Sh. = 1.03, Rich. = 3.53)** | **Forb (Sh. = 0, Rich. = 0.13)** | *Galium triflorum* |
| *Alnus crispa* | *Listera caurina* | |
| *Gaultheria shallon* | *Moneses uniflora* | **Grass (Sh. = 0.04, Rich. = 0.13)** |
| *Lonicera involucrata* | | *Bromus sitchensis* |
| *Malus fusca* | **Grass (Sh. = 0.07, Rich. = 0.47)** | *Luzula parviflora* |
| *Rosa nutkana* | *Calamagrostis nutkaensis* | |
| *Rubus parviflorus* | *Luzula parviflora* | **Shrub (Sh. = 0.03, Rich. = 0.60)** |
| *Rubus spectabilis* | | *Gaultheria shallon* |
| *Salix scouleriana* | **Shrub (Sh. = 0.42, Rich. = 1.40)** | *Merzeansia feruginea* |
| *Sambucus racemosa* | *Alnus rubra* | *Vaccinium parvifolium* |
| *Symphoricarpos albus* | *Gaultheria shallon* | |
| *Vaccinium parvifolium* | *Merzeansia feruginea* | |
| | *Vaccinium parvifolium* | |

**Table S3.** – ANOVA tables of the models explaining the mass, carbon and nitrogen loss according to the litter composition and the decomposition place.

| Model | F-value | p-value |
|---|---|---|
| **Mass loss in fine-mesh bags ~** | | |
| Composition | 117.36 | **<0.001** |
| Decomposition place | 3.02 | **0.05** |
| Composition * Decomposition place | 1.08 | 0.37 |
| **Mass loss in coarse-mesh bags ~** | | |
| Composition | 9.49 | **<0.001** |
| Decomposition place | 4.54 | **0.01** |
| Composition * Decomposition place | 0.80 | 0.53 |
| **C loss ~** | | |
| Composition | 108.78 | **<0.001** |
| Decomposition place | 2.44 | 0.09 |
| Composition* Decomposition place | 1.03 | 0.40 |
| **N loss ~** | | |
| Composition | 17.53 | **<0.001** |
| Decomposition place | 1.15 | 0.32 |
| Composition * Decomposition place | 0.03 | 1 |

821 **Table S4.** – ANOVA tables of the models explaining carbon and nitrogen loss according to the
822 decomposition place and the CWM litter C:N.
823

| Model | F-value | p-value | $R^2$ |
|---|---|---|---|
| **C loss ~** | | | |
| CWM | 11.49 | **9.4 $e^{-4}$** | |
| Decomposition place | 0.99 | 0.38 | 0.098 |
| CWM* Decomposition place | 0.09 | 0.92 | |
| **N loss ~** | | | |
| CWM | 119.75 | **$2e^{-16}$** | |
| Decomposition place | 1.77 | 0.18 | 0.505 |
| CWM* Decomposition place | 0.96 | 0.38 | |

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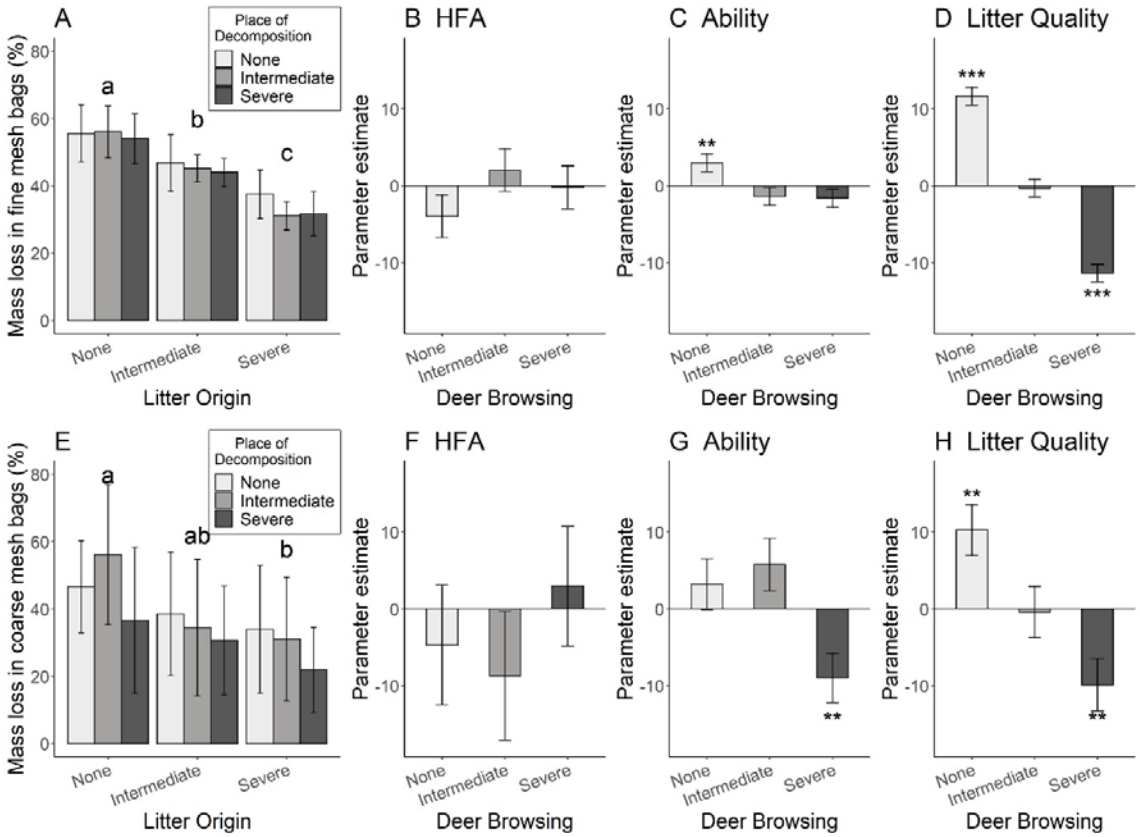


**Figure S2.** – Mass loss after one year of the plant litter among herbivory treatments for fine-mesh litterbags (top) and coarse-mesh litterbags (bottom) observed in the translocation experiment. Shades of barplots represent the herbivory treatment with: light grey = no browsing (no deer), grey = intermediate (deer present for over 70 years but exposed to significant culls between 1997 and 2010) and dark grey = severe browsing intensity (deer present for over 70 years but not exposed to hunting). Asterisks indicate estimates significantly different from zero with *<0.05, ** <0.01, ***<0.001. Panel A and Panel E represent mass loss among treatments in fine and coarse-mesh litter bags respectively with bars grouped according to litter origin (X axis) and shades corresponding to the place of decomposition. Panel B to D and F to G represent the parameter estimates (± SE) calculated using the Decomposer Ability Regression Test proposed by Keiser et al. (2014)

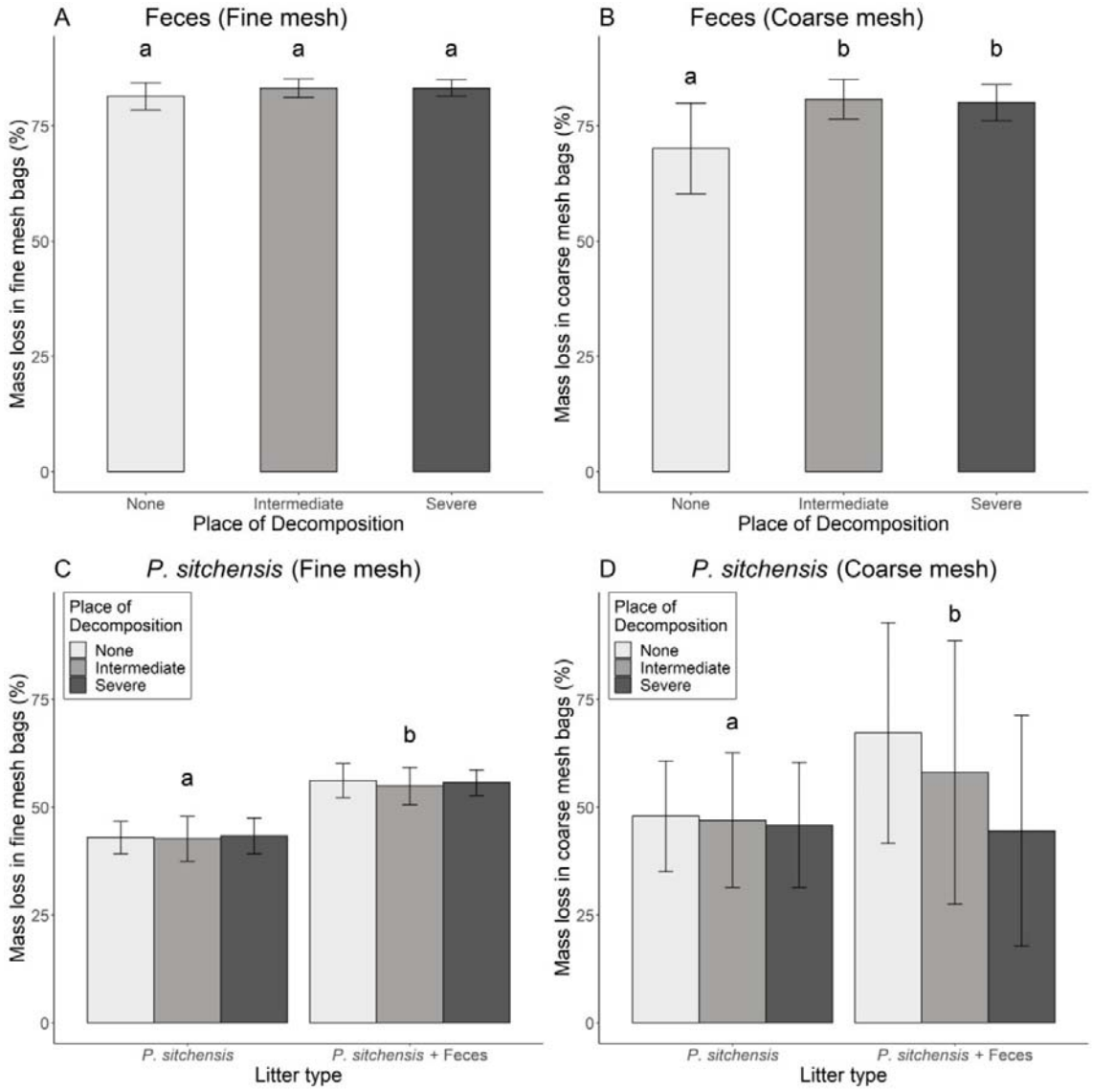


**Figure S3.** Decomposition of feces (top) and effect of feces addition on *Picea sitchensis* decomposition (bottom) for fine-mesh (left) and coarse-mesh (right) litterbags. Shades of barplots represent the browsing intensity of the place of decomposition with: light grey = no browsing (no deer), grey = intermediate (deer present for over 70 years but exposed to significant culls between 1997 and 2010) and dark grey = severe browsing (deer present for over 70 years but not exposed to hunting). Panel A – Mass loss in feces in fine-mesh litter bags; Panel B – Mass loss in feces in coarse-mesh litter bags; Panel C – Mass loss in *P. sitchensis* litter with and without the addition of feces in fine-mesh litter bags; Panel D – Mass loss in *P. sitchensis* litter with and without the addition of feces in coarse-mesh litter bags.