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Deer exclusion unveils abiotic filtering in forest understory plant assemblages

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- **Background and Aims** The role of deer (family Cervidae) in ecosystem functioning has traditionally been neglected by forest ecologists due to the animal's scarcity in most parts of the northern hemisphere. However, the dramatic rebound in deer populations throughout the 20th century has brought deer browsing to the forefront of forest ecological questioning. Today there is ample evidence that deer affect tree regeneration, understory plant and animal diversity and even litter decomposition. However, the mechanisms underlying the effects of deer on forest ecosystems remain unclear. Among others, the relative role of abiotic factors versus biotic interactions (e.g. herbivory) in shaping plant assemblages remains largely unknown.

- **Methods** We used a large-scale experiment with exclosures distributed along abiotic gradients to understand the role of black-tailed deer (*Odocoileus hemionus sitchensis*) on forest understory on the Haida Gwaii archipelago (western Canada), a unique context where most of the key ecological effects of deer presence had already been intensively studied.

- **Key Results** Our results demonstrate that 20 years of deer exclusion resulted in a clear increase in vascular plant richness, diversity and cover, and caused a decline in bryophyte cover. Exclusion also unveiled abiotic (i.e. soil water availability and fertility) filtering of plant assemblages that would otherwise have been masked by the impact of abundant deer populations. However, deer exclusion did not lead to an increase in beta diversity, probably because some remnant species had a competitive edge to regrow after decades of over-browsing.

- **Conclusions** We demonstrated that long-term herbivory by deer can be a dominant factor structuring understory plant communities that overwhelms abiotic factors. However, while exclosures prove useful to assess overall effects of large herbivores, the results from our studies at broader scales on the archipelago, suggest that exclosure experiments should be used cautiously when inferring the mechanisms at work.

Key words: abiotic factors, assembly rules, biotic interactions, bryophyte, legacy effects, overbrowsing, Sitka black-tailed deer, vascular plant.

INTRODUCTION

Growing evidence indicates that deer influence biodiversity and functioning of temperate and boreal forest ecosystems much more than previously thought. During the second part of the 20th century, most cervid (family Cervidae, hereafter deer) populations increased dramatically in many forest ecosystems of the northern hemisphere. The reasons for this recovery from severe historical population depletions are multiple. They vary among regions and include hunting regulations, restocking programs, changes in forestry and eradication of predator (Alverson *et al.* 1988; Crête and Daigle 1999; Warren 2011; Martin *et al.* 2020). As a result, deer populations became increasingly perceived as "over-abundant" in many countries (Côté *et al.* 2004; Takatsuki 2009; Carpio *et al.* 2021). Evidence indicates that abundant deer cause tree regeneration failure (e.g. Gill 1992), modify plant communities (e.g. Wiegmann and Waller, 2006), change litter decomposition (e.g. Chollet *et al.* 2021) and trigger cascading effects on animals that depend on the understory (e.g. Chollet and Martin 2013).

The studies of deer effects on forest ecosystems used a variety of methods including exclosure and enclosure experiments, experimental reduction of deer abundance through culls, comparison of sites varying in deer abundance (in a synchronic or diachronic way), the study of sites inaccessible to herbivores (rocky refuges, uncolonized islands) or simulated herbivory (i.e. clipping) (Waller 2014). However, most of the results came from exclosure experiments, with a large number of studies located in North America, Japan and Europe (Bernes *et al.* 2018). The limits of exclosure studies have been pointed out repeatedly. They include the fact that they only allow the comparison of one level of browsing with a complete lack of browsing. Furthermore, their results usually only focus on the effect of defoliation by deer and neglect their effect through trampling, soil litter disturbance/scraping, urine and faeces deposition or seed dispersal (Hester *et al.* 2000; Bergström and Edenius 2003; Waller

2014). In addition, as Mladenoff and Stearns (1993) pointed out, extrapolating the results of exclosure experiments from the stand scale to regional trends could be meaningless, because the small size of exclosures prevents information on factors (e.g. edaphic factors) other than those related to deer effect on the vegetation. In fact light availability, water stress and nutrient deficiencies are primary factors limiting plant long-term persistence and, consequently, influence community composition in most forest understories (Muller 2014; Neufeld and Young 2014). In a modelling exercise Mladenoff and Stearns (1993) suggested that the lack of hemlock (*Tsuga canadensis*) regeneration was not solely controlled by deer, and that a population reduction alone would not ensure successful regeneration. This study, among others, raised the question of the hierarchy between biotic interactions and abiotic factors in shaping plant assemblages.

In grass dominated ecosystems, large herbivores are predicted to reduce the dominance of the more competitive species and therefore to favour spatial plant coexistence (Olff and Ritchie 1998; Adler *et al.* 2001). One of the mechanisms behind this heterogeneity is that the reduction of competition due to herbivory allows a stronger control of community composition by abiotic filters. However, in boreal and temperate forests, where understories are dominated by slow growing perennial forbs and shrubs, the prediction of intense deer browsing effect on spatial vegetation heterogeneity may be quite different (Roberts and Gilliam 2014; Waller 2014). In fact, in these ecosystems, one could predict that high deer abundance would lead to a decrease in species richness and diversity, including beta diversity (i.e. measure of community heterogeneity), as understory plants may have more difficulty to withstand severe defoliation, and/or may be more palatable (Bardgett and Wardle 2003; Nuttle *et al.* 2014; Forbes *et al.* 2019). In such ecosystems, the relative role of biotic interactions and abiotic factors may be reversed, with stronger biotic than abiotic filtering. Despite such expected differences among ecosystem types, the effect of deer on vegetation spatial heterogeneity in forest ecosystems have been largely neglected, compared to grassland or savannah ecosystems (Gao and Carmel 2020). When effects of large herbivores in these systems were actually tested, some results suggested that strong abiotic gradients could actually affect the response of the forest vegetation to herbivory (e.g. Piazza *et al.*, 2016; Randall and Walters, 2011; Rhodes *et al.*, 2017 but see Suzuki *et al.* 2013). For example, Piazza et al. (2016) demonstrated that the impact of livestock on the composition and diversity of understorey vegetation increased along a precipitation gradient in *Nothofagus* forests of Argentina, with the wetter sites being more affected than the drier. In another study evaluating impacts of elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*) and cattle (*Bos taurus*) on aspen (*Populus tremuloides*) regeneration, Rhodes *et al.* (2017) highlighted a combined effect of herbivore density and abiotic factors (precipitation, elevation and stand composition).

In the present study we explore the effects of Sitka black-tailed deer (*Odocoileus hemionus sitchensis*) on the understory vegetation along abiotic gradients with the intention to evaluate the spatial heterogeneity of deer impact and vegetation response before and after deer exclusion. Specifically, our goal was to understand the relative role of abiotic and biotic filtering in the assemblage of understory plant communities. In order to achieve this, we designed a large scale exclosure experiment in a context where the ecological effects of deer presence had been intensively studied, the archipelago of Haida Gwaii in western Canada. Studies there documented a dramatic effect of deer on tree regeneration (Martin and Baltzinger 2002; Stroh *et al.* 2008), on understory and shoreline plant communities composition (Stockton *et al.* 2005; Martin *et al.* 2010; Chollet, Baltzinger, Ostermann, *et al.* 2013), on bryophyte communities (Chollet, Baltzinger, Le Saout, *et al.* 2013). They also showed a cascade of effects on insects and birds (Allombert, Stockton, *et al.* 2005; Allombert, Gaston, *et al.* 2005; Chollet *et al.* 2015), and the possibility of plant and bird communities recovery after a drastic reduction in deer density (Chollet *et al.* 2016). We used 20 exclosures placed in pairs in ten sites throughout the main island of the archipelago, Graham, where deer were initially introduced in the late 19th century resulting in the longest deer presence on Haida Gwaii (Fig. 1). Our intention here is to assess plant community recovery after twenty years of deer exclusion. Based on our previous results throughout the archipelago, we expected that after 20 years of recovery the vegetation should be more abundant, more diverse and more heterogeneous (higher beta diversity) within the deer exclosures than outside of them. In addition, a comparison of these results to those we obtained with different approaches on Haida Gwaii (Martin and Baltzinger 2002; Stockton *et al.* 2005; Chollet, Baltzinger, Ostermann, *et al.* 2013; Chollet *et al.* 2016) should give us a unique opportunity to critically assess the relative contribution of results from exclosures to the overall question of deer effects on vegetation.

MATERIALS AND METHODS

Study area and experimental design

The study took place on Haida Gwaii (formerly known as Queen Charlotte Islands, British Columbia, Canada), the largest and most isolated archipelago on the west coast of Canada. The islands (more than 150, including small islets) are largely formed of volcanic and sedimentary rock, together with intrusions of granitic rock (Sutherland Brown 1968) and are mainly covered with temperate rain forest classified in the Coastal Western Hemlock Zone (Banner *et al.* 2014). In these forests, the dominating canopy trees are Western redcedar (*Thuja plicata*), Western hemlock (*Tsuga heterophylla*) and locally Sitka spruce (*Picea sitchensis*). The shrub layer is usually dominated by regeneration of Western hemlock and shrubs like Salal (*Gaultheria shallon*), red huckleberry (*Vaccinium parvifolium*), blueberries (*Vaccinium alaskaense* and *V. ovalifolium*) and false azalea (*Menziesia ferruginea*) (Banner *et al.* 2014). Typical herb layer species are Deer fern (*Blechnum spicant*), false lily-of-the-valley (*Maianthemum dilatatum*), twayblades (*Listera ovata* and *L. cordata*), single delight (*Moneses uniflora*) and five-leaved bramble (*Rubus pedatus*) (Banner *et al.* 2014). Overall, the flora is similar to the one found in South-eastern Alaska and Northern British Columbia, but strongly impoverished due to insularity (i.e. 655 vascular plant species versus 2300, Banner et al. 2014). The climate is cool and oceanic, with a strong precipitation gradient. Mean annual precipitation ranges from 1000 mm on the east side of the islands to 7000 mm on their west side (Banner et al. 2014). Sitka black-tailed deer were introduced in the north of the largest island (Graham) in the late 19th century. In absence of their predators the population rapidly increased to reach densities higher than those found on the mainland (Martin and Baltzinger 2002). The average population density on the islands was estimated to range from 13 deer to 37 deer per km² (Engelstoft 2001; Stockton *et al.* 2005).

We used our exclosure experiment to characterize understorey vegetation change following 20 years of deer exclusion on Graham. The experiment consisted of 20 square exclosures (5 x 5 m, 25m²) set up in 1997 in 10 sites (two exclosures per site, Fig.1). We placed all exclosures in remnant old-growth forest patches dominated by Western redcedar. Each exclosure was paired with an unfenced area considered as a control plot. We chose site locations that reflected at best the forest island diversity in terms of precipitation, light availability and soil fertility. In each exclosure and associated unfenced control plot we recorded the % cover of all vascular plant species present in the 0 to 4m layer, as well as overall bryophyte cover (all species grouped) in the initial year, 1997 and in the final year, 2017. During the entire period, we checked and maintained fences regularly. Only one exclosure was destroyed in the winter 2016/2017 by tree-fall, leaving 19 intact exclosures for the 2017 survey. For each plot (inside and outside exclosure) we sampled soil in five randomly selected location in 2017 to evaluate soil fertility. From the mixed subsample we measured total carbon and nitrogen content (g / g dry soil) of freeze-dried soil using an Elementar Vario El Cube Analyzer (Elementar, Langenselbold, Germany).

Statistical analyses

Because skilled but different observers sampled the vegetation during the initial (1997) and the final (2017) monitoring sessions, we decided to minimize biases due to observer effect in species detection and in plant cover estimation by comparing characteristics of plant communities inside and outside exclosure only within a given year (i.e. in 1997 and in 2017).

For each year we compared alpha species richness, total species cover, species diversity (measured by Shannon index), beta diversity, indicator species (using IndVal, Dufrêne and Legendre 1997) and species composition (with Non-Metric Multidimensional Scaling, NMDS) for vascular plant species inside and outside deer exclosures. In addition, we compared total bryophyte cover inside and outside exclosures. Concerning beta diversity, as demonstrated by Baselga (2010), measures of dissimilarity are the resultant of two components, species turnover and nestedness, that could be partitioned. In the former the differences come from a replacement of species between assemblages but in the latter the poorest site is only a subset of the richest site (absence of replacement of species). In both case species assemblages are obviously dissimilar but not for the same reason. In addition the dissimilarity could be defined based on a qualitative (i.e. species presence) or quantitative (i.e. species abundance) dimension, which could also be partitioned (Baselga 2013). We studied beta diversity by partitioning the two components of a quantitative dissimilarity index (i.e. Bray-Curtis).

In order to study changes of assembly rules resulting from deer exclusion we evaluated the affinity of plant assemblages for soil moisture and nutrient regimes inside and outside exclosures using null models (Gotelli and Graves 1996). Species assemblage affinity was calculated as the mean value of each species affinity index present in the plot. We extracted semi-quantitative estimations of species affinity for moisture and nutrient from Klinkenberg (2020). These are equivalent to Ellenberg's indicator values in the European flora. We compared the mean species assemblage value of each plot (inside and outside) to 4,999 random assemblages drawn from the species pool (combination of all observed species). For a species richness S_i in plot i, our null model randomly sampled S_i species, each with a probability equal to its frequency in the species pool. For each plot we compared the observed value to the distribution generated by the 4,999 runs of the null model by calculating Standardized Effect Size (SES) as:

$$SES = \frac{(I_{obs} - \mu I_{null})}{\sigma I_{null}}$$

with I_{obs} the observed metric, μI_{null} and σI_{null} respectively the mean and standard deviation of the plot null distribution.

We compared treatment (inside vs. outside exclosure) and site effects on vascular species richness, Shannon index, beta diversity, total species cover and bryophyte cover with two-way ANOVAs. We studied the effect of precipitation (i.e. longitude as a proxy of the gradient, increasing form east to west), light availability (i.e. canopy cover as a proxy) and soil fertility (i.e. total soil C : N as a proxy) on vascular species richness, diversity, cover, bryophyte cover and SES with multiple regression models (including stepwise selection of explanatory variables) in 2017. To complement NMDS we tested the difference in species composition with Permutational Multivariate Analysis of Variance (PERMANOVA).

All statistical analyzes were performed in the R environment (R Core Team 2020) using the vegan (Oksanen *et al.* 2019), betapart (Baselga *et al.* 2018) and Indicspecies (Cáceres *et al.* 2020) packages.

RESULTS

At the outset of the study vascular species richness, Shannon diversity index, vascular plant cover and bryophytes cover were similar inside and outside exclosures, but varied among sites (Fig. 2 Supplementary data Table S1). After 20 years of deer exclusion the three metrics assessing vascular species were significantly higher inside than outside. Differences among sites remained significant (Fig. 2, Supplementary data Table S1). At the end of the period bryophyte cover had significantly decreased inside exclosures with an absence of differences among sites (Fig. 2, Supplementary data Table S1).

Multiple regression models indicated that at the end of the study variation in soil fertility (C : N) explained the among site variation in species richness, vascular plant cover, diversity (Shannon) and to a lesser extent moss cover variations in the exclosures (Fig. 3, Supplementary data Table S2). Conversely, outside of the exclosures, only species richness could be explained by C : N and this to only a limited extent (Fig. 3, Supplementary data Table S2). For vascular plants, the higher the soil fertility the higher the three studied community metrics, whereas the opposite pattern was observed for moss cover.

Our null models indicate non-random filtering for mean soil moisture and nutrient affinity index of plant assemblages inside exclosures (Fig. 4). Assemblages located on the west coast (i.e. higher precipitation record) were composed of species with a higher need for soil humidity (Fig. 4A) and species assemblages of more fertile sites were composed of species with a higher affinity for soil nutrient (Fig. 4B). These non-random trends in community assembly we observed inside the exclosures were lacking or weaker in plots placed outside of the exclosures (Fig. 4).

We found that only eight of the 44 species were significantly associated with a treatment, and it was only for the inside of exclosures in 2017 (Table 1). Among these species were two trees (*Chamaecyparis nootkatensis, Thuja plicata*), three shrubs (*Gaultheria shallon, Menziesia ferruginea, Vaccinium parvifolium*), two forbs (*Cornus canadensis, Rubus pedatus*) and one fern (*Blechnum spicant*).

In 1997 beta diversity (as measured with Bray-Curtis index) did not differ between the inside and outside of exclosures ($F= 0.44$, $p>0.05$, Fig. 5A), and there was no significant difference among sites ($F= 1.04$, $p>0.05$). Twenty years later beta diversity was significantly lower for plots sampled inside the exclosures than outside ($F= 20.37$, $p<0.001$, Fig. 5B) but again without any difference among sites ($F= 0.28$, $p>0.05$). The higher dissimilarity observed in 2017 outside of the exclosures mainly reflected a difference in species abundance, as some individuals were lost from one site to the other but without substitution [significant difference in nestedness (Bray-Curtis gra component, Fig 5F) but not in turnover (Bray-Curtis bal component, Fig 5D)].

The Non Metric Multidimensional Scaling shows that the composition of plant communities were totally overlapping at the beginning of the study (in 1997) but that this was no more the case at the end (in 2017, Fig. 6, Supplementary data Table S3). This result is confirmed by the PERMANOVA where we found no significant differences between inside and outside plots in 1997 ($R^2=0.007$, $F=0.56$, $p>0.05$) but a difference in 2017 ($R^2=0.20$, $F=11.7$, $p<0.001$). The site effect was important in 1997 ($R^2=0.63$, $F=5.07$, $p<0.001$) as well as in 2017 ($R^2=0.35$, $F=2.23$, $p<0.001$). In 2017, the heterogeneity among plots was lower inside than outside exclosures, indicating increased similarity after 20 years of deer exclusion (Fig. 6).

DISCUSSION

Deer as dominant biotic filter

Plant community assembly is classically considered as the result of the interplay of dispersal, and of abiotic and biotic hierarchical filtering (Keddy 1992; Lortie *et al.* 2004). The key result in this study is that abundant deer presence can act as a strong biotic filter overwhelming abiotic factors in the control of the vegetation. While the presence of deer resulted in low vegetation cover outside of the exclosures, the increases in species richness, diversity and plant cover inside the exclosures depended not only on deer exclusion for 20 years, but were also strongly dependent on soil fertility. The most fertile sites (i.e. low C : N) benefited the more from deer exclusion, whereas sites with low fertility showed weaker response to deer exclusion. This lack of change in plots with the lower amount of nutrient is key because it shows that recovery from deer overabundance will only be possible, at least in the medium term, on relatively richer sites. Outside of the exclosures, only species richness was influenced by soil fertility, and to a lesser extent to what we observed inside of the exclosures. These differences in plant community response to soil fertility when deer are abundant suggest that they act as a strong biotic filter in the assembly of plant communities, overwhelming abiotic filters. This interpretation is confirmed by our results testing the change in plant assemblage affinity for soil moisture and nutrients (Fig. 4). In fact, we found that in absence of deer, assemblages were non-random, with wet and fertile sites harbouring communities characterized by species with higher affinity for wet and rich soils respectively. However, in presence of deer (i.e. outside of exclosures) these trends fade away.

Deer differentially affect community characteristics

More generally, our results confirm that abundant deer can be a dominant factor controlling understorey vegetation in Haida Gwaii forests. Twenty years of deer exclusion resulted in a clear increase of vascular plant cover and diversity. This increase of understorey vegetation was concomitant with a reduction in bryophyte cover, probably resulting from increased competition for light and for growing space because of the developing vascular plant cover (Chollet *et al.* 2013; Chollet *et al.* 2016). Interestingly we documented only a relatively small increase in alpha species richness, suggesting that deer, although strongly controlling plant abundance, have a comparatively smaller effect on species presence. However, this interpretation could be challenged by previous results we obtained at broader scales on the archipelago (Stockton *et al.* 2005; Chollet, Baltzinger, Ostermann, *et al.* 2013). These showed a positive effect of deer absence on plant species richness on islands never colonized by deer (Stockton *et al.* 2005), on refuges inaccessible to deer (Chollet, Baltzinger, Ostermann, *et al.* 2013) or at the landscape scale after a severe experimental reduction in deer density (Chollet *et al.* 2016). We hypothesize that the relatively small increase in species richness observed in our small-size and isolated exclosures after twenty years of deer exclusion may reflect a deficit in colonization. Woodland specialist-plant species, in particular, are indeed known to be poor colonists (Bossuyt *et al.* 1999; Rooney and Waller 2003; Verheyen and Hermy 2004; Waller 2014). Nevertheless, the changes we observed in the vegetation are consistent with the results obtained throughout the northern hemisphere where deer population greatly increased during the 20th century (Rooney and Waller 2003; Côté *et al.* 2004; Takatsuki 2009; Habeck and Schultz 2015; Ramirez *et al.* 2018) or in places where deer were introduced (Tanentzap *et al.* 2009; Nuñez *et al.* 2010).

Deer effects are selective

The species which benefited the more from deer exclusion (as revealed by the IndVal analyses) were mainly shrubs and tree species, all considered as typical from the Coastal Western Hemlock Zone and highly palatable to deer (Pojar *et al.* 1980). One of this species, Western redcedar, is of particular interest as it represents an essential element of Haida culture (Turner 2004). The negative effect of deer on Yellow cedar (*Chamaecyparis nootkatensis*) is also important because this species has been recently found to be also negatively affected by global warming on Haida Gwaii (Comeau *et al.* 2019) as well as on the mainland (Hennon *et al.* 2012), questioning the future of this important species on the islands. The three shrub species which benefited from deer exclusion (*Gaultheria shallon*, *Menziesia ferruginea*, *Vaccinium parvifolium*) are also widely used by first nations as food or medicine and are considered as diagnostic elements of the Coastal Western Hemlock Zone forest type (Turner 2004; Banner *et al.* 2014).

Deer exclusion leads to local biotic homogenization

Twenty years after deer exclusion, vegetation heterogeneity was lower inside than outside of the exclosures (Fig. 5 and 6), suggesting a local biotic homogenization (Olden and Rooney 2006). This pattern of dominance of some species inside exclosures could reflect the fact that large herbivores, by reducing the dominance of the more competitive species (browsing effect), or by creating microhabitat (trampling effect), or by moving seeds (dispersal effect), create heterogeneity that could lead to increased beta diversity. This has often been documented in grass dominated ecosystems (Olff and Ritchie 1998). An alternative hypothesis is that the dominance of competitive species observed inside the exclosures was partly an artifact linked to past overbrowsing (i.e. legacy effect). Under this hypothesis, species dominance could be understood as the result of the better recovery of a minority of species that had a higher ability to withstand the prolonged presence of deer. This would confer them an initial advantage once protected, and limit the increase of poor colonizing species initially absent or more suppressed. Although we cannot fully affirm which of these non-exclusive hypotheses prevails, our results on beta diversity partitioning support the second hypothesis. In presence of deer, the higher beta diversity is explained by heterogeneity in abundance, and not by species replacement (Fig. 5). In other words, species present outside of the exclosures were also present inside, but with less variation in their abundance among sites. This suggests that herbivory, trampling or dispersal are not creating heterogeneity, but that, after deer exclusion, the abundance of the species already present increases and converges to similar cover values among sites. This understory homogenization inside the exclosures could be illustrated by the strong increase in cover of competitive and relatively fast growing species like *Gaultheria shallon* (Fraser *et al.* 1995; Bennett *et al.* 2011). That dominance of a small number of competitive species may disappear in the long term and at larger scale. This is actually what we observed in the already mentioned landscape-scale experiment of deer density reduction which, ultimately, triggered an increase in both vegetation and bird community heterogeneity at the broader scale (Chollet *et al.* 2016).

CONCLUSION

Our study demonstrates that deer, when overabundant, could overwhelm abiotic factors controlling plant communities (here soil water availability and fertility). In addition, deer reduced alpha species richness, diversity and the cover of understory plants typical from the studied costal rainforest. Despite consistency with other studies on the archipelago using different methodologies, this study based on a twenty-year exclosure experiment provided results not entirely in agreement with those observed at more broader and more realistic spatial and/or temporal scales. The less dramatic increase in species richness or the decrease in beta diversity we observed after (only) 20 years of excluding deer from small sections of forests (25 m²) could be patterns sensitive to study length or scale. We actually highlighted the key importance of addressing questions at the appropriate temporal scale in a research conducted in the same study system on deer effects on soil physicochemical properties and bacterial communities (Maillard *et al.* 2021). This called caution when using even 20 year-long exclosure experiments to assess the interactions between deer and vegetation or other ecosystem components and properties. We could overcome the difficulty by combining the exclosure experiment with other approaches involving islands with deer and islands never colonized by deer, or the vegetation in natural refuges protected from deer browsing, or the experimental reduction of deer density. But this was only made possible, on one hand, by the rare and unplanned experimental situation created by the introduction of deer to Haida Gwaii and, on the other hand, by the also rare ability to thoroughly study this system for decades.

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Tables

Table 1. Indicator species (measured by Indicator Value, Dufrêne and Legendre 1997) per treatment (Inside/Outside exclosures) per year (1997: onset; 2017: last monitoring).

	Inside	**Outside**
1997	No species associated to this treatment	No species associated to this treatment
2017	*Chamaecyparis nootkatensis* *Thuja plicata* *Gaultheria shallon* *Menziesia ferruginea* *Vaccinium parvifolium* *Cornus canadensis* *Rubus pedatus* *Blechnum spicant*	No species associated to this treatment

Figure captions

Figure 1. Study area and study sites

Figure 2. Comparison of vascular species richness, diversity (Shannon index), vascular plant cover and moss cover inside and outside deer exclosures in 1997 (left) and 2017 (right). Statistical differences were tested with two way ANOVAs. *:p-value<0.05, ***: p-value<0.001.

Figure 3. Linear model inside (black dots) and outside (open triangles) deer exclosures in 2017 for variables selected in stepwise regression (see Supplementary data Table S2 for statistical models). Statistical significance was tested with Linear Regression Models. (*): p-value<0.1, *: p-value<0.05, ***: p-value<0.001.

Figure 4. Standardized Effect Sized (SES) of the mean soil moisture index (A) and soil nutrient index (B) as a function of respectively precipitation gradient (Distance to West Coast as a proxy) and soil fertility (soil C : N as a proxy) in 2017. Black dots correspond to plots inside deer exclosures and open triangles to plots outside deer exclosures. Statistical significance was tested with Linear Regression Models. (*): p-value<0.1, *: p-value<0.05.

Figure 5. Beta diversity measure with Bray-Curtis index (A, B) and partitioning in its two components: 1) balanced variation in abundance (Bray-Curtis bal) representing substitution of species (C, D), and 2) abundance gradients (Bray-Curtis gra) representing the change in abundance of the same species between plot (E, F) inside and outside deer exclosures in 1997 (left) and 2017 (right). Statistical differences were test with one-way ANOVA. ***: p<0.001.

Figure 6. NMDS analysis in 1997 (stress =0.21) and 2017 (stress =0.15). Open triangles are plots outside exclosures and black dots are plots inside exclosures.

Figure 1

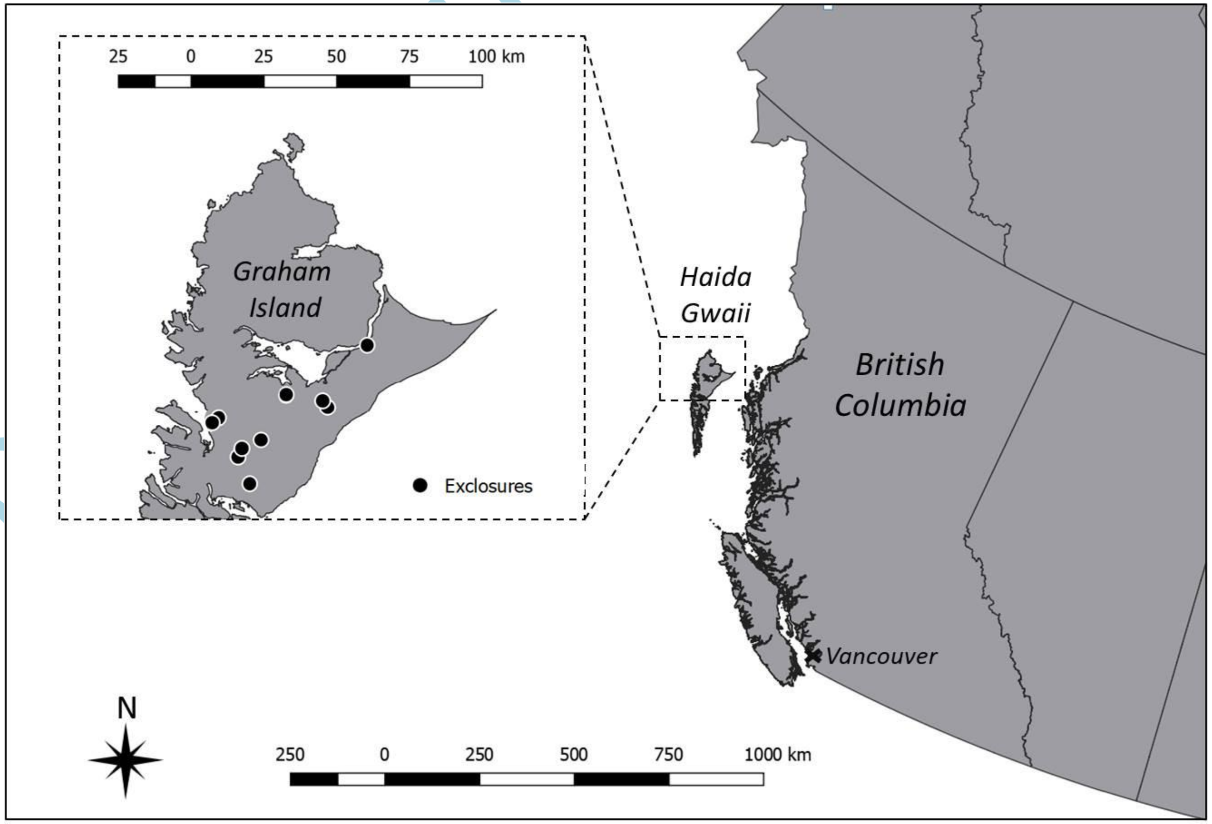
25 0 25 50 75 100 km
Graham Island
● Exclosures
Haida Gwaii
British Columbia
Vancouver
N
250 0 250 500 750 1000 km

Figure 2

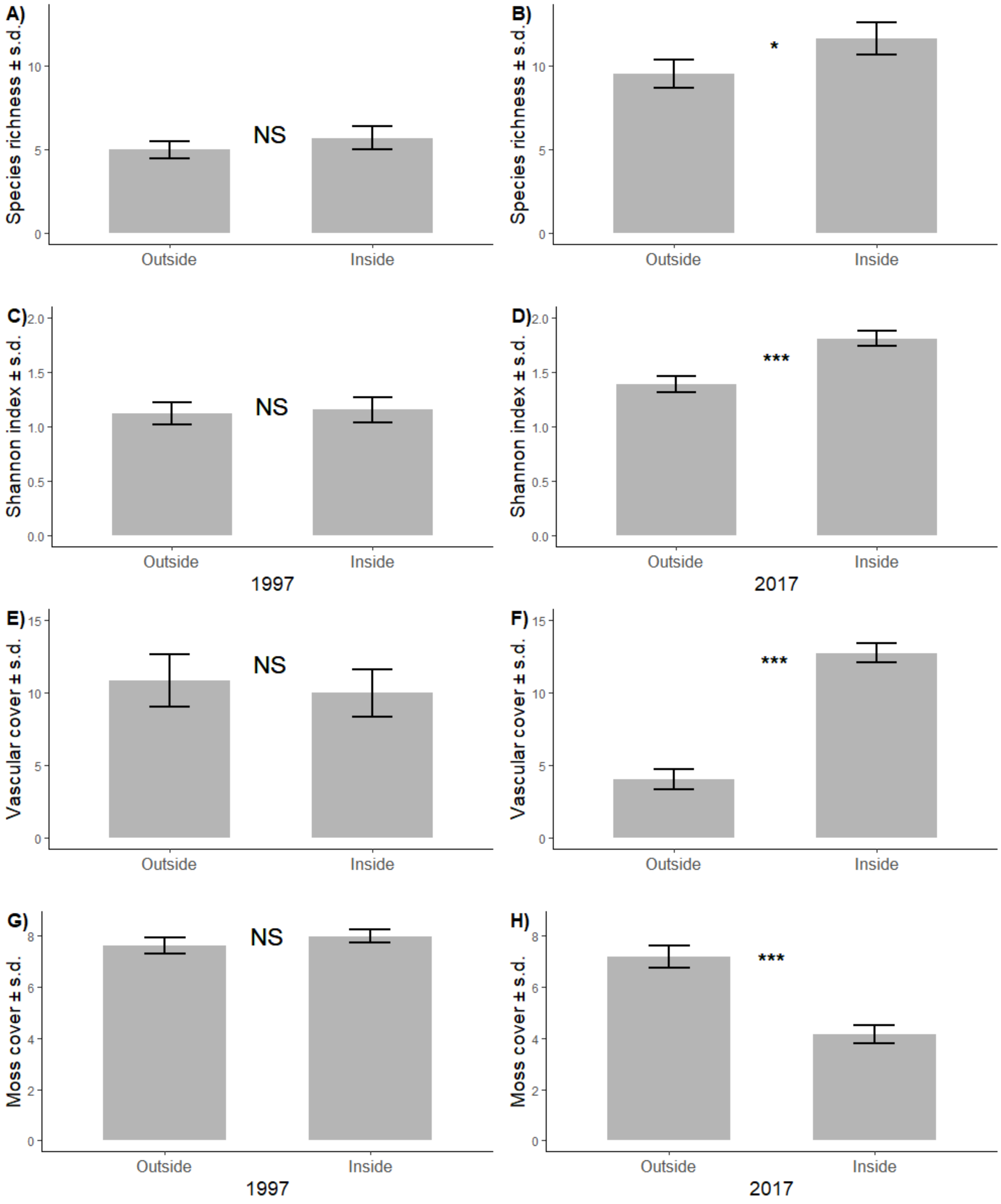
A)
Species richness ± s.d.
0
5
10
NS
Outside
Inside
B)
Species richness ± s.d.
0
5
10
*
Outside
Inside
C)
Shannon index ± s.d.
0.0
0.5
1.0
1.5
2.0
NS
Outside
Inside
1997
D)
Shannon index ± s.d.
0.0
0.5
1.0
1.5
2.0
***
Outside
Inside
2017
E)
Vascular cover ± s.d.
0
5
10
15
NS
Outside
Inside
F)
Vascular cover ± s.d.
0
5
10
15
***
Outside
Inside
G)
Moss cover ± s.d.
0
2
4
6
8
NS
Outside
Inside
1997
H)
Moss cover ± s.d.
0
2
4
6
8
***
Outside
Inside
2017

Figure 3

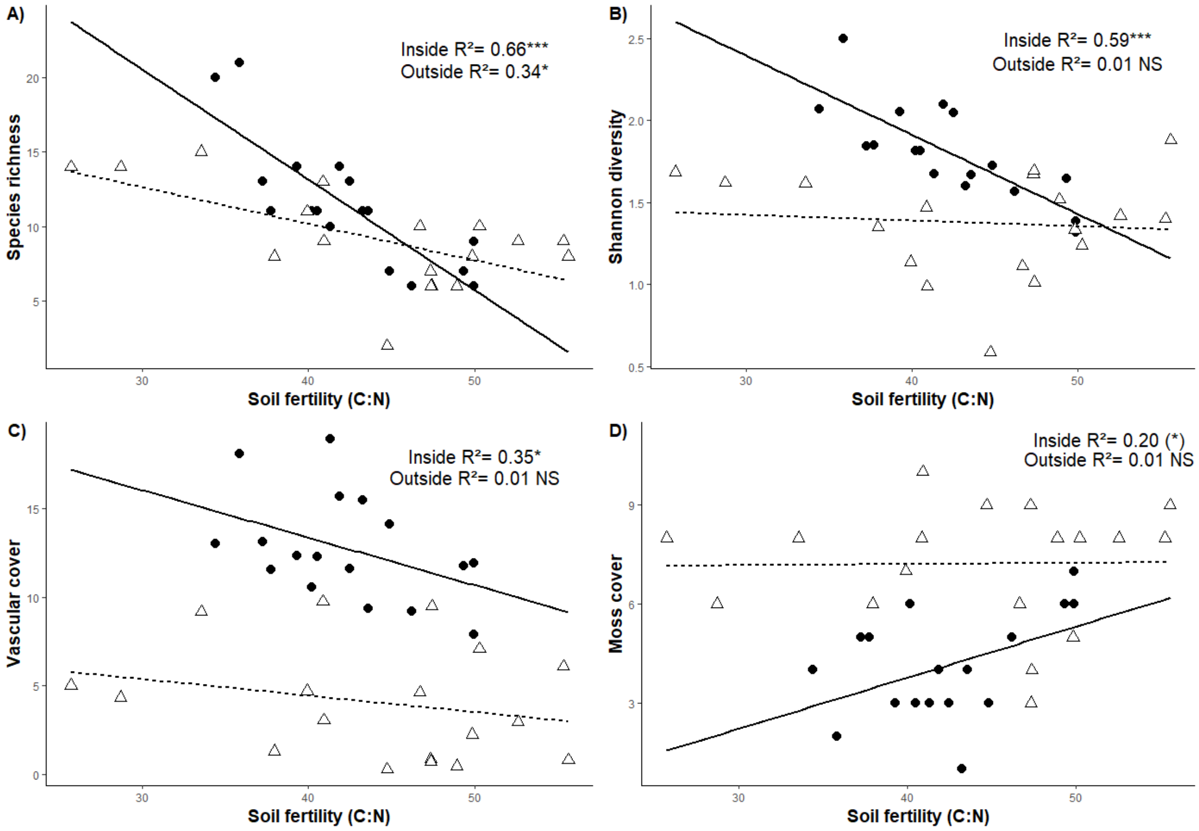
A)
Inside R²= 0.66***
Outside R²= 0.34*
Species richness
5
10
15
20
30
40
50
Soil fertility (C:N)
B)
Inside R²= 0.59***
Outside R²= 0.01 NS
Shannon diversity
0.5
1.0
1.5
2.0
2.5
30
40
50
Soil fertility (C:N)
C)
Inside R²= 0.35*
Outside R²= 0.01 NS
Vascular cover
0
5
10
15
30
40
50
Soil fertility (C:N)
D)
Inside R²= 0.20 (*)
Outside R²= 0.01 NS
Moss cover
3
6
9
30
40
50
Soil fertility (C:N)

Figure 4

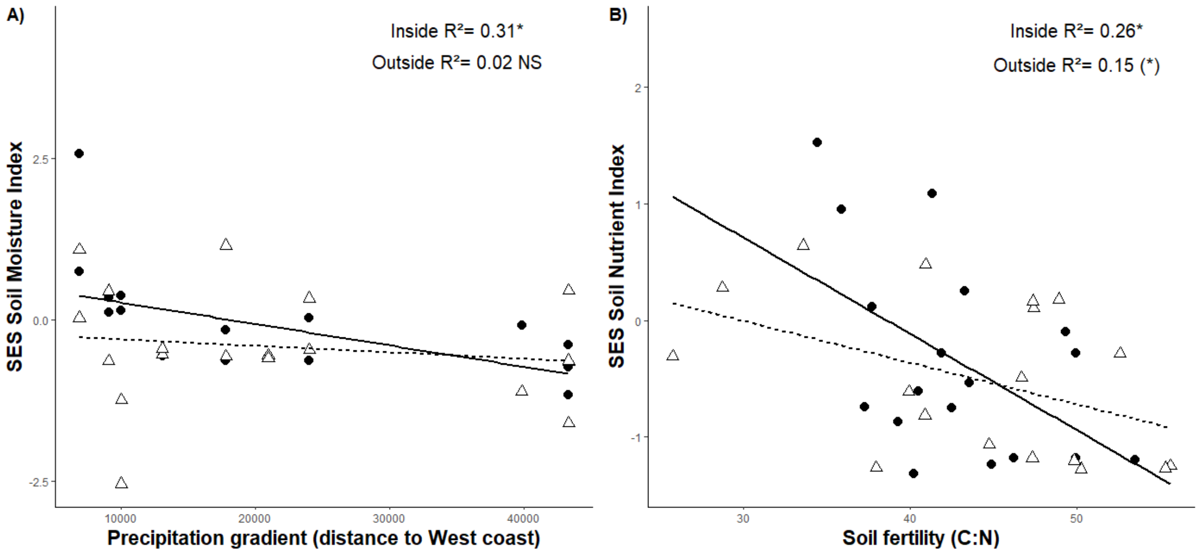
A)
Inside R²= 0.31*
Outside R²= 0.02 NS
SES Soil Moisture Index
2.5
0.0
-2.5
10000
20000
30000
40000
Precipitation gradient (distance to West coast)
B)
Inside R²= 0.26*
Outside R²= 0.15 (*)
SES Soil Nutrient Index
2
1
0
-1
30
40
50
Soil fertility (C:N)

Figure 5

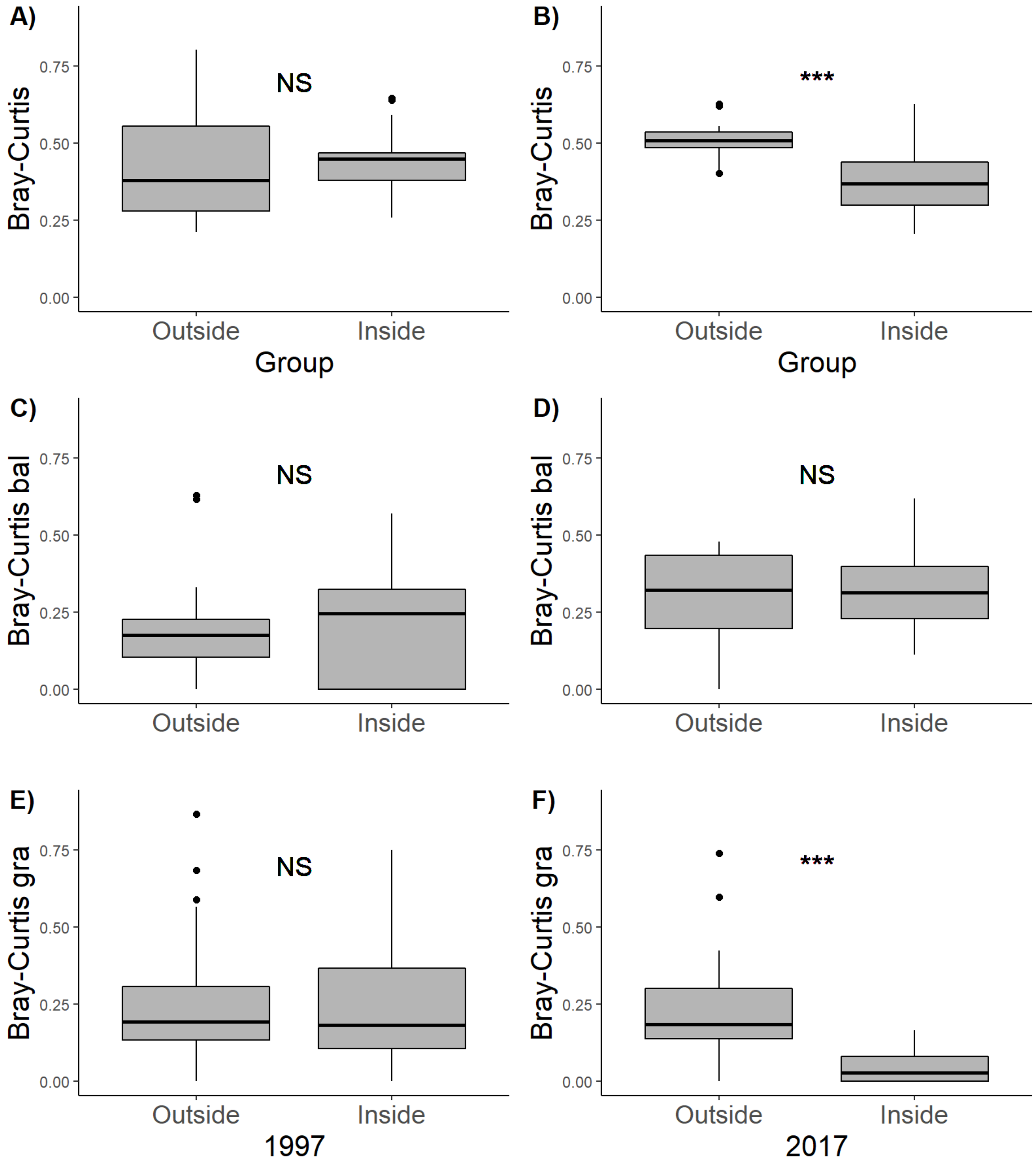
A)
Bray-Curtis
0.75
0.50
0.25
0.00
NS
Outside
Inside
Group
B)
Bray-Curtis
0.75
0.50
0.25
0.00
***
Outside
Inside
Group
C)
Bray-Curtis bal
0.75
0.50
0.25
0.00
NS
Outside
Inside
D)
Bray-Curtis bal
0.75
0.50
0.25
0.00
NS
Outside
Inside
E)
Bray-Curtis gra
0.75
0.50
0.25
0.00
NS
Outside
Inside
1997
F)
Bray-Curtis gra
0.75
0.50
0.25
0.00
***
Outside
Inside
2017

Figure 6