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CAN THE MISSING UNDERSTORY IN OLD-GROWTH FORESTS ON HAÏDA GWAII (BRITISH COLUMBIA, CANADA) RECOVER AFTER DEER EXCLUSION?

Section №10 «Ungulates Animals and Carnivorous Mammals and their Role in Ecosystems»

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Introduction

Herbivory is a critical process when studying plant community structure and diversity in many ecosystems [1,2] Large herbivores and deer in particular can have a profound impact on ecosystem structure and act as keystone species in many forest systems [3]. Extirpation of natural predators (wolf and cougars), changes in silvicultural and agricultural practices as well as introductions of exotic deer species led to a dramatic increase in abundance of deer populations worldwide. In the absence of other control than food availability, overabundant deer populations can strongly impact its environment [4,5,6]. At high densities, deer is assumed to determine the structure and composition of forest herb layers, subcanopy and ultimately forest canopy through their impacts on regeneration, generally with a decline in the abundance and distribution of palatable species and an increase in unpalatable, resistant or browse-tolerant species [7,8,9,10]. As a consequence, deer exert cascading effects on animals (small mammals, birds, invertebrates) both by competing directly for resources and by indirectly modifying the composition and physical structure of habitats [11,12,13,10].

Taking the opportunity provided by the introduction of the Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on the Haïda Gwaii archipelago we studied the effects of predator-free deer populations on previously unbrowsed old-growth forest understory vegetation. Previous observations mentioned that overbrowsing by introduced deer apparently radically altered the vegetation of Haïda Gwaii, and greatly reduced or virtually eliminated preferred forage species in many areas [14,15,16]. An enclosure experiment revealed that Sitka black-tailed deer had a drastic impact on redcedar (*Thuja plicata*) regeneration and that the recovery following deer exclusion although highly significant required a reduction of deer abundance over a long period of time [17].

The same enclosure experiment was used here to characterize the impact of introduced deer on the whole understory vegetation and to test the potential for recovery after a prolonged exclusion of deer. Our **hypothesis #1** is that deer limit the development of accessible vegetation under the browse line in terms of both biomass and height. Our **hypothesis #2** is that deer browsing may then have an impact on average species richness by either driving species elimination and/or limiting the settlement/colonization of new species.

Methods

Study area The Haïda Gwaii archipelago is the largest and the most isolated archipelago on the west coast of Canada and is covered with temperate rain forest [figure 1]. The flora is similar to the one found in South-eastern Alaska but species richness is lower on the archipelago than on the mainland. The experimental sites were distributed across the largest island, Graham, in the North of the archipelago, where enclosures and control plots were installed in remnant old-growth forest patches. Prior to European settlement, there were no deer and none of their major non-human predators. Sitka black-tailed deer were introduced to the archipelago in the North of Graham Island in the late 19th century and the population rapidly increased to reach higher densities than those found on the mainland [18,19]. Average population density on the larger islands has been estimated

at about 13 deer per km² [20]. Since their arrival deer have dramatically altered the understory vegetation which has become sparse in most localities [21, 22].

Experimental design Our experiment was designed to characterize the impact of deer on forest understory vegetation and to monitor the changes following deer exclusion. The experiment consisted of 20 square enclosures (25m²) set up in 1997 in 10 sites (two enclosures per site). Each enclosure was paired with an unfenced area of the same size considered as a control zone. Pairs of enclosure and unfenced area will be referred hereafter as to pairs.

Data collection occurred each year in late summer, early autumn from 1997 to 2001 and then in 2005. **To test hypothesis #1**, we estimated to the nearest percentage the cover of any species present inside and outside (=unfenced area) the enclosures using a 0.25m² frame within three defined vegetation strata : up to 0.5m above the ground, from 0.5m to 1.5m and from 1.5 to 4m, hereafter referred as to lower, medium and upper stratum respectively. The lower and medium strata were below the browse line and the upper stratum was above. The browse line was estimated to be at about 1.5m above the ground and to correspond to the maximum height a deer can reach [23]. Cover percentage data were then grouped according to three species groups, defined as trees, shrubs and herbs (= palatable herbs, ferns and grasses). We also recorded the maximum height reached by each species within 8 distinct height layers ranging from below 0.05m up to 2 to 4m. **To test hypothesis #2**, we measured the species richness as the number of vascular plant species found within each enclosure and unfenced areas on a studied site.

Statistical analysis

- Data used in this study are *i*) hierarchically structured because of the experimental design and *ii*) repeated over time on the same pairs of enclosures and unfenced areas in the same study sites, thus displaying temporal correlation. We thus used linear mixed-effect model to analyze our data and test for an enclosure (=treatment) effect on richness and percentage cover.

- Considering the species present both inside and outside the enclosure from 1997 until 2005 at the pair's scale, we qualified the change in the maximum height reached by the species inside and outside the enclosure and recorded the number of cases observed into 4 categories:

Category “=” the species changed similarly both in the enclosure and its paired unfenced area

Category “+” the species gained a different number of vegetation layers inside and outside the enclosure

Category “++” the species *either* grew up in one area and remained stable in the other *or* remained stable in one area but decreased in the other

Category “+++” the species grew up in one area but decreased in the paired one

We then compared the number of cases more favourable to enclosures to the one in favour of the unfenced areas using χ^2 test.

- We looked at the presence/absence pattern of each species observed at the pair's scale: when a species was observed at least once inside the enclosure or in the unfenced area, its pattern was followed in both areas (enclosure and unfenced area). We then defined 5 standard patterns:

“AS” Appearance and Stay: the species not initially present appears and remains so until 2005.

“AD” Appearance and Disappearance: the species not initially present appears but disappears before 2005.

“OLY” Observed Last Year: the species is only seen the last year of sampling (*i.e.* 2005).

“P” Persistency: the species is seen each year from 1997 to 2005.

“D” Disappearance: the species is first seen but is then absent the following years.

The three standard patterns (AS, AD and OLY) are considered as appearance patterns.

We first recorded the occurrence of each appearance pattern for a treatment (enclosure or unfenced area) when the species was always absent in its paired area and we tested for a treatment effect using χ^2 test. Then, we recorded the occurrence of any appearance pattern for a treatment when the

species was already present in the paired area (persistence or appearance patterns). We could then test for a potential time lag in the appearance patterns between enclosure and unfenced area using χ^2 test.

Results and discussion

Protection from deer browsing only had a positive effect on vegetation cover percentage in the strata below 1.5m (lower and medium strata); however there was no effect of deer exclusion when we separately consider each predefined species group (trees, shrubs, herbs).

Now considering the maximum height reached by the species at the pair's scale, we identified 61 cases. Sixteen cases showed a similar change inside and outside the enclosure whereas divergent changes occurred in 45 cases. The scenarios were significantly more favourable inside the enclosures (36 versus 9 cases; $\chi^2_{(1)} = 7.63$, $p < 0.01$, [figure 2]). The protection from deer has thus a positive effect on the height reached by the vegetation, particularly for trees and shrubs. In addition, the (++) category was the most represented category ($\chi^2_{(2)} = 7.14$, $p < 0.05$) inside and outside the enclosures.

Average species richness in enclosures and unfenced areas increased similarly over the study period regardless of deer exclusion [figure 3]. Species richness doubled between 1997 and 2005 both inside and outside the enclosures from 6 to 11 species per site on average. Species appearances mainly concerned herbs (18 species) such as cleavers (*Galium aparine*), the purple-leaved willowherb (*Epibolium ciliatum*) and Queen Charlotte Island false rue-anemone (*Isopyrum savilei*). The number of all recorded species both treatments considered remained rather stable from 1997 to 2000 but then strongly increased from 2001 to 2005, potentially stressing an increase in observers' expertise.

Stable appearance events (AS) occurred preferentially and first inside enclosures. Considering cases when a species appeared whereas it remained absent in the paired area, there was a significant difference in the type of appearance patterns between paired enclosure and unfenced area ($\chi^2_{(2)} = 7.75$, $p = 0.02$). 42% of the appearance patterns occurring in the enclosures were AS patterns, whereas they only represented 21% in the unfenced areas. However, the proportion of OLY patterns was higher within the unfenced areas (61%) than inside enclosures (30%).

Furthermore, when a given species appeared in both treatment areas, it tended to appear first inside the enclosure [figure 4]. In 35% of the appearance events in the unfenced areas, the species was already present inside the enclosures whereas the opposite situation occurred only for 16% of the appearance events inside the enclosures. This trend was significant when all species were considered together ($\chi^2_{(1)} = 12.4$, $p < 0.001$) and for the herbs group ($\chi^2_{(1)} = 5.07$, $p = 0.02$) but was significant neither for trees ($\chi^2_{(1)} = 1.97$, $p = 0.16$) nor for shrubs ($\chi^2_{(1)} = 1.0$, $p = 0.31$). Within the herbs group, the trend remained significant when we separately considered palatable herbs ($\chi^2_{(1)} = 4.39$, $p = 0.04$).

Conclusions

Our study reveals that the exclusion of deer has a general positive effect on the understory vegetation cover and dynamic. We actually showed that the vegetation cover was greater inside the enclosure than outside in the two height strata below the browse line. In addition, this positive effect has also been observed on the vegetation height for individuals that were present on site from the beginning of the study, which tend to grow inside the enclosures whereas vegetation height in the unfenced area rather remained stable or decreased. Finally, although no browsing effect on species richness has been detected, appearance events analysis revealed that the vegetation dynamic is more complex and encouraged by the exclusion of deer which seem to prevent new species from settlement on a site. We can thus assume that the understory vegetation is able to recover from deer browsing damages when the pressure is temporarily removed.

We also suggest that deer enclosures may be considered as stable source patches for the settlement of new species in the surrounding understory vegetation.

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Figures captions

Figure 1. Localisation of the Haïda Gwaii archipelago on the west coast of Canada (taken from [22]).

Figure 2. Number of divergent cases globally and by each height category of change (+, ++, +++) concerning the maximum height reached by species between 1997 and 2005. Black bars represent cases in favour to enclosures as opposed to white bars more favourable to unfenced areas. (+ : the species gained a different number of vegetation layers inside and outside the enclosure; ++ the species *either* grew up in one area and remained stable in the other *or* remained stable in one area but decreased in the other; +++ the species grew up in one area but decreased in the paired one).

Figure 3. Change in average number of species from 1997 till 2005 according to 2 initial species richness categories. R1 defines sites where species richness in 1997 was below 4 species whereas R2 identifies sites where initial species richness varied between 4 and 8 species. Solid lines represent enclosures whereas dashed lines stand for unfenced areas.

Figure 4. Number of scenarios at the pair's scale, all species considered (global) and by species group (trees, shrubs and herbs) when a given species either appears in the unfenced area whereas it was already present in the paired enclosure (black bars) or appears in the enclosure whereas it was already present in the paired unfenced area (white bars).

Figure 1.



Figure 2.

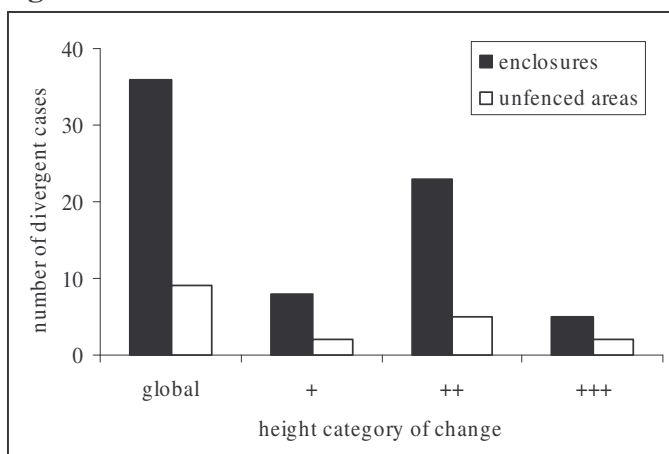


Figure 3.

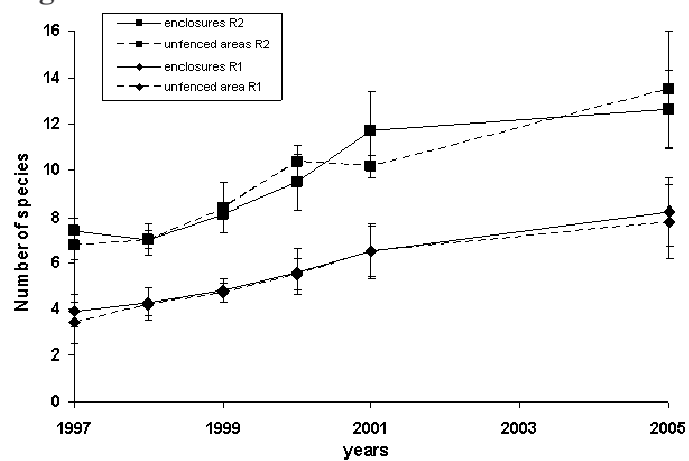
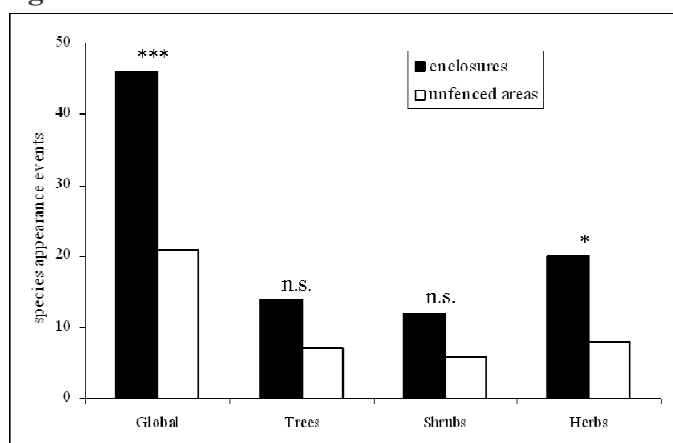


Figure 4.



n.s.: non-significant, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$