

A natural experiment on the effects of high deer densities on the native flora of coastal temperate rain forests

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Abstract

The introduction of Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Merriam) to Haida Gwaii (Queen Charlotte Islands, BC, Canada) in the late 19th century, provided an opportunity to understand the long-term effects of deer populations on the vegetation of temperate rain forests in the absence of their natural predators wolves (*Canis lupus* L.), and cougars (*Puma concolor* L.). Using seven small islands with different browsing histories (no deer, deer for <20 years, deer for >50 years), we tested the long-term effects of high deer densities on plant cover and species richness in the understorey of forest interior and forest edge habitats. Overall vegetation cover exceeded 80% in the lower vegetation layers on islands without deer and was less than 10% on the islands with deer for more than 50 years. Although overall plant species richness was similar on islands with or without deer, plant species richness at the plot scale (314 m²) was reduced by 20–50% on islands with deer for >50 years. The differences were most pronounced for the species-rich edge communities and among herb and shrub species. These results suggest that in the absence of predators, deer have the potential to greatly simplify the forest ecosystem.

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1. Introduction

Deer populations, unregulated by natural predators, have become a major factor affecting forest ecosystem dynamics in many parts of North America (Sullivan et al., 1990; Diamond, 1992; McShea et al., 1997) and Europe (Hester et al., 1991; Baines et al., 1994; Gill, 1999). Understanding the long-term consequences for plant diversity has become important to forest conservation around the world.

In eastern North American hardwood forests, where the increase of white-tailed deer (*Odocoileus virginianus* Zimmerman) population has been facilitated by the

extirpation of the principal non-human predators, wolves (*Canis lupus* L.) and cougars (*Puma concolor* L.) (Crête, 1999) and changes in silvicultural, agricultural and game management practices (Kuiters et al., 1996; Waller and Alverson, 1997; Côté et al., 2004) deer have affected plant abundance and diversity (Frelich and Lorimer, 1985; Alverson et al., 1988; Tilghman, 1989; Hobbs, 1996; deCalesta, 1997; Waller and Alverson, 1997; McShea and Rappole, 2000) and in some instances caused the extirpation of woody plant species (Hough, 1965; Whitney, 1984; Rooney and Dress, 1997a). Deer have been associated with a shift in plant community composition from shrubs and forbs to grasses and ferns (Horsley and Marquis, 1983) and with the reduced frequency of many plant species listed as threatened or endangered (Miller et al., 1992; Anderson, 1994; Rooney and Dress, 1997a; Augustine and Frelich, 1998).

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In contrast, most of the remaining western coastal forest, north of 49°N latitude, still supports predators (Harbo and Dean, 1983; Kirchoff, 1991) and few studies have examined the effects of mule deer (*Odocoileus hemionus* Rafinesque) (McArthur et al., 1988; Singer and Renkin, 1995), Columbia black-tailed deer (*Odocoileus hemionus columbianus* Richardson) (Woodward et al., 1994) or Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Merriam) (Klein, 1965; Pojar et al., 1980), on western forests, although they are known to become overabundant with reduced predation (Leopold, 1943; McCullough, 1997).

The forests of the Haida Gwaii archipelago differ from those of mainland British Columbia in possessing neither native deer, nor their non-human predators (Cowan, 1989). Hence, the introduction of deer in the late 1800s (Osgood, 1901; Munro, 1935) provided a rare opportunity to study the effects of predator-free deer on previously unbrowsed habitat. As deer spread through the archipelago, Vila et al. (2004a,b) demonstrated that islands were colonized at different times. However, once islands were colonized, the effect of deer was continuous to the present and did not show signs of temporal fluctuations. This unique situation provides a natural laboratory (*sensu* Diamond, 1983; A.R. Wallace in Whittaker, 1998) with a temporal gradient of deer browsing history.

We used this “natural experiment” to study the cumulative effects of high deer densities on plant cover and species richness in relation to the length of deer browsing history. We selected seven islands of similar size, all covered with primary forest but differing in their history of deer browsing: three showed no evidence or history of deer browsing, on two islands deer had been present for less than 20 years, and on two for more than 50 years (Vila et al., 2004a,b).

2. Methods

2.1. Study area

The Haida Gwaii archipelago (Queen Charlotte Islands) of British Columbia, situated 80 km west of the mainland of British Columbia and 50 km south of the Alexander Archipelago of Alaska, occurs within the per-humid temperate forest zone of the coastal temperate rain forest (Alaback and Pojar, 1997). It is the largest and most isolated archipelago on the west coast of Canada and contains over 540,000 ha of intact habitat, over 230,000 ha of it within protected areas (Ricketts et al., 1999). The vegetation of these islands is similar to that of adjacent Southeast Alaska (Banner et al., 1989) but the flora is relatively impoverished with only 665 recorded vascular plant species (Lomer and Douglas, 1999), compared with over 2300 vascular plant species on the adjacent mainland (Douglas et al., 1998). The fauna also is impoverished relative to the mainland (Ricketts et al., 1999). Except for an extinct relict population of caribou (*Rangifer tarandus dawsoni*), there were no deer and none of their major non-human predators in the pre-European period (Cowan, 1989).

Laskeek Bay, situated on the east coast of Haida Gwaii (Fig. 1), contains 15 islands of various size and proximity. The seven islands included in our study: Low, South Low, Lost, West Skedans, South Skedans, Haswell, and West Limestone were selected to control, as much as possible, for island area and to include islands that varied in the length of time deer have been present. They are located within 17 km of one another and range in area from 4.5 to 16 ha (Table 1). West Limestone Island, West and South Skedans Islands, and South Low and Low Islands are part of a British Columbia Wildlife Management Area

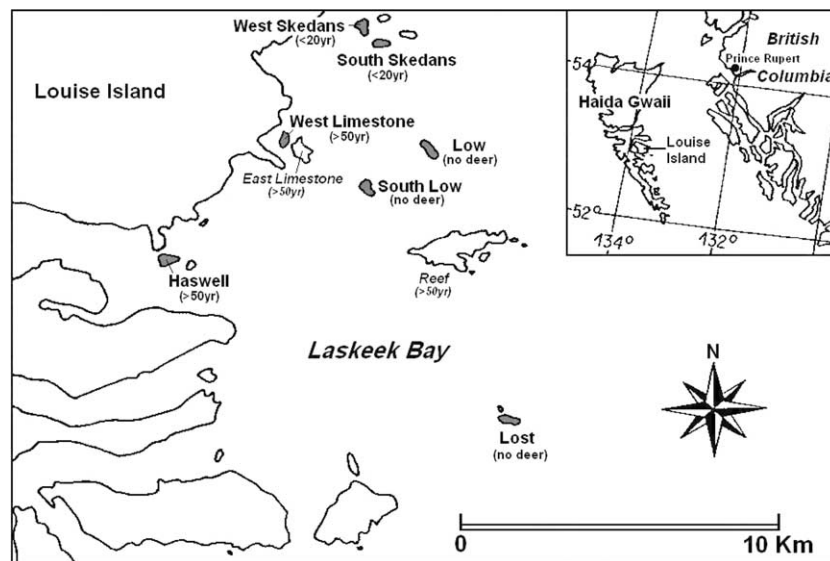


Fig. 1. Study area, showing the position of the 7 study islands in grey and the length of their browsing history (none, <20 years; >50 years). Also shown are Reef and East Limestone islands.

Table 1

Island characteristics, showing *isolation*, measured as the distance to the main island chain and *area* (both from Martin et al., 1995); *browsing history*, the duration of deer presence (from Vila et al., 2004a,b), *pellet groups*, pellet group density (means \pm SE), based on four 135-m transects for each island; and *deer*, deer density, calculated as pellet group density multiplied by 33.3/0.19 (deer density of E. Limestone as calculated by Daufresne and Martin (1997)/the measured pellet group density for E. Limestone)

Island	Isolation (m)	Area (ha)	Browsing history (years)	Pellet groups (m ⁻²)	Deer (km ⁻²)
S. Low	2900	4.5	None	0	0
Lost	7300	5.3	None	0	0
Low	5400	9.6	None	0	0
S. Skedans	2400	5.6	<20	0.17 \pm 0.04	30 \pm 7
W. Skedans	1350	8.2	<20	0.12 \pm 0.02	21 \pm 4
Haswell	150	13.3	>50	0.12 \pm 0.02	21 \pm 4
W. Limestone	350	16.0	>50	0.21 \pm 0.03	37 \pm 5

while Lost Islands fall within the northeastern perimeter of Gwaii Haanas National Park Reserve and Haida Heritage Site. None of the seven has been commercially logged. All maintain primary forest cover.

2.2. Deer density and history of deer browsing

In the years following the introduction of Sitka black-tailed deer to Haida Gwaii, the population expanded and spread until it colonized all but the most remote islands (Munro, 1935; Pojar, 1999). On East Limestone Island and Reef Island, also in Laskeek Bay (Fig. 1), deer densities in 1996 were estimated at about 32 deer km⁻² (Daufresne and Martin, 1997). A similar estimate was obtained at Reef Island as a result of a cull (Gaston et al., In press). On each of the seven islands, as well as on the larger East Limestone Island, we assessed the density of deer pellet groups along four, 2 m \times 135 m transects (Bennett et al., 1940) throughout July 2000. We determined the relative deer density on each island, by comparing pellet group density to the pellet group density of East Limestone Island where we knew deer density from direct count obtained by a line of 10 observers covering the entire area of the island accompanied by a roving observer, who ensured that these very tame deer were not pushed by the line, and an observer circumnavigating the island (to cover shorelines and small cliffs). Observers communicated by VHF radios.

The length of time deer had been present on the different islands in Laskeek Bay (Table 1) was estimated (Vila et al., 2004a,b) by analyzing shrub stem age through an analysis of tree ring patterns and by dating the earliest fraying scars (created by deer rubbing their antlers on trees). Vila and coworkers showed that deer never colonized Low, South Low and Lost islands, have had a measurable impact on West and South Skedans for less than 20 years but have had a measurable impact on Haswell and West Limestone islands for more than 50 years. Their results also indicated that after the initial phase of colonisation deer maintained constant and high browsing pressure on the vegetation, suggesting a lack of marked fluctuations in deer densities over the periods considered.

2.3. Habitat types and study plots

We recognized two distinct habitat types on these islands: the forest edge and the forest interior. They differed principally in available light and exposure to wind and salt-spray (Calder and Taylor, 1968). The forest edge vegetation had a greater component of herbaceous species, many with conspicuous flowers, the interior had a larger component of shade-tolerant shrub species. The transition between the two occurred within 25 m of the high-tide line. We sampled each island with 10 randomly spaced 10-m radius circular plots along the forest edge (10–15 m from the high-tide line) and five 10-m radius circular plots within the forest interior. The latter had to be at least at 50 m from the forest edge and 50 m from one another. As a result of these constraints no more than 5 plots could be placed on the smaller island. Sampling covered 3–10% of smaller islands. Light availability in the interior was largely a function of canopy cover, and could vary from plot to plot.

2.4. Measurement of understorey vegetation

We sampled the vegetation in 2000, throughout the month of July, the period of maximum cover of herbaceous plants in this region. Vascular plants were identified according to Pojar and MacKinnon (1994), and verified with Hitchcock and Cronquist (1973). We defined three vegetation strata: 0–50, 50–150, and 150–400 cm. The first two strata were below the browse line and the third was above. The browse line was estimated to be at about 150 cm (Martin and Daufresne, 1999). We used standard spot charts (Mueller-Dombois and Ellenberg, 1974) to estimate the percent cover of each species and the total cover of vegetation in each stratum. We analysed the variation of total vegetation cover independently for each strata within each habitat type to provide a synthetic picture of vertical vegetation structure and of how the effect of deer browsing rippled through the vegetation layers. We calculated the total cover for each plant in the 0–50 and 50–150 cm layers (those within deer reach) and added up these cover values for all the plants within each of three main vegetation types (herbs,

shrubs and young trees) and for the main shrub Salal (*Gaultheria shallon*) and studied the variation of vegetation type cover below 150 cm in relation to deer browsing history.

2.5. Species richness at multiple scales

Plot species richness was measured as the number of vascular species found within each 314-m² sample plot. Island species richness was estimated as the total number of plant species found in all 15 plots on individual islands with each species counted only once. To estimate how species richness and turnover increased with increasing sample size we generated species accumulation curves using the software EstimateS 6.01 b (Colwell, 1997). Estimates were generated from 500 random combinations of *n* samples ($n=1,2,\dots,15$). Resampling of the data was conducted with replacement to balance the effects of rare species, which are known to affect the accuracy of species accumulation curves (Kempston, 2002), and to allow for meaningful variation with sample sizes near to the total sample (Gotelli and Colwell, 2001). Confidence intervals for the resulting curves were calculated as $est \pm t_{0.05}sd/\sqrt{15}$. We used the number of plots on each island (15) to determine degrees of freedom instead of the number of sampling iterations (500), which constituted an overestimate of real sample size.

2.6. Statistical analysis

We used a general linear mixed-model, GLMM (GENMOD procedure of SAS, release 6.09, 1993) to test the effect of deer browsing history (tested at the level of islands), habitat type (edge or interior) and of their interaction on overall vegetation cover in different strata, on cover of the main plant types and of salal below 150 cm as well as on plot species richness. "Island" was considered a random effect nested in the fixed effect of "browsing history" (three durations of deer browsing). For the analyses of the effects of these explanatory variables on vegetation cover we arcsine transformed % cover values (Sokal and Rohlf, 1995) and fitted the transformed values to a GLMM with a log-link function and gamma error term. Species counts per plot were fitted to a GLMM with a log link function and Poisson error term. We conducted Chi-squared tests to test the heterogeneity of island totals and to test for any difference in effect between edge and interior habitat.

3. Results

3.1. The effect of browsing history on vegetation cover

Estimates of current deer densities did not appear to depend on time since deer colonisation. They ranged

from 21 to 31 deer km⁻² on islands with deer for less than 20 years and from 21 to 37 deer km⁻² on islands with deer for over 50 years (Table 1).

3.1.1. 0–50-cm stratum

Browsing history had a highly significant effect on vegetation cover in the first stratum (Table 2). Cover was greatest on islands with no history of deer browsing and lowest on the islands with more than 50 years of deer browsing (Fig. 2). There was a significant island effect nested within browsing history (Table 2). GLMM parameter estimates show that this effect resulted from variation in cover between islands with over 50 years of browsing ($p < 0.001$; Fig. 2). There was no island effect within the other island categories. Cover of vegetation below 50 cm differed significantly between the forest interior and forest edge (Table 2). The effect of deer differed between interior and edge plots (Table 2, significant interaction between browsing history and habitat). On islands without deer and on islands with over 50 years of deer browsing, vegetation cover in the 0- to 50-cm stratum was, on average, slightly greater in edge plots. On islands with less than 20 years of deer browsing it was greater in interior plots.

3.1.2. 50–150-cm stratum

Browsing history had a highly significant effect on vegetation cover (Table 2). Cover was again greatest on islands with no history of deer browsing and lowest on islands with over 50 years of deer browsing (Fig. 2). There was a significant island effect nested within browsing history (Table 2), which also resulted from differences in cover between islands with over 50 years of browsing history ($p < 0.001$; Fig. 2). Habitat type, independent of

Table 2

Statistics for GLMM analysis of the impact of deer on cover of vegetation in relation to *browsing history* (fixed effect), *island* (random effect nested within *browsing history*), and *habitat* type (fixed, effect, edge or interior) for three strata (0–50, 50–150, 1.5–4 m)

Effects	χ^2	df	<i>p</i>
<i>0–50 cm stratum</i>			
Browsing history	116.83	2	***
Island (browsing history)	51.87	4	***
Habitat	11.91	1	***
Browsing history * habitat	31.95	2	***
<i>50–150 cm stratum</i>			
Browsing history	83.26	2	***
Island (browsing history)	57.74	4	***
Habitat	0.13	1	n.s.
Browsing history * habitat	8.65	2	*
<i>150–400 cm stratum</i>			
Browsing history	6.43	2	*
Island (browsing history)	2.28	4	n.s.
Habitat	2.45	1	n.s.
Browsing history * habitat	5.45	2	n.s.

p, probability associated to test; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s. = non-significant.

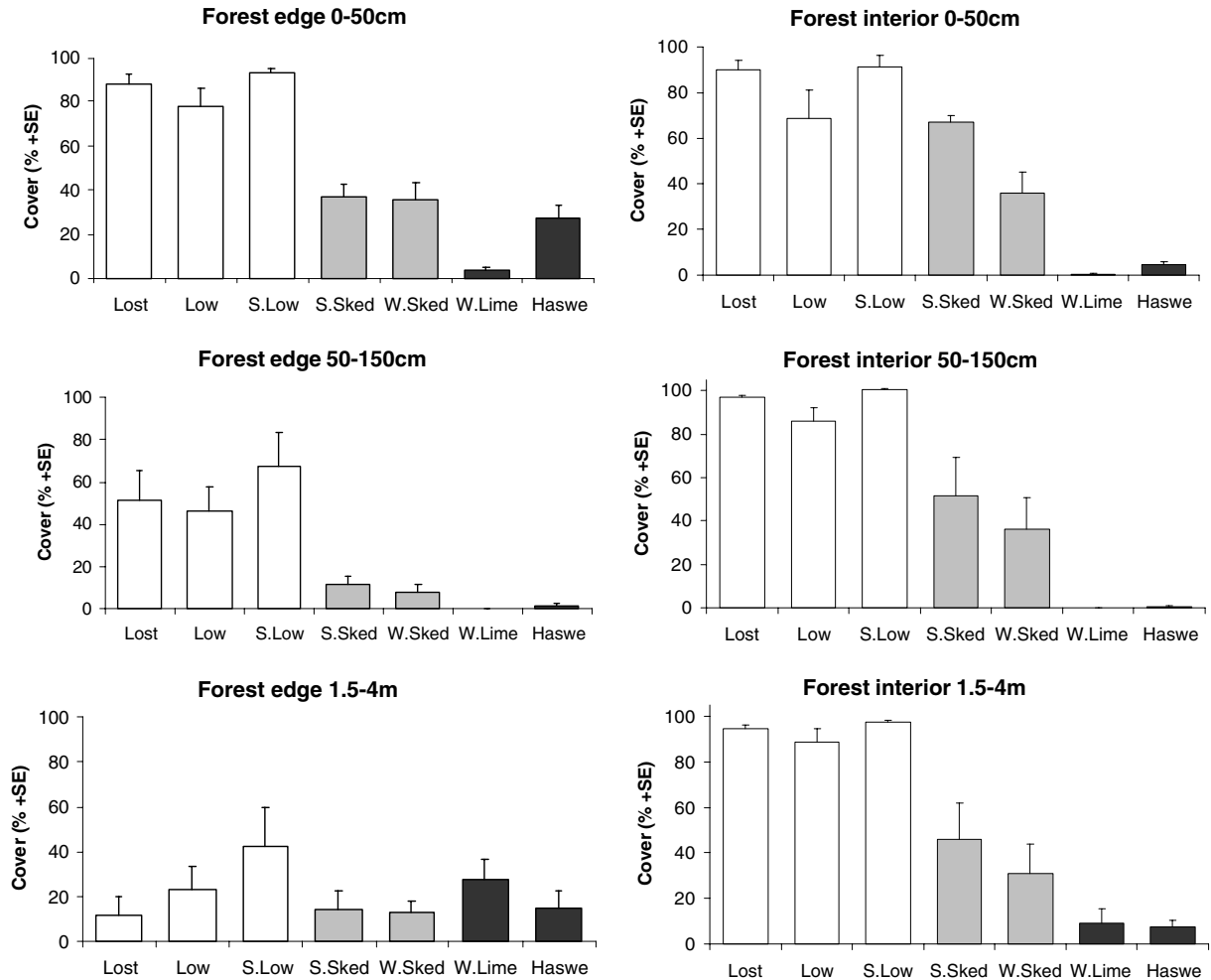


Fig. 2. The cover of vegetation in edge ($n = 10$ plots for each island) and interior ($n = 5$ plots for each island) habitat from 0 to 50 cm, 50 to 150 cm and 150 to 400 cm on each of seven islands in relation to length of browsing history. White = no deer, grey = deer for less than 20 years, black = deer for over 50 years (means + SE).

browsing history, had no significant effect on vegetation cover in this stratum. However, the effect of browsing history differed between edge and interior plots (significant interaction between habitat and browsing history, Table 2). On islands with no history of deer browsing and on islands with less than 20 years of deer browsing, cover was much greater in interior plots than in edge plots. In edge plots, the effect of deer browsing on vegetation cover was strong on all islands with deer, whereas for interior plots the effect of deer browsing was pronounced only on the islands with over 50 years of browsing.

3.1.3. 150–400-cm stratum

Browsing history also had a significant effect on vegetation cover in the highest stratum analyzed (Table 2). There was no island effect nested within browsing history. There was no habitat effect (Table 2) and no significant effect of the interaction of habitat with browsing history. On islands with no history of deer browsing and on islands with less

than 20 years of browsing, cover was greater in interior plots than in edge plots. In contrast to the first two strata, the amount of vegetation cover in edge plots on islands without deer did not exceed 50% in this strata (Fig. 2).

3.2. Browsing history and cover of main vegetation components

3.2.1. Herbs

Herb cover was inversely correlated to the length of browsing history (Fig. 3; Table 3). Habitat and its interaction with browsing history had significant effects on herbaceous vegetation cover. On islands with no history of deer browsing and on islands with deer for less than 20 years, herbaceous cover was similar in both interior and edge habitats (Table 3; Fig. 3). On islands with deer for more than 50 years it was greater at the edge than in the interior. In edge plots, one of the graminoid species dominant on islands without deer, Dunegrass *Elymus mollis*, was virtu-

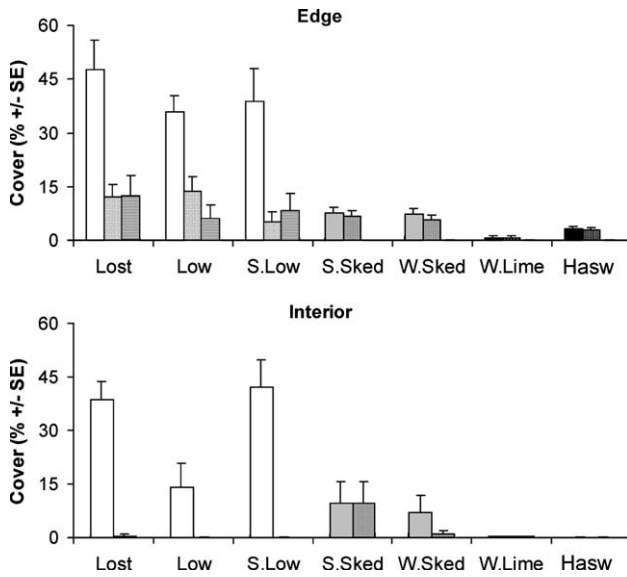


Fig. 3. The cover of herbaceous vegetation in edge ($n = 10$ plots for each island) and interior ($n = 5$ plots for each island) habitat from 0 to 150 cm on each of seven islands in relation to length of browsing history. White = no deer, grey = deer for less than 20 years, black = deer for over 50 years (mean + SE). Edge: Also shown are the contributions to herb cover of the grass *Elymus mollis* (horizontal stripes), and all other graminoids (dots). Interior: Also shown are the contributions to herb cover of graminoid species (dots).

Table 3
Statistics for GLMM analysis of the impact of deer on cover of vegetation grouped by plant type (herbs, shrubs, trees) in relation to *browsing history* (fixed effect), *island* (random effect nested within *browsing history*), and *habitat* type (fixed effect, edge or interior)

Effects	χ^2	df	<i>p</i>
<i>Herbs</i>			
Browsing history	63.39	2	***
Island (browsing history)	1.24	4	n.s.
Habitat	7.51	1	**
Browsing history * habitat	9.64	2	**
<i>Shrubs</i>			
Browsing history	57.18	2	***
Island (browsing history)	25.13	4	***
Habitat	1.10	1	n.s.
Browsing history * habitat	19.18	2	***
<i>Salal</i>			
Browsing history	56.77	2	***
Island (browsing history)	7.58	4	n.s.
Habitat	16.73	1	***
Browsing history * habitat	39.56	2	***
<i>Trees</i>			
Browsing history	14.15	2	***
Island (browsing history)	19.43	4	***
Habitat	1.23	1	n.s.
Browsing history * habitat	7.17	2	*

p, probability associated to test; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, n.s., non-significant.

ally eliminated on all islands with deer. However the other graminoids represented the bulk of the herbaceous vegetation that remained on islands with deer (Fig. 3).

3.2.2. Shrubs

Browsing history had a highly significant effect on the cumulative cover of all shrub species below 150 cm (Table 3). Shrub cover was inversely correlated to the length of browsing history (Fig. 4). Island nested in browsing history had a significant effect on shrub cover (Table 3). This effect resulted from variation in cover between islands with over 50 years of browsing (parameter estimates within the GLMM $p < 0.001$; Fig. 4). The interaction between habitat and browsing history had a highly significant effect on shrub cover (Table 3). Shrub cover was greater in the interior than at the edge on islands with no deer and on islands with less than 20 years of browsing; shrub cover was lower in the interior than at the edge on islands with more than 50 years of deer browsing (Fig. 4). Salal (*Gaultheria shallon*) was the most abundant shrub species on all seven islands. Browsing history, habitat type and their interaction had a highly significant effect on the cover of salal (Table 3). Salal cover was similar on islands with no deer and on islands with deer for less than 20 years but was much lower on islands with deer for more than 50 years (Fig. 4). On islands without deer, other shrub species accounted for a significant proportion of shrub cover, both in edge and interior plots. On islands with deer, shrub cover was almost exclusively made of salal (Fig. 4). Cover of salal was greater in the interior than at the edge

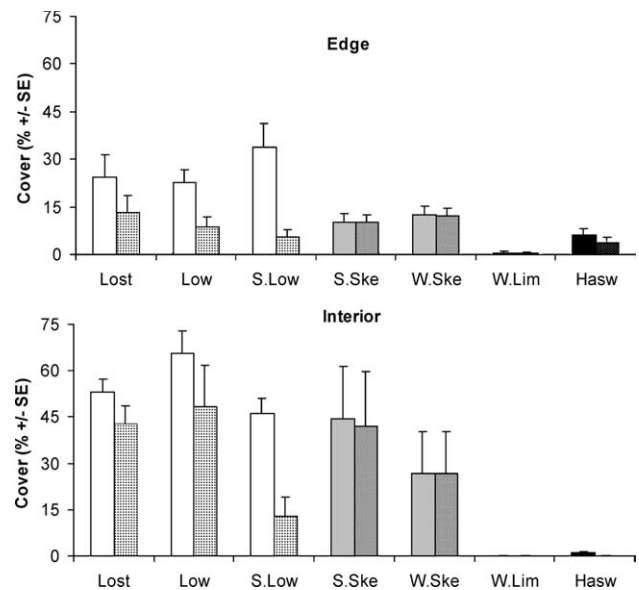


Fig. 4. The cover of shrubs in edge ($n = 10$ plots for each island) and interior ($n = 5$ plots for each island) habitat from 0 to 150 cm on each of seven islands in relation to length of browsing history. White = no deer, grey = deer for less than 20 years, black = deer for over 50 years. Also shown is the contribution to shrub cover of *Gaultheria shallon* (dots) below 150 cm (means + SE).

on islands with no deer and on islands with less than 20 years of browsing, but was lower in the interior than at the edge on islands with more than 50 years of browsing.

3.2.3. Young trees

Browsing history had a significant effect on the cover of young trees below 150 cm (Table 3). Island had a significant effect on tree cover within island categories. Habitat type had no significant effect but the interaction between “habitat” and “browsing history” had a significant effect (Table 3).

3.3. Browsing history and plant species richness

3.3.1. Plot

Browsing history, habitat type and their interaction had a significant effect on plant species richness per plot

Table 4

Statistics for GLMM analysis of impact of deer on plot (314 m²) species richness in relation to *browsing history* (fixed effect), *island* (random effect, nested within *browsing history*), and *habitat* type (fixed effect, edge or interior)

Effects	χ^2	df	<i>p</i>
Browsing history	127.73	2	***
Island (browsing history)	4.67	4	n.s.
Habitat	9.21	1	**
Browsing history * habitat	12.90	2	**

p* < 0.05; *p* < 0.01; ****p* < 0.001 and n.s., non-significant.

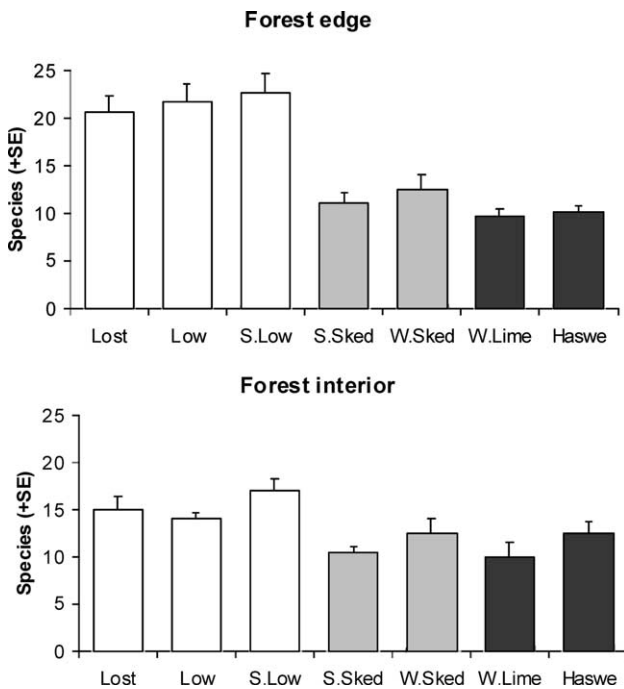


Fig. 5. The species richness in edge (*n* = 10 plots for each island) and interior (*n* = 5 plots for each island) habitat on each of seven islands in relation to length of browsing history. White = no deer, grey = deer for less than 20 years, black = deer for over 50 years (means + SE).

(Table 4). The number of species recorded per plot (314-m²) was lower on average on islands with deer than on islands without (Fig. 5). On islands without deer species richness per plot was, on average, significantly greater in forest edges than in the forest interior (GLMM parameter estimates, *p* < 0.001). On islands with deer, species numbers were similar in edge and interior plots (Fig. 5).

3.3.2. Island

The total number of species recorded per island (15 plots; 4710-m²) was higher on islands without deer (Table 5). Species accumulation for all seven islands rose quickly for sample sizes of one to four plots (Fig. 6). In samples with more than seven plots, species accumulated far more gradually, indicating an adequate sampling intensity. The accumulation curves formed three discrete groups that were consistent with browsing history. Islands with no history of deer browsing showed the highest estimates of species richness at all scales. Confidence intervals (95%) for islands with no deer showed no overlap with other islands, for the entire span of the curve. Species accumulation on islands with less than 20 years of browsing was consistently greater than species

Table 5

Number of plant species (γ -diversity) recorded in ten, 314-m² edge plots (3140-m²), five 314-m² interior plots (1570-m²) and all 15 plots (4710-m²), on each of seven islands in relation to length of browsing history

Island	Browsing history	Edge species	Interior species	Total species
S. Low	None	59	24	64
Lost	None	53	25	59
Low	None	51	21	57
S. Skedans	Less than 20 years	37	18	48
W. Skedans	Less than 20 years	42	22	49
Haswell	Over 50 years	36	22	44
W. Limestone	Over 50 years	32	19	41

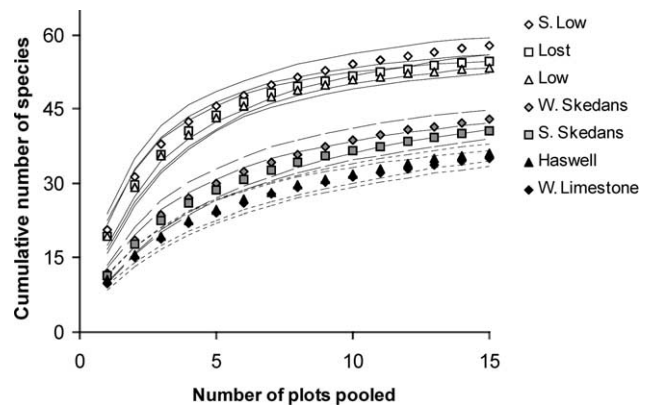


Fig. 6. Species accumulation curves for vascular species occurring on seven islands (*n* = 15 plots for each island). Symbols represent estimates of mean species richness and lines represent 95% confidence intervals for 500 random combinations of *n* sample plots (*n* = 1, 2, ..., 15).

accumulation on islands with more than 50 years of browsing, but the confidence intervals overlapped for small sample sizes. Overall we recorded an identical total of 71 species on the three deer-free islands and on the four islands with deer. However, when non-native species were removed from the comparison, 70 native plant species had been recorded on deer-free islands and 65 native species on islands with deer.

4. Discussion

The long-term presence of deer had a strong effect on plant cover and plant species richness. Both cover and richness decreased with increasing length of browsing history. The effect was greatest in the species-rich forest edge and among shrub and herb species.

Decreased plant diversity and/or abundance have been recorded for many forest systems affected by moderate to high deer densities (Klein, 1965; Alverson et al., 1988; Anderson and Katz, 1993; Woodward et al., 1994; deCalesta, 1997). However, these studies have generally occurred in contexts where other factors (forest industry, agriculture, urban development, hunting, predators and other large herbivores) may have played a role in the emerging pattern (but see Hough, 1965 and Rooney and Dress, 1997b). In our study, the absence of other human driven factors affecting the interaction of deer and vegetation, allowed us to clearly determine the role of the deer in ecosystem modification. Although the small size of the islands selected, with their large edge-to-interior ratios, may result in a more acute effect, the pattern is similar on the large islands in the archipelago (Pojar et al., 1980; Engelstoft, 2001). The sparse understorey noted in Haida Gwaii by several observers (Calder and Taylor, 1968; Banner et al., 1989; Pojar et al., 1980; Pojar, 1999) contrasts with the dense understorey noted by early foresters and visitors (Gregg, 1923; Hopkinson, 1931; Hall, 1937; Carr, 1951). This change is contemporary with the spread of deer (Vila et al., 2004a,b).

4.1. Variation in impact

On islands without deer, edge plots had more species than interior plots, but this difference did not exist on islands with deer, suggesting deer have removed a number of plant species from the forest edge. In the coastal temperate forest, edge habitat usually has a larger component of herbaceous vegetation (Calder and Taylor, 1968), which makes up the bulk of deer summer diets (McCaffery et al., 1974; Bunnell, 1990) and is highly susceptible to repeated browsing (Miller et al., 1992).

Forest interior vegetation appeared to be more resistant to deer modification. On islands with deer for less than 20 years, extensive patches of salal remained, making up most of the total cover. These patches were

apparently thinned by deer browsing, allowing light to penetrate to the lowest stratum and to produce dense growth throughout. On islands without deer the lowest stratum in the interior was often deeply shaded and produced little foliage. However the increased growth resulting from decreased competition for light did not fully compensate for the vegetation lost through browsing. Finally, on islands with deer for more than 50 years, most shrubs had disappeared.

4.2. The browse zone

Deer impact creates a browse-line when deer are abundant in a forest (Rhoads, 1997). Sitka black-tailed deer feed mainly between 0 and 150 cm (Bunnell, 1990; Daufresne and Martin, 1997). Plants above this browse-line are generally only indirectly affected, when young stems are unable to replace older stems (Vila et al., 2004a,b) or young long-lived canopy species are unable to recruit (Alverson et al., 1988; Anderson and Loucks, 1979; Anderson and Katz, 1993; Martin and Baltzinger, 2002). In Laskeek Bay the effect on interior vegetation in the 150 to 400 cm stratum resulted also from the ability of deer to push shrubs over in order to reach their upper branches.

4.3. Deer-modified plant communities

The effect of unconstrained deer browsing on community composition results from the combined effects of diet preference and differential recovery among species (Huston, 1979). Wildflower and shrub abundance generally show reduced abundance (Woodward et al., 1994; Pojar, 1999), while grasses often increase under herbivory (McNaughton, 1984). We observed a small decrease in cover for most graminoids but an increased dominance relative to most herb and shrub species. On islands with deer for more than 50 years, little vegetation cover remained in either the edge or interior habitat, but significantly more cover occurred on the shoreline, where grasses provided the dominant cover. Most grasses have their meristem tissue low to the ground, which spares it from browsing, a high root-to-shoot ratio that maintains reserves for rapid regrowth, and lateral spread to out compete other species (McNaughton, 1984). These features have been attributed to co-evolution of their morphology with grazing animals (Olf and Ritchie, 1998). The only grass species that had much lower cover on islands with deer than on islands without was dunegrass (*Elymus mollis*), the only grass with extensive above-ground structure.

We recorded lower cover of young trees below 150 cm. on islands with deer. Cover of young trees was lowest on islands with deer for more than 50 years, and in plots from the interior habitat; it varied greatly from island to island within island categories (Stockton, 2003).

This is not consistent with Daufresne and Martin's (1997) suggestion that reduced competition with depleted shrub species could favour regeneration of Sitka spruce (*Picea sitchensis*), or western hemlock (*Tsuga heterophylla*), despite the growth delays resulting from browsing (Vila et al., 2002). On Haida Gwaii, deer suppress natural regeneration of western red cedar *Thuja plicata* (Pojar, 1999; Martin and Baltzinger, 2002) and have repeatedly been shown to reduce tree regeneration elsewhere (Marquis, 1974; Anderson and Loucks, 1979; Alverson et al., 1988; Anderson and Katz, 1993).

4.4. Measuring what counts

Since MacArthur and Wilson (1963) published their model of island biogeography, species lists have often been used for island studies (Quin et al., 1987). In Laskeek Bay the effect of deer on plant species richness cannot be discerned by comparing the total number of species recorded on the three islands without deer as a whole, and on the four islands with deer considered together. Differences in species richness between islands become striking only when examined at a higher resolution. Species accumulation curves showed that the difference in species density is greatest between six and seven 314-m² plots, indicating that small areas may be highly susceptible to species loss. In addition, failure to take into account the relative frequency and abundance of species fails to capture the ecological processes within an island. At the scale of the individual plot, deer have greatly reduced the cover of vegetation and virtually eliminated many species and plant types.

4.5. Implications for management and conservation: Crying wolf?

The end-point of unconstrained, long-term deer modification appears to be the open cathedral-like forests found over much of Haida Gwaii (Calder and Taylor, 1968). These contrast with the dense understorey found in mainland coastal forests where wolves and cougars still occur (Pojar et al., 1980).

Our results confirm that, in the absence of predators, or where predator pressure is severely reduced, deer have a strong impact on vegetation structure and diversity. These changes may greatly modify ecosystem functions with cascading effects to plant-plant and plant-animal species interactions and far reaching impacts, not only to the vegetation but also to the fauna that could have long-term effects affecting even the process of recovery when deer populations can be curbed. In Haida Gwaii, which retains one of the largest protected tracts of coastal temperate rain forest in North America, the effects may create serious conservation problems for both plant and animal species. Moreover, many of these species are rare (Ogilvie, 1994; Taylor, 1989) and/or

culturally significant (Turner, 1998) and these modifications have both ecological and cultural repercussions. Hence, the remaining forest areas without deer have a high conservation value. The same applies to areas elsewhere with intact predator complexes. These areas may provide refuge for rare or endemic species sensitive to the effects of uncontrolled deer browse. Preservation of these refuges may be critical in maintaining biodiversity. Careful maintenance of predator populations and other deer population control mechanisms, where they exist, and their restoration where they have been eliminated, should be a global conservation priority.

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