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Large herbivores strongly slow down litter decomposition in temperate forests

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Abstract

In temperate forest ecosystems, the role of large herbivores in litter decomposition, a key nutrient cycling process, is unresolved. Herbivores may first modify litter abundance by affecting plant cover. They may also modify the decomposition process by changing litter quality and altering decomposers' ability by changing soil abiotic properties and/or decomposer communities. Using two litterbag transplantation experiments in the quasi-experimental situation resulting from the introduction of Sitka black-tailed deer to the forests of Haida Gwaii (Canada), we disentangle the relative importance of the latter modifications on litter decomposition. We demonstrate that deer strongly reduce carbon (C) and nitrogen (N) loss, a 21 and 38 % decrease respectively, mainly by altering plant community composition. We reveal other ecosystem changes induced by deer through feces deposition, abiotic soil modification or decomposer community changes that affect decomposition processes, but are outweighed by deer top-down control on vegetation quality. Thus, the large increase in deer populations in temperate forests worldwide may be considered an important factor modifying global C and N cycling.

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Introduction

Large herbivores and the functioning of temperate forests

Temperate forests, dominated either by coniferous or by broadleaved trees, cover approximately 12% of the Earth's surface (Olson et al., 2001) and include some of the most threatened forest ecoregions (e.g. temperate rainforests, (DellaSala, 2011). Until recently, the role of large herbivores in nutrient cycling processes in these forests has been relatively neglected (Tanentzap & Coomes, 2012). This may be partly because forest ungulates were largely absent from European and many North American forests as a result of hunting and/or unfavorable habitat availability (McShea, Underwood, & Rappole, 1997; Apollonio, Andersen, & Putman, 2010). The dramatic rebound in herbivore populations in the second part of the 20th century, following changes in hunting regulations and in land-use (farm abandonment and reversion to forests), and the extirpation of their natural predators, brought large forest ungulates back to the forefront of ecological thinking (Terborgh & Estes, 2013). The initial emphasis of research was on the consequences of herbivore 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 the mechanisms of herbivore effects on forest aboveground communities has dramatically improved recently, the critical repercussions on belowground patterns and processes are still only insufficiently understood (Bardgett & Wardle, 2003; Hobbie & Villéger, 2015). Belowground effects will be partly mediated by the effects large herbivores have on litter decomposition. From an ecosystem perspective, litter decomposition plays a 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 few studies on how large forest herbivores affect different aspects of litter decomposition.

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Large forest herbivores and litter decomposition

Large herbivores may modify belowground processes by affecting two of the main controls on decomposition: litter quality and decomposers ability (Prescott, 2010). Through plant removal, combined with selective foraging, large herbivores modify plant community composition, plant stoichiometry, as well as the relative contribution of canopy and understory vegetation to litter composition (Côté, Rooney, Tremblay, Dussault, & Waller, 2004). These changes in plant litter quality and quantity will, consequently, modify decomposition processes and nutrient cycling (Bardgett & Wardle, 2003). In addition, large herbivores also produce high quality litter through dung and urine deposition that may enhance microbial activity, and thus, decomposition (Sitters et al., 2017). Independently from litter quality, recent evidence indicates 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" due to decomposer specialization may partly compensate the aforementioned changes in decomposition caused by large herbivores, but studies explicitly testing this hypothesis are scarce, and provide contrasting results (see Olofsson & Oksanen, 2002; Penner & Frank, 2018).

The second potential way large herbivores modify belowground processes is through alteration of decomposers ability. This could happen through change in soil properties, such as compaction, pH, moisture, that affect microclimates and consequently decomposition rates (Gass & Binkley, 2011; Z. Wang et al., 2018). In addition, large herbivores may also modify the development and functioning of decomposer communities [soil fauna (Andriuzzi & Wall, 2017) and microorganisms (Cline, Zak, Upchurch, Freedman, & Peschel, 2017; Eldridge et al., 2017)], changing the rate of litter decomposition (Handa et al., 2014).

There is recognition of the multiplicity of pathways through which large herbivores 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 has led to apparent contradictions in

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observed results. To better identify the mechanisms behind the effect of large herbivores on litter decomposition we designed a study that combined approaches able to disentangle the relative effects of multiple pathways on the process.

A unique quasi-experimental study site

Our long term study of how deer introduced to the archipelago of Haida Gwaii (British Columbia, Canada) affected the ecology of its forests (Table S1), provided a unique opportunity and critical background knowledge for an integrated study of large herbivore effects on litter decomposition. Sitka black-tailed deer (*Odocoileus odocoileus sitkensis*), native to coastal British Columbia's temperate rainforests, were introduced to Haida Gwaii from the nearby mainland in the late 19th century (Golumbia, Bland, Morre, & Bartier, 2008). Deer colonized most, but not all, islands, resulting in a quasi-experimental situation with islands colonized by deer early on, and a limited number of small isolated forested islands never colonized. The occurrence of reference islands without deer made it possible to demonstrate that, on all islands where deer were present, deer herbivory was the main factor structuring plant, invertebrate and songbird communities, overwhelming other biotic or abiotic factors (i.e. islands areas, soil and micro-habitats diversity (Chollet, Baltzinger, Ostermann, Saint-André, & Martin, 2013; Gaston, Stockton, & Smith, 2006; Martin & Baltzinger, 2002; Martin, Stockton, Allombert, & Gaston, 2010) and Table S1). In addition, the monitoring of islands subject to recurrent experimental culls allowed us to document the potential for recovery of the aboveground vegetation and songbirds that followed the severe reduction in deer herbivory (Chollet et al., 2016).

We made use of this exceptional situation to assess via two litterbag experiments how deer affected litter decomposition, and the mechanisms involved. First, we assessed the effect of deer presence on litter decomposition at the community scale. We used a reciprocal translocation of litterbags containing litters representative of three herbivory levels: strong on sites with deer, absent on sites without deer, and intermediate on sites with deer population subject to recent recurrent culls. The objective was to discriminate among the effects deer have on litter decomposition, either through

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their impact on litter quality or through their effect on decomposers' ability (including effects on soil properties and decomposer community composition), through an approach that explicitly includes home field advantage. Second, we added deer feces in a set of litterbags to assess how the deposition of high quality litter in the form of feces, affected the rate of litter decomposition.

Material and Method

Study site and vegetation sampling

Haida Gwaii is characterized by a humid temperate-oceanic climate, with mean annual temperature of 8.5°C and precipitation which varies greatly from 1,350 mm on the east coast to 7,000 mm on the west coast (Banner et al., 2014). The archipelago is covered by temperate rainforest dominated at low elevation by western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and Sitka spruce (*Picea sitchensis*). The location of our study sites are in the coastal western hemlock wet hypermaritime BEC subzone, CWHwh1, which occupies 49% the archipelago, and ranges from sea-level to 350m in elevation (Banner et al., 2014). Soil bedrock geology is volcanic and sedimentary, together with intrusions of granitic rock (Sutherland Brown, 1968).

We selected three islands in Laskeek Bay (52°53'12"N, 131°35'20"W, Figure S1 in Supporting Information). We selected sites with similar parent material and 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 for a synthesis of previous studies). Low Island, 9.6 ha, has never been colonized by deer. Louise Island, 25,000 ha, was colonized by deer for over 80 years ago (Vila, Torre, Guibal, & Martin, 2004) and has a current deer density estimated at 30 deer / km². Reef Island, 249 ha, was also colonized by deer more than 80 years ago, but its deer population has been regularly culled between 1997 and 2010. Reef Island has a current deer population density estimated at about 15 deer / km² and a partially recovered understory vegetation (Chollet et al., 2016). Low, Reef and Louise Islands therefore represent three distinct deer herbivory treatments: absence of current and historic browsing pressure, intermediate browsing pressure and strong browsing pressure, respectively. Our

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rigorous selection of sites with similar bedrock and similar forest types but representative of all three browsing regimes prevented us to control also for island size. To take this into account we selected all sampling plots in the coastal sites on all islands. On each island we established and sampled 15 vegetation plots of 10 m x 10 m, leading to a total of 45 plots. Adjacent plots were separated by at least 100 m. In each plot we estimated the percentage cover of vascular plants and bryophytes in three strata, ground, understory and canopy, using the Londo scale (Londo, 1976).

Litter and feces collection, litter bag construction and translocation experiment

We measured litter decomposition rates using the litter bag method. To obtain our litter samples, we collected summer senescent leaves from 33 plants species on the three islands (representing the three distinct deer herbivory levels). We dried these litter samples at 30°C for a week before using them. We collected fresh deer feces from another deer inhabited island in Laskeek Bay (East Limestone, 48 ha) in order to standardize feces quality. For litter decomposition we used 15 cm * 15 cm bags made of polypropylene mesh with two different mesh sizes. We used litterbags with a 0.2 mm mesh size to target the decomposition solely due to soil microfauna and microorganisms. We used litterbags with a 3.7 x 4.45 mm mesh size to assess litter the additional effect of mesofauna and macrofauna on decomposition.

We developed two complementary experiments in order to study the various mechanisms by which deer could affect the decomposition process.

Experiment 1. To investigate the decomposition of the plant community litter present in each given plot, we collected litter from all plant species covering more than 5% of the plot area. The objective was to produce litterbags for each plot that contained plant material in the same proportion as in the plot. We fixed total mass of litter per litterbag at 4g. Hence, the mass of each plant species litter was calculated according to its relative abundance in the plot. For each plot we made three identical litterbags for each of the two mesh-sizes. For each mesh size we placed one litterbag on the plot the litter came from (“Home”). We placed the two remaining bags per mesh-size on the plots on the two

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other islands ("Away"). This translocation allowed us to independently test for the effects of home field advantage, of decomposers ability (soil properties and decomposer community composition), and of litter quality on litter decomposition (Figure S1). Litter bags were numbered with aluminum tags and placed randomly on the surface of the forest floor on each plot, and held in place using U pins at each corner of the bag.

Experiment 2. To investigate the influence of deer feces on litter decomposition, we placed on each of the 45 plots a litterbag containing 2 g of deer feces and 2 g of a standardized litter (litter from one of the dominant tree species on all islands, *P. sitchensis*) for each of the two mesh-size bags. As controls, we used a litterbag only filled with 5g of deer feces and a litter bag exclusively filled with 2 g of *P. sitchensis* litter, again using the two mesh-size bags. We placed control litter bags on each plot. To avoid any biases from potential inter-treatment differences in spruce litter quality, we used a mix of *P. sitchensis* litter collected from the three islands for this set of litterbags.

Thus we placed a total of 12 litterbags ([3 community compositions + 1 feces + 1 *P. sitchensis* + 1 mix of feces and *P. sitchensis*] * 2 mesh size) at each plot, representing a total of 540 litterbags (12 bags * 45 plots). We fixed the litterbags at soil surface in July 2017 and collected them in July 2018, one year later. After collection we dried the contents of the litterbags at 70°C for 48h prior to weighing the contents and then performing chemical analyses.

Structural and chemical analyses

We measured initial C and N contents of dried litter from eight individuals of each plant species (vascular and bryophytes) from each island (with varying deer herbivory). Additionally, we measured initial C and N contents of eight deer pellet groups that were previously dried at 70°C for 48h. C and N contents were determined with an Elementar Vario El Cube Analyzer (Elementar, Langenselbold, Germany) using 3.5 mg of ground material. Based on these values and on the relative proportion of each litter in the bags, we calculated initial C and N content for each litterbag.

We further calculated carbon and nitrogen loss after one year in the small mesh litterbags only. At the end of the experiment we finely ground dried litter from the small mesh litterbags, and measured C

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and N content. We calculated carbon and nitrogen loss by subtracting the amount of carbon and nitrogen content after one year of decomposition from the initial amount.

We measured soil bulk density at the surface of the soil with five replicate measures per plot. For this, we collected soil with a 5.4 cm depth x 4.1 cm diameter (71.29cm^3) copper core hammered into the soil using a mallet. We took care to not change the structure of the soil while sampling. We removed any coarse woody debris from core samples and subtracted their volume from the volume of the core. We then dried soil at 105°C for 24h. We used data on soil pH, C:N and organic horizon depth collected from another study located on the same islands (Maillard et al. unpublished data) in different plots (but located in the same area). The data was collected from five plots on Low Island, five plots on Louise Island and six plots on Reef Island. Soil organic horizon depth was measured from a soil pit dug within each plot. Soil was sampled within the plots with a 2.5 cm diameter x 30 cm depth core. Approximately 100 samples per plot were composited and sieved with a 5 mm sieve to ensure homogenization. We measured soil pH in a 0.01 M $CaCl_2$ solution using a 1:10 ratio (air dried soil: solution). Soil C:N ratio was determined from 3 mg of freeze-dried and ground soil using an Elementar Vario El Cube Analyzer.

Statistical analysis

In order to evaluate the effect of deer herbivory on plant community composition we used Correspondence Analysis. In addition we calculated the Community Weighted Mean (CWM) of the litter C:N ratio at each plot using the formula $CWM_i = \sum_1^j (C_j \times p_j) \,/\, \sum_1^j (N_j \times p_j)$ with i representing the plot, j the plant species on this plot, C_j and N_j the C and N content of the corresponding litter, and p_j the relative abundance of the corresponding plant species on the plot.

We compared litter CWM C:N ratio, soil bulk density, soil pH, soil C:N ratio and organic horizon depth between the three islands using one way ANOVA with permutation tests.

Analyses of decomposition experiment 1 (plant community). We used two way ANOVA to compare mass loss, carbon loss and nitrogen loss between litterbags with the three litter sources (island with no, intermediate or strong deer herbivory) and the three decomposition place (island with

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no, intermediate or strong deer herbivory). To disentangle the relative importance of the two main ways deer may modify C and N decomposition, we used the Decomposer Ability Regression Test proposed by (Keiser, Keiser, Strickland, & Bradford, 2014) using SAS 9.4 (SAS Institute, Cary, NC). This method statistically discriminates among effects of litter quality (i.e. 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 capacity of decomposer communities]) and Home Field Advantage (i.e. the acceleration of decomposition of litter when decomposing in the plot the litter comes from as a result of specialization of the decomposer community). Compared to the classically used Structural Equation Modeling (SEM), the Decomposer Ability Regression Test offers the additional possibility to explicitly test HFA 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 two way ANOVA to compare mass loss, C loss and N loss of *Picea sitchensis*, feces and combination of both.

For all analyses when homoscedasticity and normality of the distribution of the residues were not respected (i.e large mesh litterbags) we used ANOVA with permutation tests instead of classical ANOVA (lmPerm package, (Wheeler, 2010).

We performed all statistical analyses (except Decomposer Ability Regression Test) in the R 3.4.1 environment (R Core Team, 2017).

Results

Deer modify aboveground and belowground characteristics

The first axis of the Correspondence Analysis clearly discriminated the plant species composition and abundance in the plots according to deer browsing level (Fig. 1A). In the absence of deer, vegetation cover was higher and there was greater shrub diversity. The vegetation on plots with strong deer

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herbivory was characterized by a high cover and diversity of bryophytes (Fig. 1A). Plots under intermediate deer herbivory showed intermediate plant species diversity and cover. We found no significant difference in the C:N ratio of the plant litter among deer herbivory treatments (Fig. 1B, p-value = 0.2).

Soil bulk density was significantly higher on plots from islands with deer (Fig. 1C, p-value < $2.2e^{-16}$). Soil pH and depth of the organic horizon measured in the plots significantly decreased with increasing deer browsing pressure (Fig. 1D and F, p-value = 0.037 and 0.0054 respectively). Soil C:N was not significantly different among treatments (Fig. 1E, p-value = 0.32).

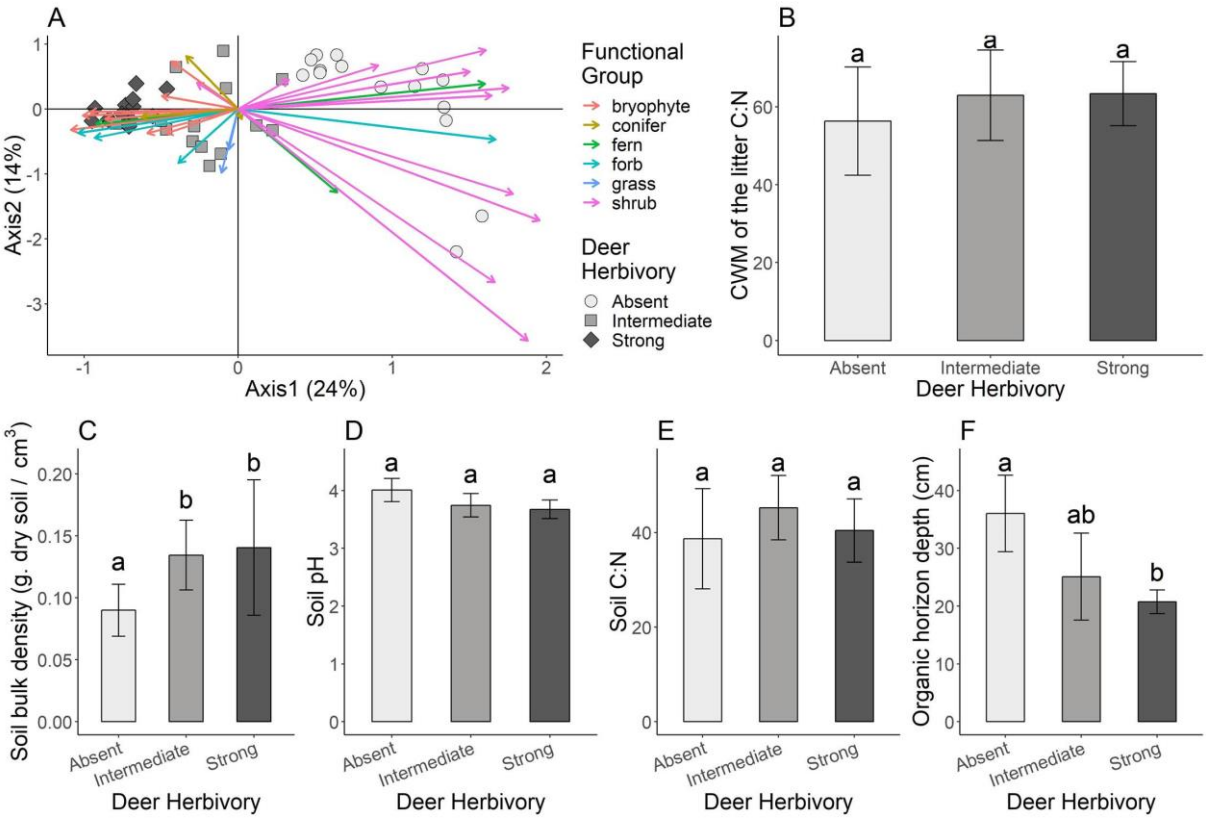

Figure 1. Effect of deer herbivory on aboveground (A, B) and belowground (C to F) parameters. Shades of dots and barplots represent the deer herbivory treatment with: light grey = no herbivory (deer absent), grey = intermediate (deer present for over 80 years but exposed to significant culls between 1997 and 2010) and dark grey = strong herbivory (deer present for over 80 years and not exposed to hunting). Small letters on each barplot indicate differences tested by post-hoc test. Panel A- Correspondence Analysis on the plot vegetation data. Dots represents the plots and arrows indicate the species contributions to axis. Plot symbols refer to the three deer herbivory treatments. Plant species are classified according to their functional group ; Panel B- Average 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.

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Decomposition of plant community litter

The loss of carbon in the litter was highest for litter originating from islands without deer and lowest for litter from islands with the most severe browsing pressure (Fig. 2A, F = 108.78, p-value = $<2e^{-16}$). When compared to litter originating from the island with no deer, Carbon loss was reduced by 12% in litter collected from the island with intermediate herbivory, and by 30% in litter collected from the island with strong herbivory, this independently of the decomposition context (Fig. 2A). Home field advantage was not significant, indicating that decomposers were not more efficient in decomposing litter carbon when it originated from their own environment rather than from other sites (Fig. 2B). The ability of the micro-fauna and microorganisms to decompose carbon was significantly higher for litter placed in plots without deer than in plots on islands with deer (Fig. 2B, p-value = 0.008). All litters decomposed 5% slower when incubated in the plots from the island with strong deer herbivory than in those from the island without deer. Litter quality was the main driver of carbon loss. Litter mixes originating from the island with no deer had the best quality index, followed by the litter mixes originating from the island with intermediate deer herbivory and then by litter mixes originating from the island with strong deer herbivory (Fig. 2B).

Litter mixes from the island without deer had significantly higher nitrogen loss than litter mixes from islands with deer. However, unlike C loss, nitrogen loss was lower for litter mixes originating from the island with intermediate deer herbivory than that originating from the island with strong deer herbivory (45% and 30% respectively, Fig. 2C, F = 17.53, p-value = $2.07e^{-07}$). We detected no home field advantage for N loss (Fig. 2D). In addition, none of the decomposer communities were better at decomposing and releasing nitrogen.

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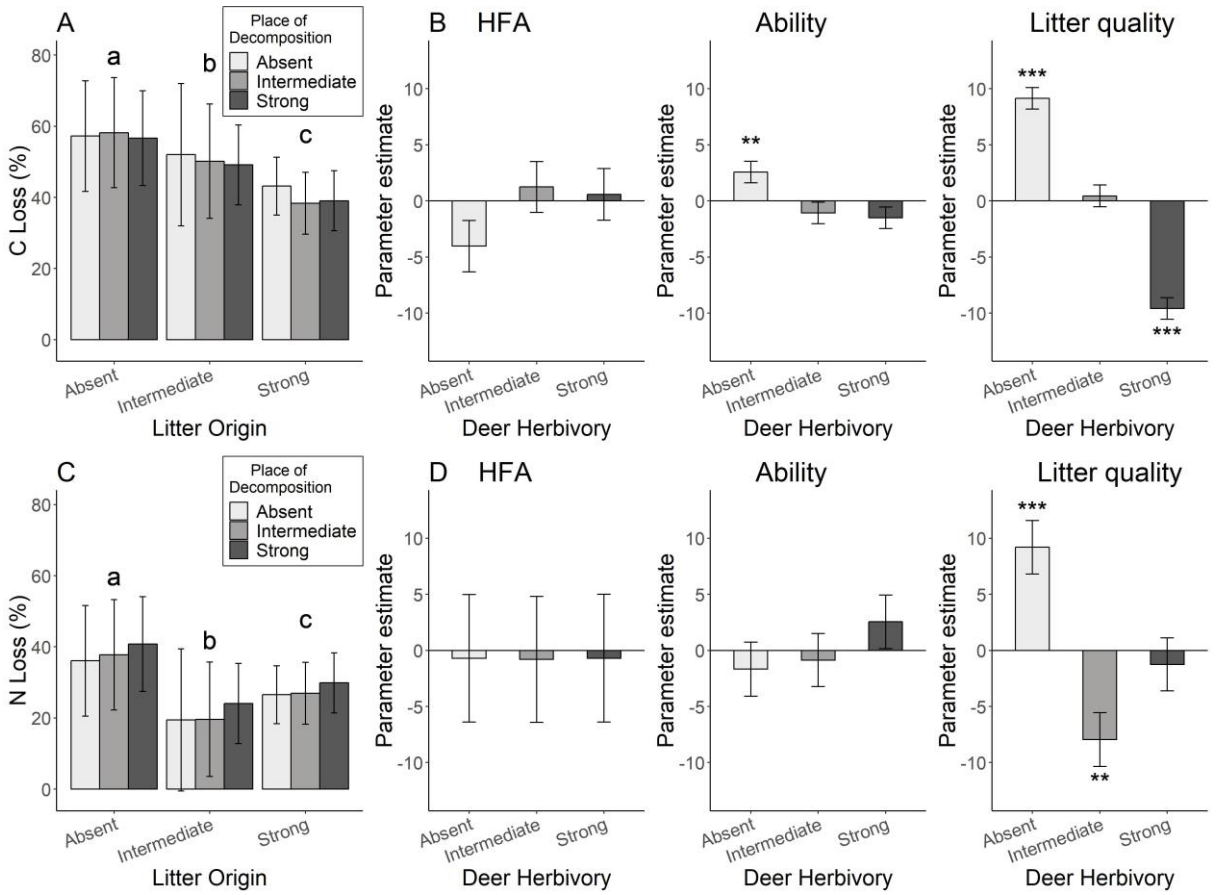

Figure 2. Decomposition rate of the plant community litter among deer herbivory categories for carbon (top) and nitrogen (bottom) in small mesh litterbags evaluated by translocation experiment. Shades of barplots represent the deer herbivory with: light grey = no herbivory (deer absent), grey = intermediate (deer present for over 80 years but deer density reduced by culls between 1997 and 2010) and dark grey = strong herbivory (deer present for over 80 years but not exposed to hunting, highest deer density). Asterisks indicate estimates significantly different from zero with *<0.05, ** <0.01, ***<0.001. Small letters in each barplots indicate differences tested by post-hoc test. Panel A and Panel C represent carbon and nitrogen loss among treatments respectively with bars grouped according to litter origin and shades corresponding to the category of deer herbivory where the litter bags were placed. Panel B and D represent the parameter estimates (± SE) calculated using the Decomposer Ability Regression Test proposed by Keiser et al. (2014).

Carbon and nitrogen loss were significantly and negatively related to the C:N ratio Community Weighted Mean (CWM) of the litter (Fig. 3). Litter nitrogen loss was strongly linked to C:N CWM, which explained 50% of its variability (Table S2). This link was stronger than the one observed for carbon, for which C:N CWM explained only 10% of its variation (Table S2).

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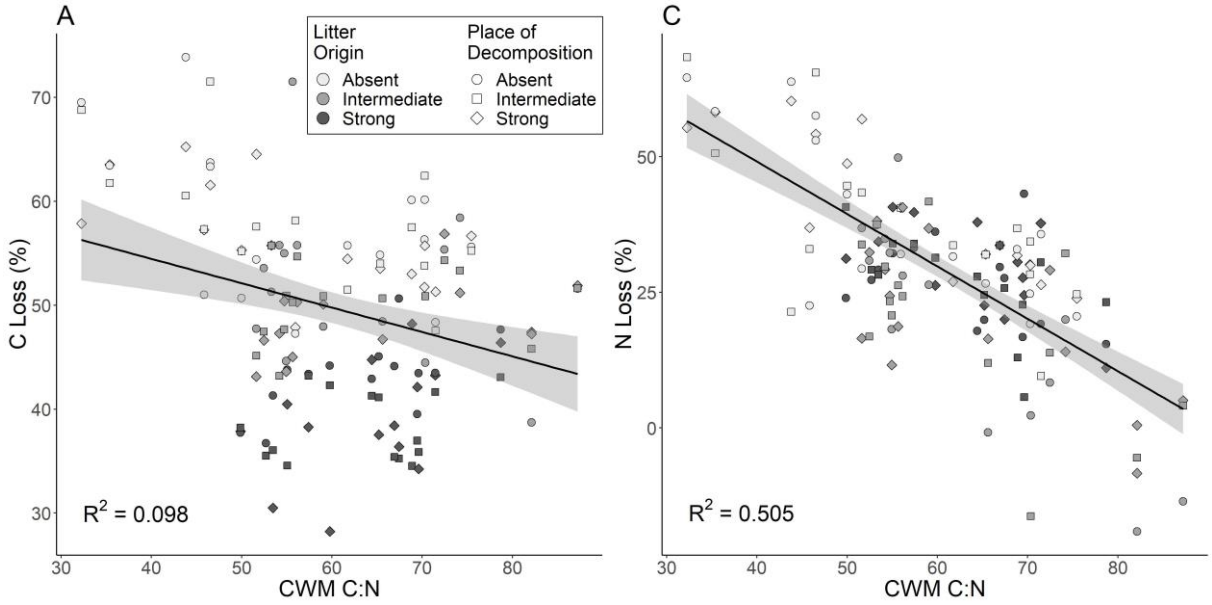

Figure 3. Linear regression of carbon (left) and nitrogen (right) loss variability with plant C:N Community Weighted Mean. Shades of dots represent the deer herbivory on the island where the litter came from, with: light grey = no herbivory (deer absent), grey = intermediate (deer present for over 80 years but not exposed to hunting, highest deer density) and dark grey = strong herbivory (deer present for over 80 years but not exposed to hunting, highest deer density). The shape of the symbols refer to the browsing category of the island where we placed the litterbags. Details on regressions models are given in Table S2

Results of mass loss in coarse mesh litterbags were similar to those from fine mesh litterbags, although variability between replicates was greater (Table S2). Mass loss in litter mixes originating from islands with intermediate and strong deer herbivory were respectively 26% and 38% lower than in litter mixes originating from the plots on the island without deer (p-value < $2e^{-16}$). Decomposers in the plots from the island with strong deer herbivory had significantly lower decomposition ability in large mesh bags. We observed a 25% decrease in mass loss in large mesh bags placed on the island with strong deer herbivory compared to bags placed on the island without deer (Figure S2 D, p-value = 0.006).

Feces decomposition

There were no differences in carbon and nitrogen loss from feces placed among the islands with different deer herbivory (Fig. 4A and B, F = 1.386, p-value = 0.26 and F = 0.416, p-value = 0.66 respectively). Feces addition significantly increased the decomposition of *P. sitchensis* litter by 31% for carbon and 47% for nitrogen (Fig. 4C and D, F = 175.62, p-value < $2e^{-16}$ and F = 66.39, p-value = $3.56e^{-}$

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^{12} respectively). The ability of the decomposer community (= decomposition place) had no effect on carbon lost (Fig. 4C, F = 0.752 and p-value = 0.47) by *P. sitchensis* litter. However, for nitrogen loss by *P. sitchensis* litter, the presence of deer feces together with, improved the decomposition ability of the decomposer community in the plots from the islands subject to herbivory (Fig. 4D, F = 20.10, p-value = $7.89e^{-08}$).

In coarse mesh litterbags we found that mass loss from feces was 15% higher on islands with deer than on islands without deer (Figure S3, p-value = $2.2e^{-16}$). The addition of feces also enhanced the decomposition of *P. sitchensis* litter in coarse mesh litterbags (Figure S2, p-value = 0.047).

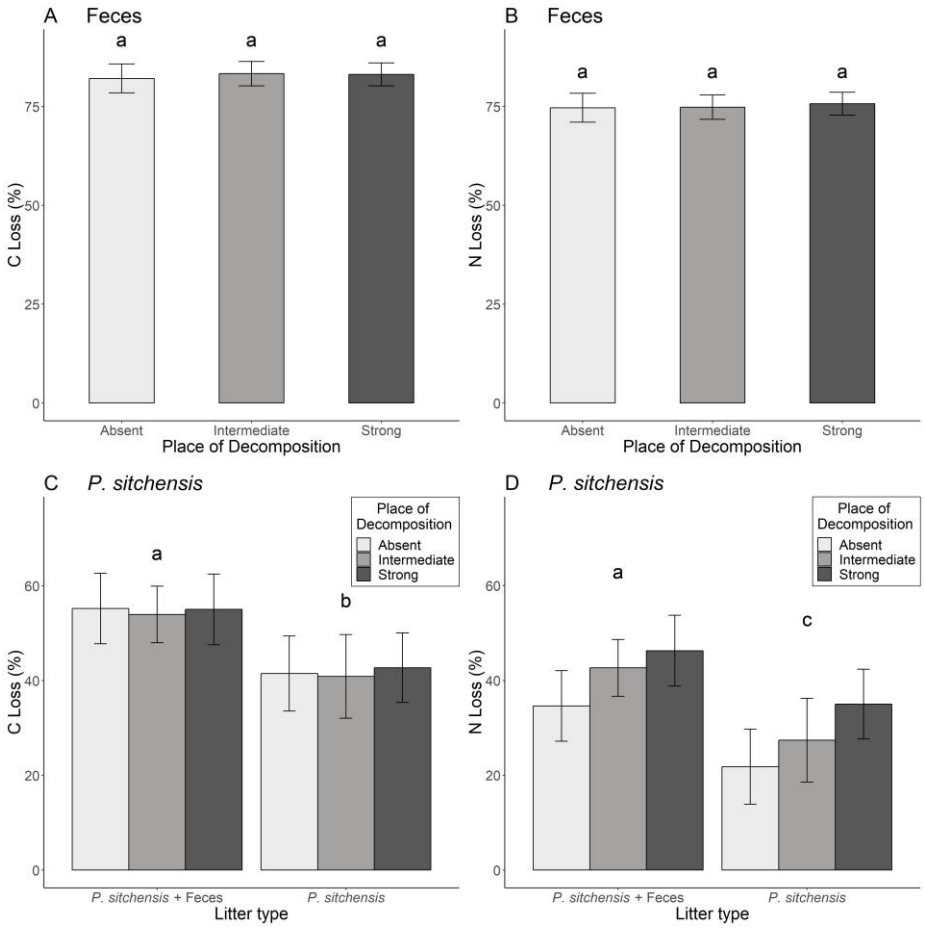

Figure 4. Decomposition of feces (top) and effect of feces addition on decomposition of *Picea sitchensis* litter (bottom) in small mesh litterbags. Shades of barplots refer to the deer herbivory category of the place of decomposition with: light grey = no browsing (deer absent), grey = intermediate (deer present for over 80 years but not exposed to hunting, highest deer density) and dark grey = strong deer herbivory (deer present for over 80 years but not exposed to hunting, highest deer density). Panel A – Carbon loss in feces; Panel B – Nitrogen loss in feces; Panel C – Carbon loss in *P. sitchensis* litter with and without the addition of feces; Panel D – Nitrogen loss in *P. sitchensis* litter with and without the addition of feces. Small letters above each barplots indicate differences tested by post-hoc test.

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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 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 (decomposers ability). Previous research focused on decomposers' 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 litter quality 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. In fact, the major shift in litter quality caused by deer browsing was a 25% reduction in carbon loss and a 27% reduction nitrogen loss in litter, independent of the location where the litter bags were placed (island with no, intermediate or strong herbivory). 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).

The prevailing importance of change in litter quality that resulted from deer herbivory on decomposition in the temperate forests we studied is in agreement with the microcosm study of (Harrison & Bardgett, 2003) who showed that decomposition of birch (*Betula pubescens*) litter, originating from inside deer exclosures (unbrowsed) in the Scottish Highlands decomposed faster than litter from outside of the exclosures (browsed), irrespective of the origin of the soil (inside or outside of exclosures). Conversely, (Olofsson & Oksanen, 2002) in a field translocation experiment assessing the decomposition of four plant species dominating the vegetation of lightly and heavily grazed tundra demonstrated a positive effect of herbivory on decomposition rate.

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The dramatic change in litter quality found in our study is the result of an alteration in the understory plant community. Intense and prolonged deer browsing dramatically changed the understory plant composition and cover, resulting in up to a 90% reduction in understory shrub cover, leading to a dramatic reduction in litter quality. These modifications not only confirm the severe effect of ungulates on the understory vegetation of Haida Gwaii (Chollet et al., 2013; Martin et al., 2010) but are consistent with results in other temperate forests (Côté et al., 2004; Boulanger et al., 2018).

We found that the reduction in litter quality, and the associated modifications in decomposition pattern, were only partly driven by the variation in the litter C:N ratio. The decline in litter quality affected carbon and nitrogen cycles differently. For carbon, litter quality decreased as deer herbivory increased. For nitrogen, litter quality was poorer in the intermediate deer herbivory than on the island with strong herbivory. The decline in litter C loss could be explained by the shift from an understory dominated by more decomposable species (shrubs) towards an understory of less decomposable species (conifers and bryophytes) as the level of deer herbivory 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 decomposability of the litter from islands with deer herbivory and thus the slight effect of CWM of litter C:N (≈10% of variation explained). The contrasting result we obtained for N loss in litter decomposition 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, which explains the lowest N loss values observed in this treatment (≈50% of variation explained by CWM litter C:N).

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Deer also modify decomposers ability

Although the change in litter quality caused by deer herbivory was 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. The contrast between carbon and nitrogen decomposition among islands, and the similarity in C and N decomposition when using large, rather than fine mesh litterbags, suggest 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 or lower pH. 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. 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 shrub cover may have reduced the root exudate which stimulate bacterial activity (Ekberg, Buchmann, & Gleixner, 2007). Contrary to carbon, the ability of decomposers to decompose nitrogen in litter did not vary among islands with different patterns of deer herbivory. This may be explained by the selection of microorganisms better able to exploit N in environments where this element is the most limiting ("nitrogen mining hypothesis", (Craine, Morrow, & Fierer, 2007) compensating for the switch in bacterial:fungal ratio. This hypothesis is supported by our control experiment, where we used a standardized quality of litter (*Picea sitchensis*), and found a greater ability of decomposers to decompose N in litter samples incubated on sites with deer.

Interestingly, we also found that the inclusion of the soil macro and mesofauna (hereafter fauna) in litter decomposition affected decomposition rates at the community scale (Figure S2). Specifically, we

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found that litter decomposition was reduced on the island with the highest deer density, suggesting a negative effect of high deer density on the faunal decomposer communities. Previous studies documented negative effects of large herbivores on the abundance and diversity of the soil fauna (see review by (Andriuzzi & Wall, 2017)), but the consequences on litter decomposition were not studied. As most previous studies on the effects of large herbivores on decomposition only considered the role of microbes, we feel more attention needs to be paid to the role of the soil fauna in order to better understand ecosystem nutrient cycling.

Soil fauna also plays an important role on the decomposition of feces, with evidence of Home Field Advantage (HFA). Indeed deer feces decomposition in our study was more rapid on islands with deer (home) than on the island without (away), but only when including the effects of fauna (large mesh bags, Figure S2). We infer that deer have a positive effect on animals decomposing dung. Such a positive effect of large herbivores on this specialized fauna has been recently demonstrated in Japan where (Iida, Soga, & Koike, 2018) found a positive relationship between the populations of dung beetles and deer density. In our study, we demonstrated that, litter fauna, but not microorganisms, were selected for decomposition of a particular litter type. This is an important result as most literature on HFA only considered microorganisms, and this suggests a potential underestimation of fauna on HFA.

Most knowledge on the effect of high quality litter deposition (dung and urine) by large herbivores on nutrient cycling comes from the study of domestic animals and/or grassland ecosystems (McNaughton, Banyikwa, & McNaughton, 1997; Frank & Groffman, 1998; Christenson, Mitchell, Groffman, & Lovett, 2010). We demonstrate that in these temperate forests dung decomposed faster, and released more nitrogen, than observed for plant litter. Also, the addition of feces increased the rate of *Picea sitchensis* decomposition, increasing C loss by 24% and N loss by 32%. This may be explained by the presence of labile nutrients in dung, which enhance the development of microbial communities, increasing rates of nutrient cycling (Bardgett, Keiller, Cook, & Gilburn, 1998). However, despite these results, we found that high quality litter deposition did not affect global decomposer ability (no higher decomposer

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ability on islands with deer dung/urine). This is partly surprising as recent studies demonstrated that feces deposition was responsible for changes in soil nutrient availability and plant productivity (Barthelemy, Stark, & Olofsson, 2015; J. Wang et al., 2018). The explanation for the lack of effect in the forests we studied likely rests with the patchy distribution of solitary deer, in contrast to herding species like reindeer or livestock, and thus reflects the patchy, and limited, amounts of dung deposited locally, amounts that are not sufficient to influence the nutrient cycling at the ecosystem level (Pastor, Naiman, Dewey, & McInnes, 1988).

Conclusion

Although given relatively little attention until recently, we demonstrate that deer in temperate forests are a key component 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 forest ungulates 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 an urgent need to expand our results to other temperate forest of the world to assess the overall consequences of these changes in ungulate abundance on global carbon storage (Tanentzap & Coomes, 2012) and nitrogen cycling in soils (Hobbie & Villéger, 2015).

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Statement of authorship

SC conceived the ideas and designed methodology; SC, MM, JS and J-LM collected the data; SC and MM 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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Supporting Information

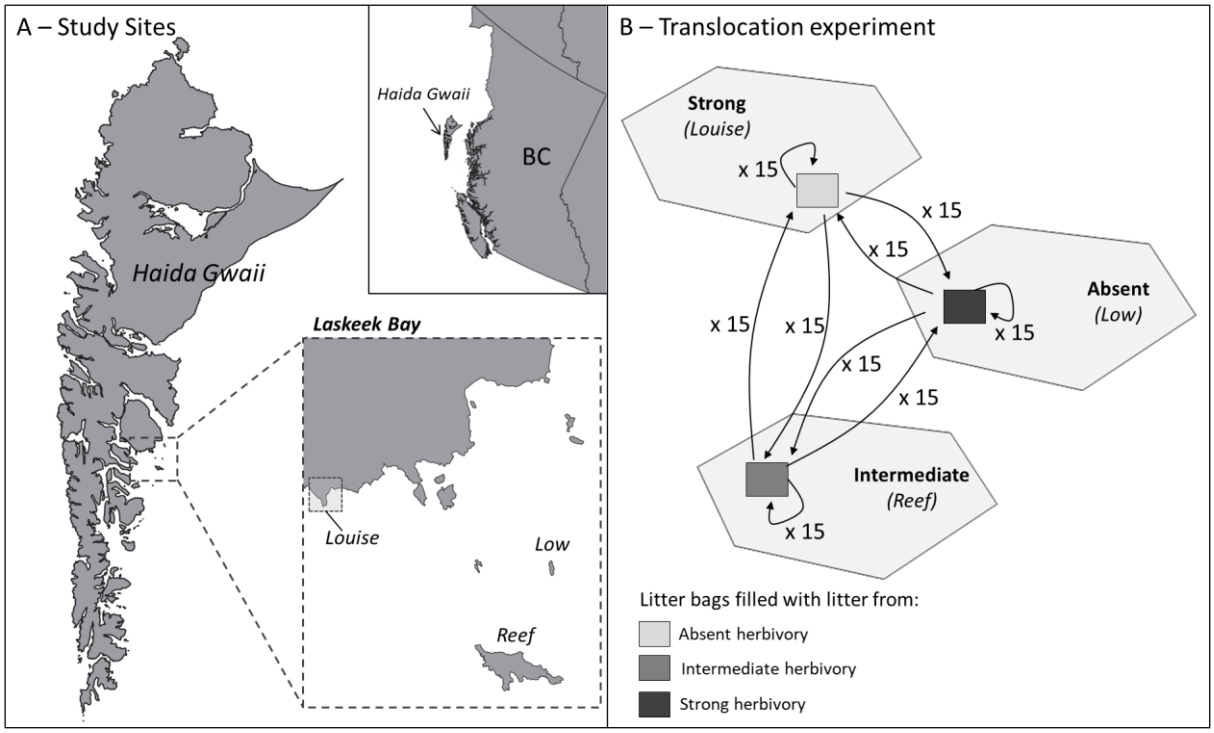

Figure S1. Study area and experimental design. A – Map of the study sites, B – Translocation pattern in the experiment 1. Absent = no deer, Intermediate = deer present for over 80 years but exposed to significant culls between 1997 and 2010, Strong = deer present for over 80 years but not exposed to hunting

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Table S1. Table synthesizing previously published results on the effect of deer on aboveground ecology of Haida Gwaii o islands covering the entire range of island sizes found 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.

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Table S2. – ANOVA tables of the models explaining carbon and nitrogen loss according the decomposition place, the CWM and the Rao litter :N

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	

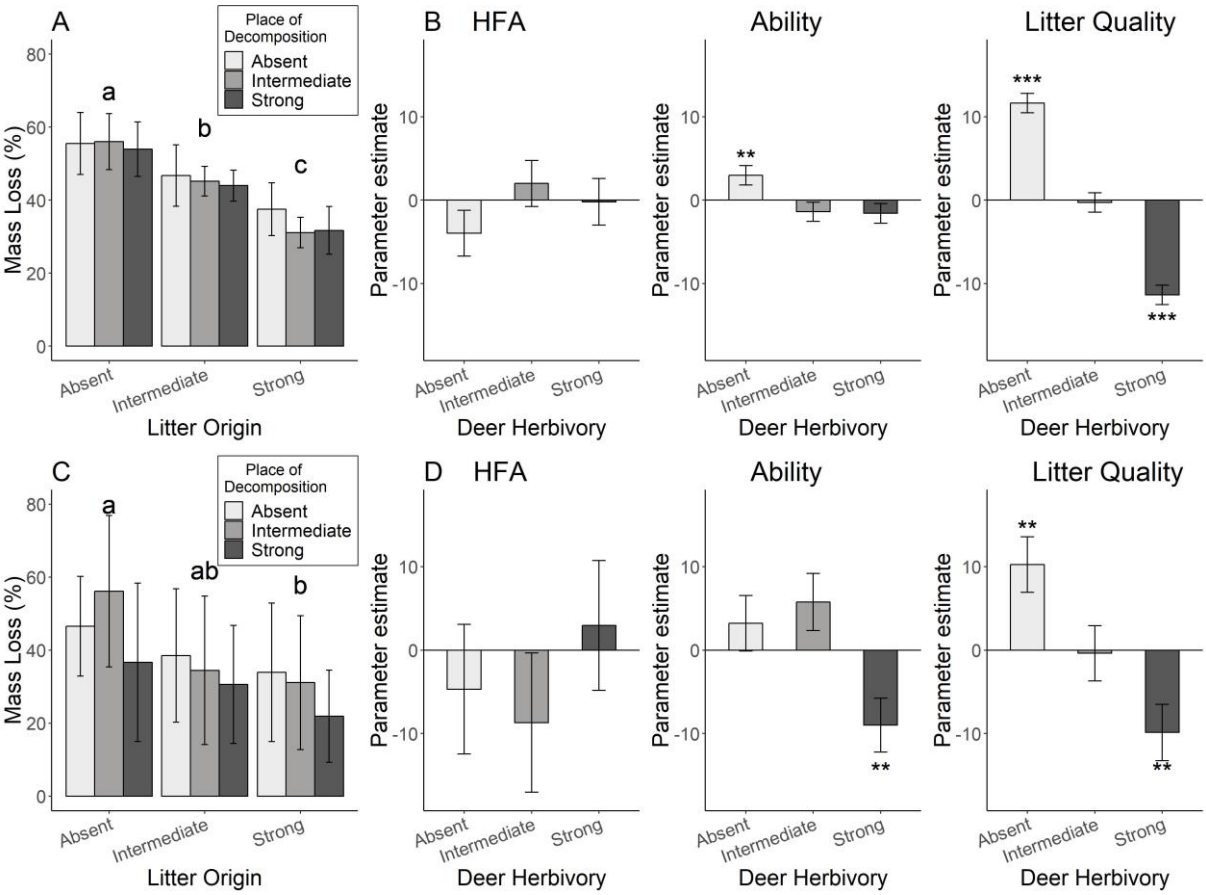

Figure S2. - Decomposition rate of the plant community litter among herbivory treatments for fine mesh literbags (top) and large mesh literbags (bottom) evaluated by translocation experiment. Shades of barplots represent the herbivory treatment with: light grey = no browsing (no deer), grey = intermediate (deer present for over 80 years but exposed to significant culls between 1997 and 2010) and dark grey = strong herbivory treatment (deer present for over 80 years but not exposed to hunting). Asterisks indicate estimates significantly different from zero with *<0.05, ** <0.01, ***<0.001. Panel A and Panel C represent mass loss among treatments in fine and coarse mesh litter bags respectively with bars grouped according to herbivory treatment of litter origin and colors corresponding to the location of decomposition. Panel B and D represent the parameter estimates (± SE) calculated using the Decomposer Ability Regression Test proposed by Keiser et al. (2014)

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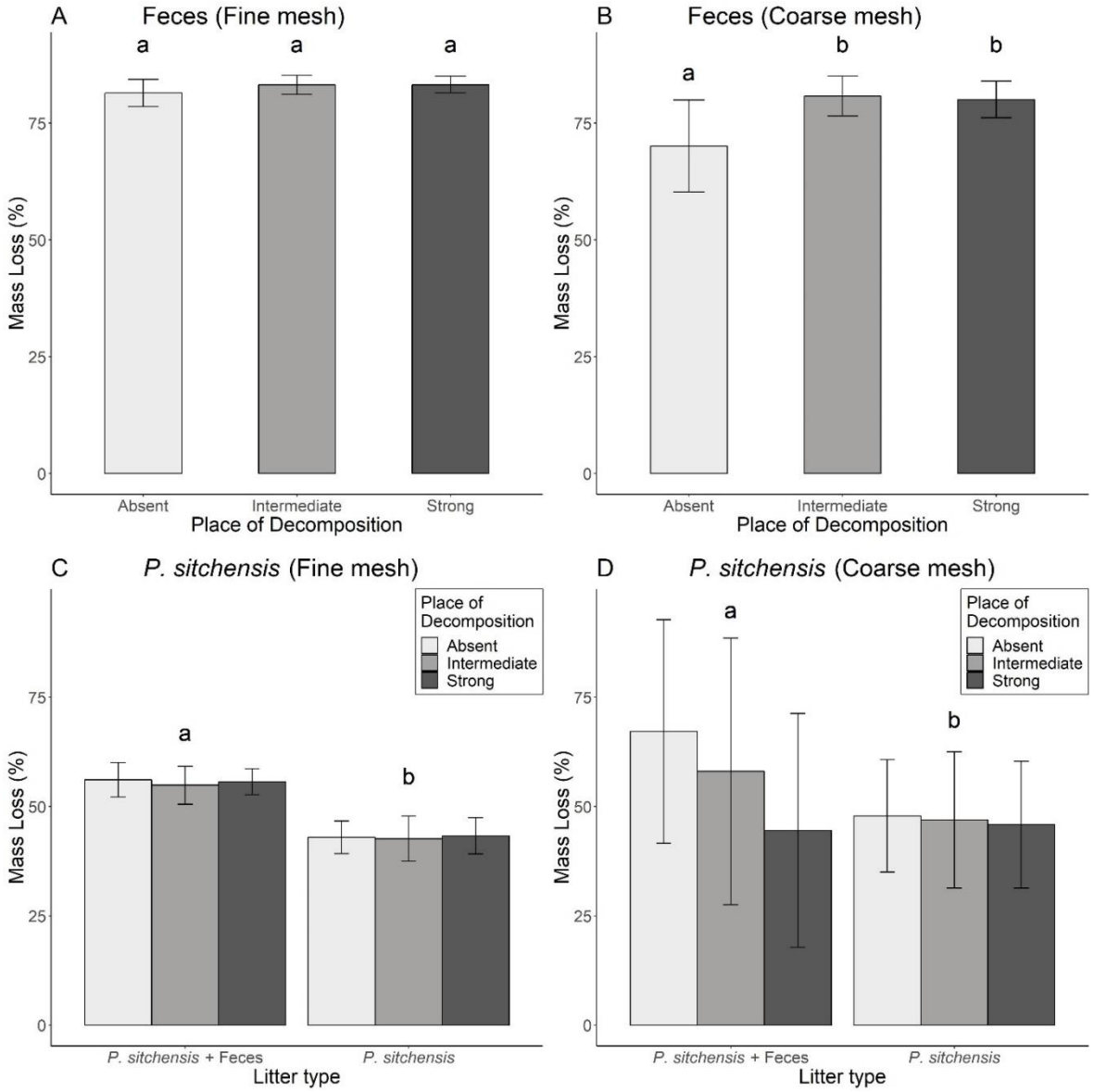

Figure S3. Decomposition of feces (top) and effect of feces addition on *Picea sitchensis* decomposition (bottom) for fine mesh (left) and large mesh (right) litterbags. Shades of barplots represent the herbivory category of the place of decomposition with: light grey = no browsing (no deer), grey = intermediate (deer present for over 80 years but exposed to significant culls between 1997 and 2010) and dark grey = strong herbivory treatment (deer present for over 80 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.