

Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: lessons from a deer introduction

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Received: 28 January 2009 / Accepted: 20 August 2009 / Published online: 13 November 2009
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Abstract Debate on the relative importance of competition for resources and trophic interactions in shaping the biological diversity of living communities remains unsettled after almost a century. Recently, dramatic increases in ungulate populations have provided a useful quasi-experiment on the effects of unrestrained ungulates on forest ecology. The islands of Haida Gwaii (Canada) offer a unique situation to investigate the potential of large herbivores to control temperate forest community structure and diversity. Black-tailed deer *Odocoileus hemionus* Merriam, native to adjacent mainland areas of British Columbia, were introduced in 1878 and spread to all but a few islands. Because deer were not native to the

archipelago, islands that still lack deer provide a rare instance of temperate forest vegetation and fauna that developed in the absence of large herbivores. The colonisation of different islands at different times, and the absence of significant predation allow us to assess whether and how a large herbivore can exert “top-down” control on vegetation and its associated fauna. We studied plant communities in forest interior and shoreline, on seven small islands of varying browse history. Three islands were untouched by deer, deer had been resident for about 15 years on two, and on another two deer had been present for more than 50 years. Without deer, vegetation in the understorey and/or shrub layer was dense or very dense. Structure and composition varied markedly within and between shoreline and interior communities. Without deer, shoreline communities were dominated by species absent from islands with deer. Where deer had been present for less than 20 years most plant species characteristic of shorelines on islands without deer were already absent or scarce, but in the forest interior species richness was less affected and extensive shrub thickets remained. On islands where deer had been present for >50 years vegetation below the browse line was extremely simplified, converging in both forest interior and shoreline towards an open assemblage of a few deer-tolerant species, basically two coniferous trees. This top down effect on the plant community reflected up the food chain so that understorey invertebrate and shrub-dependent songbird communities became simplified. In contrast, species densities of

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litter arthropods (especially weevils and millipedes) were highest where deer were present for >50 years. Canopy birds were unaffected by deer presence. In the absence of predators, major climatic stress or other means to control the herbivore, deer browsing created greatly simplified plant and animal communities.

Keywords Deer · Forest herbivores · Habitat diversity · Herbivory · Plant and animal community simplification · Top down · Bottom up

Introduction

What is the relative importance of competition for resources (Gause 1934) and other trophic interactions (herbivory and predation) (Elton 1927) in the shaping of biological diversity in living communities? The debate is not settled after almost a century. The competition paradigm (MacArthur and Levins 1967) initially dominated. It began to be questioned when the numerous indirect effects at work inside food-webs and their effects on community composition became apparent (Paine 1969; Estes and Palmisano 1974). Questions about the extent to which top or intermediate levels in the food webs will and can affect lower or primary trophic levels started to fuel a debate on “top-down” or “bottom-up” control of food-web components and thus on what controls species abundance and diversity in a given community.

The “bottom-up” hypothesis, derived from the competition paradigm, assumes that vegetation abundance and diversity is limited only by the abundance of nutrients, water and light and by competition (Huston 1979; Polis 1999), the impact of herbivores on plants being controlled by the ability of plants to produce defences. The “top-down” hypothesis (Hairston et al. 1960; Pace et al. 1999) in its most extreme rendition, supposes that plants are unable to control herbivory and that part of the world is green only because predators directly or indirectly control herbivores.

The dramatic increases in deer populations in many parts of the world over the past century have triggered renewed efforts to understand the potential of large herbivores to affect the diversity and abundance of plants (Alverson et al. 1988; Waller 2008) and, through indirect effects, those of animals (DeCalesta 1994; Côté et al. 2004). Over large parts

of North America and Europe, this increase has been attributed to the extirpation of large predators (Breitenmoser 1998), and to changes in silviculture, agriculture and game management.

There is strong evidence to suggest that the increases in deer populations have triggered large-scale modifications of the vegetation (McShea et al. 1997; Waller and Alverson 1997; Horsley et al. 2003 for North America; Kuiters et al. 1996; Gill and Fuller 2007 for Europe; Putman 1996 and Côté et al. 2004 for reviews). In eastern North America deer have been associated with a shift in forest 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; Rooney and Dress 1997; Augustine and McNaughton 1998).

As changes in deer populations typically occurred simultaneously with changes in land use, early studies suggesting negative effects of deer overabundance on understorey biodiversity were met with skepticism (Mladenoff and Stearns 1993; Waller and Alverson 1997). Furthermore, no study had access to reference forests that had never been exposed to deer browsing. Thus, the question of what a temperate forest would look like without large herbivores, and of how plant and animal diversity would change in situations where deer were only controlled by their food resources have lacked the kind of unambiguous answer that might be provided by quasi-experimental situations.

The archipelago of Haida Gwaii (Queen Charlotte Islands), British Columbia, Canada, provides one such natural experiment (*sensu* Diamond 1983). No mammalian forest herbivores are native to these islands. Sitka black-tailed deer *Odocoileus hemionus sitkensis* Merriam were introduced to the northern end of the archipelago in 1878 and spread rapidly to most of the islands (Golumbia et al. 2008). However, a few small islands show no sign of ever having been visited by deer. In addition, Vila et al. (2004a, b, 2005), based on growth rings and rubbing scars on woody vegetation, identified islands where deer had been present for different lengths of time. Despite a few endemic species (Taylor 1989) and some degree of species impoverishment, the flora of Haida Gwaii is a comparable subset of that found on the adjacent mainland (Alaback 1990) where it is exposed to browsing by black tailed deer. In a companion paper, Stockton et al. (2005) provided a detailed analysis of

the effects of deer on the native flora of these islands and showed how deer browsing was associated with a dramatic reduction in plant cover and plant species richness. Allombert et al. (2005a, b) discussed the indirect effect of variation in browsing history on invertebrates and birds of the same set of islands.

In this paper we used the same data sets to provide a comprehensive analysis on how the presence or absence of a large herbivore affects plant community composition and structure within and between two ecotopes (shoreline and forest interior habitats). We then analysed how these modifications are summarized in indices of plant species density (*sensu* Gotelli and Colwell 2001), overall cover and diversity and echoed by a cascade of changes in species density, abundance and diversity of invertebrates and songbirds. We considered the following questions: (1) whether uncontrolled deer populations affect the abundance, diversity and structure of understorey vegetation; (2) whether they affect tree regeneration; (3) whether there is an overall negative relationship between presence of uncontrolled deer populations and animal diversity; (4) whether the effects of deer on animals is highest in species that depend on understorey vegetation; (5) whether the magnitude of the effects increases with duration of deer presence.

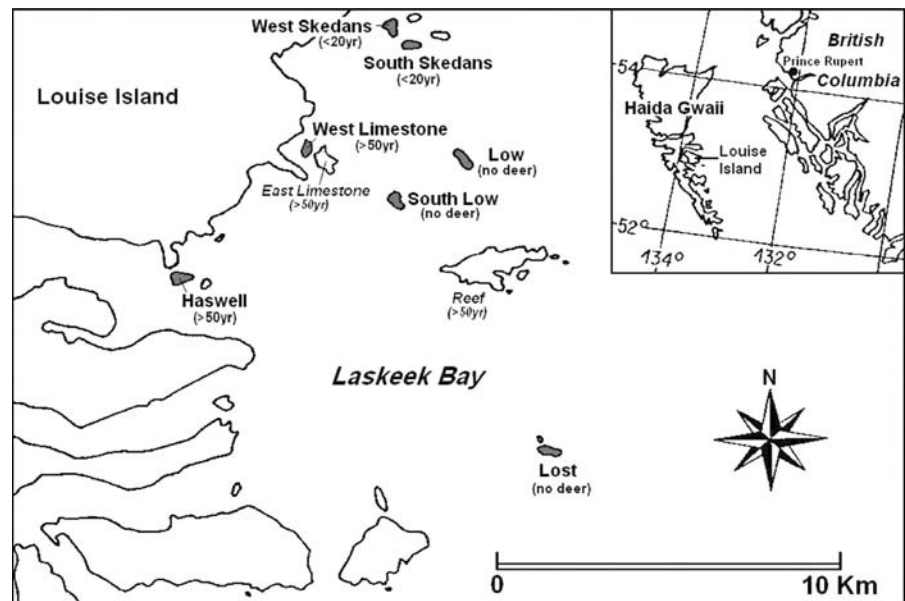
Methods

Study area

Haida Gwaii, the largest and most isolated archipelago on the west coast of Canada, is situated 80 km west of mainland British Columbia and 50 km south of the Alexander Archipelago of Alaska. It falls within the perhumid temperate forest zone of the coastal temperate rain forest. The flora is similar to that of adjacent Southeast Alaska (Banner et al. 1989), but is relatively impoverished with only 665 recorded vascular plant species (Lomer and Douglas 1999). The fauna also is impoverished (Ricketts et al. 1999) and, except for an extinct relict caribou population, there were no deer and none of their major non-human predators at the time of European contact, in the eighteenth Century (Cowan 1989). The deliberate introduction, in the late nineteenth century (Osgood 1901; Munro 1935), of Sitka black-tailed deer from populations native to similar forests on the adjacent mainland, created a situation where unconstrained deer populations could affect large areas of forest.

Our study sites were all situated in Laskeek Bay on the east coast of Haida Gwaii (Fig. 1). None of the islands studied has been substantially affected by human activities (Martin and Daufresne 1999). They

Fig. 1 Map of Study area



have no large predators and no major climatic constraints (Pojar 1999) to interfere with the relationship between deer and their habitat.

The analysis of age structures in shrub-stems and the dating of the oldest fraying scars through tree ring measurement (Vila et al. 2004a, b, 2005) revealed that, among our study islands, some had been occupied by deer for >50 years, while others had been occupied for <20 years. Independent observations confirmed that on the islands identified by Vila et al. as colonized within the past 20 years, deer were present in 1989 (~10 years prior to this study, personal observation) but not recorded in 1983 by Rodway et al. (1988). Hence colonization probably took place ~15 years before the start of our studies, in 1998.

We studied seven islands, selected to control, as much as possible, for island area: South Low, Low, and Lost (deer-free; 4.5, 5.3 and 9.6 ha in size, respectively), South Skedans, West Skedans, (deer present for <20 years; 5.6 and 8.2 ha, respectively), Haswell and West Limestone (deer present for >50 years; 13.3 and 16.0 ha, respectively). All are located within 17 km. The islands without deer are the most isolated from the larger islands (between 3 and 7 km). The islands where deer were present for less than 20 years were at 1.3–2.4 km from the larger islands and the islands with deer for over 50 years were situated between 350 and 150 m from the larger islands. The two latter were therefore easily accessible to deer even for brief visits lasting less than a day. All supported the same type of primary forest dominated by western hemlock and Sitka spruce and were unaffected by commercial logging or other human activity. Sitka spruce tended to be more prevalent on the offshore islands and western redcedar was more frequent on inshore islands. Pellet counts (Stockton et al. 2005) indicated that densities were comparable between the two island categories with deer and suggested deer densities ranged from 21 to 37 deer per km⁻². As the unbrowsed islands are much further out from the main islands than the browsed islands, they are less protected from oceanic influences and have a greater exposure to wind. The greater isolation and the distinctive disturbance histories, which suggest harsher environmental conditions, could have negative effects on species diversity or abundance by limiting the presence of species sensitive to salt spray or to drier conditions.

The islands with the longest browsing history were the largest and least isolated of the study islands so, all else being equal, might be expected to have higher species richness than the other islands (MacArthur and Wilson 1967). However, in contrast with these expectations, plant species richness was highest on the smallest and most isolated islands (Stockton et al. 2005; Gaston et al. 2006), which were also those without deer. Overall geology, soils and topography were similar among the islands studied.

Ecotopes and study plots

We recognized two distinct structural habitat types: the shoreline and the forest interior (see Stockton et al. 2005 for details). These ecotopes differed principally in available light and exposure to wind and salt-spray. They presented major differences in vegetation composition in the absence of deer (dominance of herbaceous vegetation at the shoreline and of shrubs in the forest interior, see Stockton et al. 2005). The transition between the two occurred within 25 m of the high-tide line.

Because of the high edge-to-interior ratio on small islands, we sampled the shoreline vegetation on each island with ten 10-m radius circular plots regularly spaced along the shoreline (10–15 m from the high-tide line) and five 10-m radius circular plots placed within the forest interior at least 50 m from the forest edge, at least 50 m from one another and with similar light levels (closed canopy cover). Vegetation sampling covered 3–10% of the area of each island.

Measurement of understorey vegetation

Vascular plants were identified according to Pojar and MacKinnon (1994), and verified with Hitchcock and Gronquist (1973). We defined two strata: 0–50 cm and 50–150 cm. These zones were chosen to highlight the effects of deer, which feed primarily below 150 cm (Martin and Daufresne 1999). The percent cover of each species, as well as the total cover of vegetation in each of three strata, was estimated using standard spot charts (Mueller-Dombois and Ellenberg 1974). Within a stratum, cover was defined as the area covered by the projection of its foliage on an imaginary horizontal plane in that stratum. Estimates of percent cover were made to the nearest percent (a 1 m² area representing

0.3% of the plot). Plants present but with negligible cover were all given a 0.001% cover value. Sampling was performed in July 2000, the period of maximum cover of herbaceous plants in this region.

Sampling of invertebrates and identification

We sampled understorey invertebrates on the same plots used to study deer impact on vegetation. We had ten plots per island: five in the forest interior and five at the shoreline. The shoreline plots were chosen randomly among the ten used in the vegetation study.

We sampled invertebrates from the understorey vegetation in each plot with a sweep net of 38.1 cm in diameter. All the vegetation within 3.6-m from the plot center and below the browse line (1.5 m from the ground, hereafter browse-layer) was swept uniformly for 2 min in shoreline plots and for 3 min in interior plots (due to denser understorey). We collected three samples on each plot at different dates between 25 May–20 July 2001, except interior plots on Lost Island, where we collected only two. Sampling dates for the different islands were interspersed to avoid temporal bias. All arthropods (except Acari) were removed from the net with a suction aspirator, counted, and preserved for identification.

We sampled litter invertebrates in the 30 forest interior plots only. We used pitfall traps: two plastic cups fitted together with a light gray ceramic tile supported by small sticks as cover. Despite potential shortcomings (Spence and Niemelä 1994), pitfall traps are commonly used for sampling litter arthropods. They are most efficient for active groups such as ground beetles or spiders (Standen 2000) but work also for gastropods (Suominen 1999). Six traps were deployed at each plot, spread every 60° at 3-m from the plot center. We intended to leave traps for 18 days on each island. Because of logistic constraints, the average was 18.5 days for islands without deer, 19.5 days for islands with a short-browsing history and 20 days for islands with a long-browsing history. Traps were left out in May–June 2000. After collection, specimens were preserved for identification.

Specimens were identified to family and morphospecies by one of the authors (S.A.) and identifications were validated through collaboration with taxonomists (see acknowledgements in Allombert et al. 2005a). The use of morphospecies is considered suitable to

assess differences in species richness across different habitats (Oliver and Beattie 1996). All browse-layer specimens were identified to morphospecies, except Thysanoptera (thrips), and Nematocera (long-horned flies). For litter specimens we only identified gastropods and beetles. We identified larvae from heterometabolic orders to morphospecies or species and considered them as adults. We did not analyze larvae from holometabolic orders.

Sampling of song birds

Allombert et al. (2005b) studied bird assemblages of the different islands (no distinction made between shoreline and interior) by two methods: point-counts and spot-mapping. Both methods yielded similar results. Here we use only the data obtained from spot-mapping. Censuses were conducted over the entire area of each island, following the method formerly used in the UK Common Bird Census (Marchant et al. 1990; Bibby 1992). The method estimates species population densities and provides better information on the presence and abundance of rarer species and on gamma diversity (e.g., species richness at the scale of an island than point counts; see Hamel 1984; Bibby 1992). We made four 4 h visits to each island spread over the entire breeding season. The entire island was covered during each visit, we located each bird seen or heard on a map and recorded its behaviour (singing, foraging, etc.). Because of their open understorey, the larger islands, those with deer for over 50 years, were the easiest to census, especially when compared to the smaller deer-free islands with their dense understorey; so coverage was probably similar for different island categories. Island species richness was defined as the number of species recorded during the four mapping sessions. Breeding pair density was calculated by dividing the number of pairs identified during the mapping sessions by the area of the island (area data are from Martin et al. 1995). Censuses were all done by the same observer (SA).

Analyses

Variation in vegetation composition

For each ecotope we retained all plant species that were present with at least 1% cover in more than five

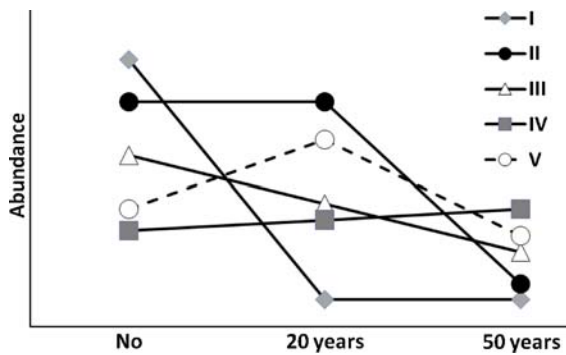


Fig. 2 Five theoretical response patterns of vegetation to modification by deer. I = plants “restricted” to islands with no deer, II = plants “restricted to islands with no deer or deer for less than 20 years, III = plants with decreasing cover with increasing length of browsing history, IV = plants not affected by browsing history or with higher cover on islands with deer, V = plants with highest cover for intermediate levels of disturbance (humped-back shaped curve). No = without deer; 20 years = deer present less than 20 years; 50 years = deer present for over 50 years

plots. We assigned these species to one of five browsing response guilds (Boutin and Keddy 1993; Wilson 1999) on the basis of their response trajectory in the strata below 150 cm (the two lower strata). These five guilds (Fig. 2) described five possible responses of the cover of a species to the presence of deer, relative to the situation on deer-free islands: (i) reduction in mean cover/plot after less than 20 years of deer presence; (ii) mean cover/plot not greatly reduced when deer had been present <20 years but greatly reduced when they had been present >50 years; (iii) a similar decline in cover from 0 to <20 years and from <20 to >50 years; (iv) cover remained unchanged or increased with length of deer presence; (v) cover highest on islands with deer for <20 years. Having assigned species to guilds based on a visual analysis of trends, we used an ANOVA (STATISTICA software) to assess the significance of the differences in mean cover/plot among island categories.

Principal component analysis

We used principal component analysis (PCA, PROC FACTOR procedure, SAS 2001) to examine the effect of deer on plant-types among treatments. PCA projects samples on a new set of axes, hence reducing

the dimensionality of the dataset while retaining those characteristics that contribute most to its variance. We selected PCA as an ordination method based on a preliminary examination of the data using a detrended correspondence analysis (DCA) which showed maximum gradient length of the data to be less than 3 SD (ter Braak and Smilauer 1998). PCA is considered appropriate for analyzing samples along short gradients such as this, especially when species are monotonically related to each other such as the species in our dataset (Jongman et al. 1995).

To minimize the number of zero abundance scores, we grouped cover estimates for each species in each plot for 0–50 cm and 50–150 cm strata according to plant-type (tree, shrub, forb, fern, and graminoid) and used them as our variables, unless cover of individual species averaged more than 2% in either stratum (salal *Gaultheria shallon* Pursh, dune grass *Elymus mollis* Trin. in Spreng and red fescue *Festuca rubra* L. for shoreline plots; salal for interior plots) in which case cover of the species was included as a separate variable in the analysis. For most species zero abundance scores occurred in plots with >50 years of deer browsing, demonstrating a unimodal response to deer presence over time. Total species richness was included as a separate variable. We standardized vegetation cover variables and the PCA was carried out on the correlation matrix to prevent the swamping of uncommon measures by common ones (Stevens 1986).

Analysis of variation in indices of species density, abundance and diversity

For the vegetation and invertebrates we analyzed changes in α -level species density (Gotelli and Colwell 2001) (number of species recorded by sampling unit), in overall taxa abundance per sampling unit (total plant cover or total number of individuals per plot for invertebrates) and in Shannon’s diversity index at the plot scale in relation to browsing history and ecotope (when applicable). For birds the sampling unit was the island and we analyzed trends in the number of bird species, total number of individuals and species diversity per island. Based on the results of Allombert et al. (2005b) we only included those bird species that were dependant on the understorey for feeding and/or nesting.

Results

Change in the vegetation

Changes in vegetation composition

In the shoreline ecotope 26 plant species had a cover of 1% or more in >5 plots. These included one coniferous tree, eight shrubs, 11 forbs, five grasses and one fern species (Table 1). Sitka spruce *Picea*

sitchensis was the only tree that met our sample size requirement. Salal and Nootka rose *Rosa nutkana* were the dominant shrub species. Fireweed *Epilobium angustifolium*, false-lily-of-the-valley *Maianthemum dilatatum* and giant vetch *Vicia gigantea* were the three most common forbs, dune grass and red fescue the main grasses. Sword fern *Polysticum munitum* was the only common fern. All 26 species were common on the islands without deer. On the islands which had had deer for >50 years our criteria

Table 1 Guild membership of vascular plant species that had a cover greater than 1% in the layers below 150 cm in more than five shoreline plots

Shoreline plots			0–50			50–150			Trend	
Plant species	Common name	Deer presence (years)			Deer presence (years)					
		No	<20	>50	0	<20	>50			
Conifer trees	<i>Picea sitchensis</i>	Sitka spruce	2.33	3.80	4.40	2.63	3.85	0.40	V	
Shrubs	<i>Gaultheria shallon</i>	Salal	9.57	16.85	4.15	7.97	5.05	0	II*	
	<i>Rosa nutkana</i>	Nootka rose	5.40	0.10	0.15	4.40	0.05	0	I***	
	<i>Lonicera involucrata</i>	Black twinberry	2.10	0	0	3.83	0	0	I***	
	<i>Arctostaphylos uva-ursi</i>	Kinnikinnik	4.27	0.20	0	–	–	–	I(*)	
	<i>Rubus parviflorum</i>	Thimbleberry	1.67	0	0	2.40	0	0	I	
	<i>Symphoricarpos albus</i>	Snowberry	1.47	0	0	2.00	0	0	I	
	<i>Rubus spectabilis</i>	Salmonberry	0.77	0	0	1.77	0	0	I*	
	<i>Vaccinium parvifolium</i>	Red huckleberry	1.10	0.05	2.35	1.30	0.10	0	IV ^a	
Forbs	<i>Epilobium angustifolium</i>	Fireweed	6.33	0.05	0	5.80	0	0	I***	
	<i>Maianthemum dilatatum</i>	False lily-of-the-valley	9.17	0.30	0	–	–	–	I**	
	<i>Vicia gigantea</i>	Giant vetch	2.57	0.05	0	2.63	0	0	I***	
	<i>Angelica lucida</i>	Seawatch	1.27	0	0	0.67	0	0	I**	
	<i>Heracleum lanatum</i>	Cow’s parsnip	0.93	0	0	0.93	0	0	I*	
	<i>Ranunculus occidentalis</i>	Western buttercup	0.73	0	0	0.23	0	0	I**	
	<i>Conioselinum pacificum</i>	Pacific hemlock parsley	0.67	0.05	0	0.03	0	0	I**	
	<i>Fritillaria camschatcensis</i>	Black lily	0.43	0	0	0.03	0	0	I*	
	<i>Achillea millefolium</i>	Yarrow	0.37	0.05	0.05	0.07	0	0	I	
	<i>Sedum divergens</i>	Spreading stonecrop	0.43	0.20	0	–	–	–	III	
	<i>Prenanthes alata</i>	Western rattlesnake root	0.37	0.10	0.15	–	–	–	III	
	Grasses	<i>Elymus mollis</i>	Dunegrass	9.00	0	0	8.63	0	0	I***
		<i>Festuca rubra</i>	Red fescue	9.77	7.25	2.40	0.20	0	0	III*
<i>Puccinellia nulkaensis</i>		Pacific Alkali Grass	3.23	0	0.85	0.03	0	0	I	
<i>Hordeum brachyantherum</i>		Meadow barley	2.27	0	0	0.80	0	0	I	
<i>Calamagrostis nutkaensis</i>		Nootka reedgrass	1.50	4.85	0	0.93	0.25	0	II	
Ferns	<i>Polysticum munitum</i>	Sword fern	0.60	0.05	0	0.30	0	0	I(*)	

Figures in table represent the average species percent cover/plot in each 0–50 and 50–150 vegetation layers. Guild attribution (I to V) were made based on the averages cover values in the 0–50 and 50–150 cm layers. These browsing response guilds are defined in Fig. 2. Statistical significance of ANOVA analyses of Trends: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. Parentheses in Trend column refer to marginal significance ($P < 0.06$)

^a REHU follows a marked type I trend in the 50–150 cm layer

retained only eight species: the spruce, three shrubs, two forbs and two grasses (Table 1).

In the interior plots 13 species met our criteria. These included two conifer trees (Sitka spruce and western hemlock *Tsuga heterophylla*), two deciduous trees (Sitka alder *Alnus crispa* and Pacific crabapple *Malus fusca*), six shrubs (mostly salal, thimbleberry *Rubus parviflorus* and salmonberry *Rubus spectabilis*), one forb (false lily-of-the-valley) and two ferns (sword fern and bracken fern *Pteridium aquilinum*). All these species were present on the islands without deer. On the islands with deer present for >50 years only the two conifer species and one shrub species (red huckleberry *Vaccinium parvifolium*) retained significant cover.

Variation in plant response to browsing

Of the 26 species retained in the analysis of shoreline plots, the guild attributions (see Fig. 2) of 16 had significant differences in the average cover/plot below 150 cm among island categories (ANOVA analysis, see Table 1). These were the plants with the highest occurrence frequencies and hence those for

which the comparisons had the best statistical power. Based on their average cover in the samples (Table 1) we assigned 19 of the 26 species to response guild I, two to guild II, three to guild III, one to guild IV and one to guild V.

Of the 13 species retained in the analysis of the vegetation in interior plots, ten had significant differences in their mean percent cover among the three deer-effect categories. Based on their average cover in the 0–150 cm layers in the samples (Table 2), we assigned nine of these species to guild I, two to guild II, none to guild III or IV and two to guild V.

Thus, most species followed a guild I pattern. Only four species followed a guild II pattern. Of the latter salal was the only one common in both ecotopes. The species that exhibited a guild III pattern (a gradual reduction with increased deer presence) in the shoreline habitat were two forbs and the red fescue. The two conifers exhibited a guild V pattern: their cover in the understorey was highest on islands with deer <20 years. One species, the red huckleberry showed marked differences in its response to browsing between the two vegetation layers considered. In

Table 2 Guild membership of vascular plant species that had a cover greater than 1% in the layers below 150 cm in more than five interior plots

Interior plots			0–50			50–150			Trend
Plant species	Common name	Deer presence			Deer presence				
		No	<20	>50	No	<20	>50		
Conifer trees	<i>Picea sitchensis</i>	Sitka spruce	0.40	0.80	0.40	1.53	2.60	0	V
	<i>Tsuga heterophylla</i>	Western hemlock	0.13	3.80	0.80	0.33	4.20	0.10	V*
Deciduous trees	<i>Alnus crispa sinuata</i>	Sitka alder	0.93	0	0	2.80	0.20	0	I*
	<i>Malus fusca</i>	Pacific crabapple	0.13	0.20	0	0.40	1.20	0	II
Shrubs	<i>Gaultheria shallon</i>	Salal	29.47	30.10	0	35.60	32.50	0	II**
	<i>Rubus parviflorus</i>	Thimbleberry	5.33	0	0	7.93	0	0	I**
	<i>Rubus spectabilis</i>	Salmonberry	3.80	1.20	0	7.80	1.20	0	I*
	<i>Symphoricarpos albus</i>	Snowberry	1.87	0	0	3.60	0	0	I*
	<i>Lonicera involucrata</i>	Black twinberry	1.60	0	0	3.53	0.30	0	I***
	<i>Vaccinium parvifolium</i>	Red huckleberry	0.93	0	1.20	2.27	0	0	I** ^a
Forbs	<i>Maianthemum dilatatum</i>	False lily-of-the-valley	13.93	0	0	0.47	0	0	I***
Ferns	<i>Polysticum munitum</i>	Sword fern	22.00	5.20	0	18.47	0.07	0	I***
	<i>Pteridium aquilinum</i>	Bracken fern	0.53	0	0	3.87	0	0	I

Figures in table represent the average species percent cover/plot in each 0–50 and 50–150 vegetation layers. Guild attribution (I to V) were made based on the averages cover values in the 0–50 and 50–150 layers. These browsing response guilds are defined in Fig. 2. Statistical significance of ANOVA analyses of Trends: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

^a REHU follows a marked type IV trend in the 0–50 cm layer

the ground layer its cover was highest on islands with deer >50 years (guild IV pattern). In the 50–150 cm layer it followed a clear guild I pattern, cover being dramatically reduced in presence of deer.

Principal components analysis

The first component of the PCA of shoreline plots and interior plots (Fig. 3a) summarized 25% of the variance, the second 21% and the third 8%. Plots with the highest positive scores on PC1 had high species richness and high cover of shrubs in both vegetation layers below 150 cm. The second principal component segregated these plots in plots with high cover of ferns in both layers (positive scores along PC2) and plots with high cover of forbs and dune grass in both layers (negative scores along PC2). Plots with medium species richness and cover (i.e., plots with scores close to zero along PC1) were segregated along PC2 into plots with a high cover in the 50–150 cm vegetation layer of the commonest shrub, salal, and a high cover of young trees in the 50–150 cm vegetation layer (positive scores on PC2) from plots with low values in these variables (negative scores on PC2).

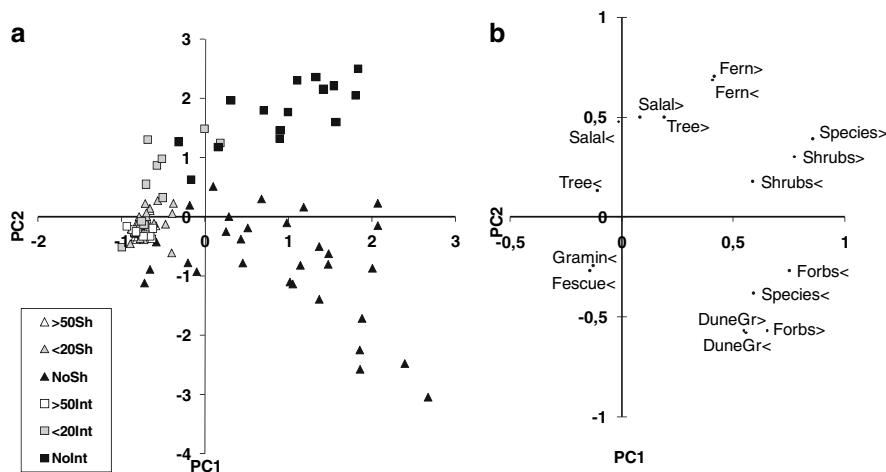


Fig. 3 Principal components 1 and 2 obtained from a Principal Components Analysis, PCA, of 70 shoreline (Sh) (triangles 14 variables measured) and 30 interior vegetation plots (Int) (squares 12 variables measured) with three different browsing histories (no deer, black symbols; deer < 20 years, grey symbols; deer > 50 years, open symbols; note that open triangles are essentially masked by the open squares). **a** Planes defined by principal component 1 (25% of total variance) and 2 (21% of total variance) for shoreline and interior plots combined; **b** variable factor loadings for shoreline and interior

plots combined. The second PC segregated plots that had slightly negative scores on PC1 (that is low vegetation cover and low species richness) into plots with a significant cover of salal in the 0–50 cm layer (positive scores) from plots with a high cover of Grasses and Red fescue (negative scores).

Islands without deer (in black) showed a wide spread of scores along PC1 (from highly positive to negative scores, Fig. 3a), reflecting a wide range of values in species richness and vegetation cover as well as variation in species composition. The plots from shoreline and forest interior segregated completely along PC2 (Fig. 3a). Plots from the shoreline on islands without deer had a wider spread along both axes than those in the interior. They had negative or slightly positive scores along PC2 and those with the most positive scores on PC1 and the most negative scores on PC2 were characterized by a high cover of forbs and dune grass, significant high cover of shrubs other than salal and high species richness in the 0–50 cm layer (Fig. 3b). The shoreline plots with the lowest positive scores or with negative scores along PC1 had lower vegetation cover and lower species richness but were characterized by a high cover of

plots combined. *Abbreviations:* Richness = species richness, Tree = tree cover (tree cover in the shoreline plots consists exclusively of Sitka spruce *Picea sitkensis*), Shrubs = shrub cover, Salal = salal *Gaultheria shallon* cover, Fern = fern cover (restricted to interior plots), Forbs = forb cover (restricted to shoreline plots), Gramin = graminoid cover, DuneGr = dune grass *Elymus mollis* cover (restricted to shoreline plots), Fescue = red fescue *Festuca rubra* cover (restricted to shoreline plots); height classes < = 0–50 cm; > = 50–150 cm

grasses and especially of red fescue in the 0–50 cm vegetation layer. The plots from the forest interior had positive scores on PC2 and those with the highest positive scores on PC1 were characterized by a high cover of shrubs other than salal, a high cover of ferns and high species richness especially in the 50–150 cm layer. Forest interior plots that had lower scores along PC1 were characterized by a high cover of salal and of young trees.

Plots from islands with the longest browsing history showed almost no spread and no segregation along the two axes. Plots from both ecotopes formed a single dense cluster of almost identical scores (negative scores on PC1 and 2; Fig. 3a). All plots on these islands had low values for the variables describing species richness and vegetation cover. Their vegetation consisted mainly of young trees (mainly Sitka spruce *Picea sitchensis*) and red fescue or other graminoids (variable loadings on Fig. 3b).

Plots from islands with deer <20 years (shown in gray on Fig. 3a) had intermediate scores along PC1. Their scores were intermediate between those of the plots from the other two classes of islands. In this category shoreline plots had scores close to those from islands that had had deer >50 years. Their vegetation cover consisted of small trees (mainly Sitka spruce), red fescue and other grasses and of a small amount of salal. Plots from the forest interior segregated into two sub-groups (Fig. 3a). Plots with negative scores on PC2 which had scores close to those from islands with deer >50 years and plots with positive scores on PC2 which had scores closer to those of plots from islands without deer that had a high cover of salal.

Overall, plots of the two ecotopes were distributed along two converging gradients of vegetation simplification (Fig. 3a). The two extremities of these gradients characterize a strong contrast in vegetation structure and composition between the two ecotopes on islands without deer (positive scores on PC1) and a total lack of segregation on islands with the longest browsing history (negative scores on PC1).

Changes in taxa species density, abundance and diversity

Plants

On islands without deer, plant species density was significantly higher in shoreline plots than in forest

interior plots. On islands with a long history of deer presence species density in shoreline plots was very low and similar to values found in interior plots (Fig. 4; Table 3). Most of that decrease was already observed on the islands with deer <20 years. In the forest interior species density per plot showed only little variation among islands with different browsing histories.

Plant cover in the understorey decreased dramatically and monotonically in both ecotopes when length of deer presence increased. The pattern was similar in both habitat types, with cover going from values around 90% on islands without deer to less than 20% on islands with deer >50 years (Fig. 4; Table 3).

Average plant diversity index per plot was highest on islands without deer and lowest on islands with deer. In the shoreline plots the decrease was monotonic. In interior plots most of the decrease occurred between islands without deer and islands with deer <20 years (Fig. 4; Table 3).

Invertebrates

Overall, understorey invertebrate species density per plot decreased with length of deer presence. Highest species density was observed in the plots from the shoreline ecotope, but the decrease was comparable in both ecotopes (Fig. 4; Table 3).

The average number of specimens of understorey invertebrates collected per plot was highest in the shoreline habitat of islands without deer and was dramatically lower on islands with deer. Sample sizes were lower for interior plots and decreased with increasing length of deer presence (Fig. 4; Table 3).

In the absence of deer, Shannon's diversity index of ground layer vegetation invertebrates was high and comparable in plots from both ecotopes. It decreased with increasing duration of deer presence. In the shoreline plots the decline was most pronounced between islands without deer and islands with deer <20 years. For interior plots this difference was reversed.

The average litter invertebrate species density per plot (only forest interior plots) and the average number of specimens caught per plot were highest on islands with deer >50 years (23 and 50% higher than on islands without deer, respectively). The gain in species and in total abundance was in part caused by an increase in occurrence and abundance of weevils and millipeds on both islands that had deer for >50 years. Shannon's index for litter invertebrate

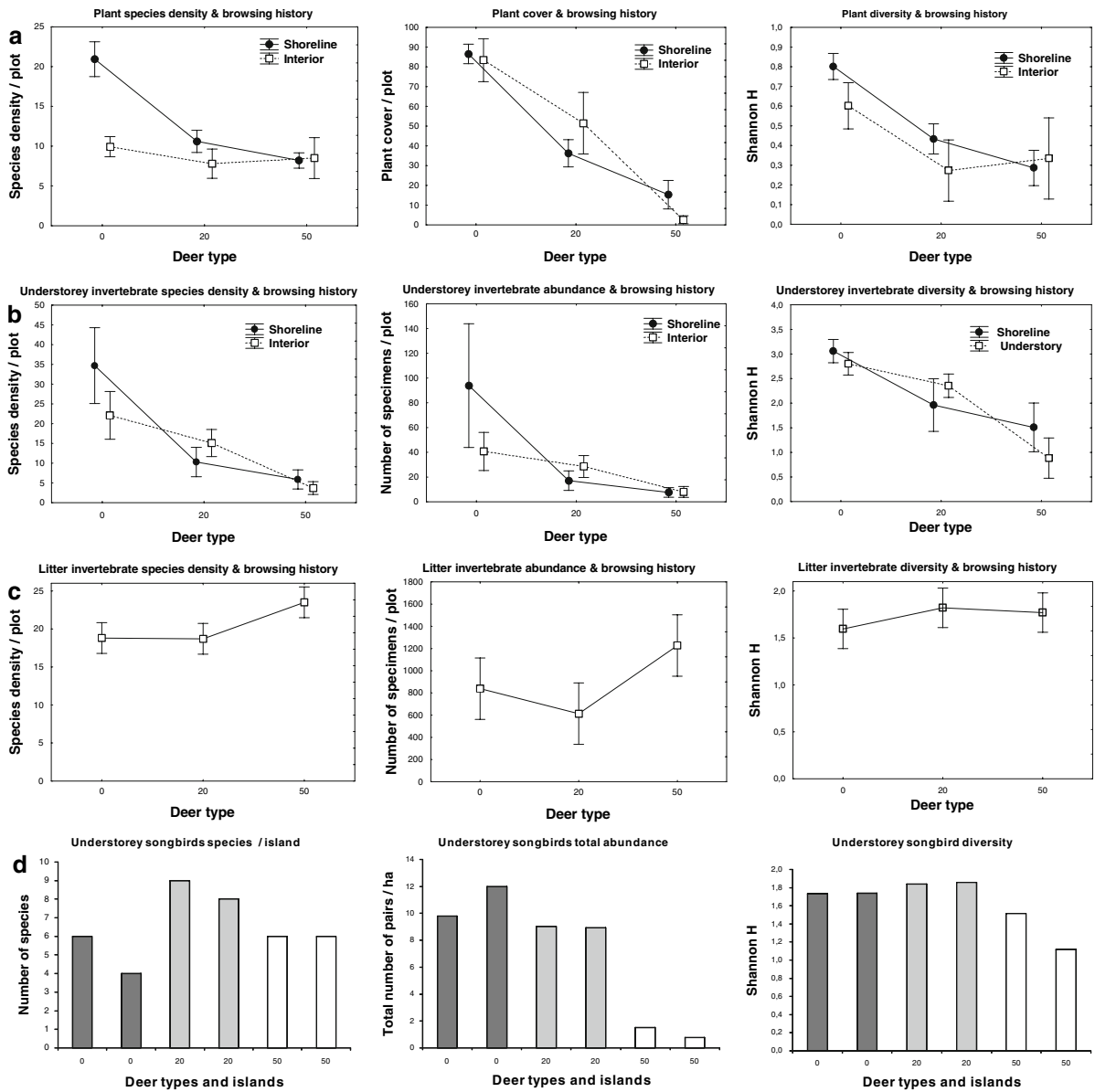


Fig. 4 Variation among islands in mean species richness per plot (species density); abundance per plot (%cover or total number of individuals), and Shannon diversity index per plot. **a** Plants; **b** understorey invertebrates; **c** litter invertebrates; **d** songbirds that depend on the understorey for feeding or

nesting. There is an overall significant negative effect of deer presence on the abundance of understorey songbirds (Table 3; Allombert et al. 2005b). Vertical bars denote 0.95 confidence intervals

species did not vary significantly among island categories (Fig. 4; Table 3). Species density, composition and invertebrate abundance did show some important variations between islands and especially so between the islands with deer for >50 years (only two species in common among the ten species that were most abundant in the two samples).

Birds

The density in bird species that depend on understorey vegetation was highest on islands with deer <20 years and there was no stark contrast in species richness between islands without deer and islands with deer >50 years. The mean number of pairs per ha was 5–10

Table 3 Results of generalized linear model (Statistica, Factorial ANOVA, LS means procedure) on the effects of deer browsing history and ecotope (shoreline or forest interior) on species richness, species abundance and Shannon diversity index

Taxa	Variable	Effect	<i>F</i>	<i>P</i>	Significance
Vegetation	Species richness	Deer	33.87	0.000	***
		Ecotope	30.17	0.000	***
		Deer × ecotope	19.50	0.000	***
	Cover	Deer	199.6	0.000	***
		Ecotope	0	0.952	NS
		Deer × ecotope	5.70	0.004	*
	Shannon index	Deer	39.97	0.000	***
		Ecotope	6.08	0.015	*
		Deer × ecotope	3.31	0.040	*
Understorey invertebrates	Morphospecies richness	Deer	54.48	0.000	***
		Ecotope	3.15	0.082	NS
		Deer × ecotope	7.23	0.002	**
	Abundance	Deer	20.21	0.000	***
		Ecotope	3.01	0.088	NS
		Deer × ecotope	6.30	0.003	*
	Shannon index	Deer	53.55	0.000	***
		Ecotope	1.41	0.240	NS
		Deer × ecotope	4.70	0.13	NS
Litter invertebrates	Morphospecies richness	Deer	7.75	0.002	**
	Abundance	Deer	0.011	5.30	*
	Shannon index	Deer	1.33	0.282	NS
Understorey songbirds	Species richness	Deer	2.29	0.248	NS
	Abundance	Deer	59.97	0.004	**
	Shannon index	Deer	–	–	

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = non significant

times lower on islands with deer >50 years than on the other island categories. Shannon's diversity was lower on islands with deer >50 years than on the two other island categories (Fig. 4; Table 3 and see Allombert et al. 2005b for a thorough statistical analysis of song bird trends in relation to deer browse).

Discussion

Plant population responses to unchecked deer browsing

Young trees

Cover of young Sitka spruce and western hemlock was highest on islands with deer <20 years and similar in the two other island categories. Cover of deciduous

trees was reduced on islands with deer. The impact of deer on the growth and survival of tree seedlings has been recognized for many years (Leopold et al. 1947). In eastern forests, eastern hemlock *Tsuga canadensis* and eastern white cedar *Thuja occidentalis* seedlings were shown highly susceptible to deer browsing (Anderson and Loucks 1979; Frelich and Lorimer 1985; Alverson et al. 1988; Epstein et al. 1999). On Haida Gwaii, Sitka spruce and western hemlock can be heavily browsed (Coates et al. 1985; Vila et al. 2002, 2003), especially in the winter (hemlock) and spring (new growth of spruce), when herbaceous vegetation is scarce (Bunnell 1990) and in sites where alternative forage has become scarce. In our study, Sitka spruce under 1.5 m, occurred often in *bonsai* form in the presence of deer, especially when growing in good light conditions, with a dense foliage within a layer of protruding dead branches. However, browsing did not

seem to significantly affect their cover over time and many young spruce and hemlock attained escape height and resumed normal growth (Vila et al. 2002). Although uncommon on the islands we studied, the third dominant conifer on Haida Gwaii, western redcedar, *Thuja plicata*, was recorded below 150 cm only on islands without deer. It is highly susceptible to browsing by introduced deer; when deer are present redcedar regeneration is eliminated in the understorey of mature forests (Martin and Daufresne 1999; Vourc'h et al. 2002; Martin and Baltzinger 2002; Stroh et al. 2008).

Shrubs

Shrubs were abundant in the shoreline and interior ecotopes of islands without deer but contributed little or no cover on islands with deer. Deer usually select new growth of woody species as it contains less lignin and more starch and is easier to digest than established branches and leaves (Bunnell 1990). This has led to the demise of many shrub species on Haida Gwaii through attrition, as suckers and buds are repeatedly browsed, preventing regeneration (Vila et al. 2004b).

Salal (guild II) was the most abundant shrub species in both ecotopes on the islands without deer, forming impenetrable thickets at several sites. On islands with deer <20 years, thickets persisted and salal was still the most abundant shrub in both habitats. On islands with deer >50 years, salal persisted only in inaccessible areas such as cliff faces and the tops of stumps.

Red huckleberry occurred mainly as fully grown individuals on islands without deer. On islands with deer only a few over-mature individuals with a limited number of stems, defoliated below 1.5 m, occurred (Vila et al. 2004b). Seedlings showed signs of repeated browsing but were relatively abundant when they were able to grow within a thick layer of moss which offered some protection. The abundance of such dwarfed huckleberry seedlings accounted for most of cover of the species that was recorded below 50 cm in the open understorey or in shoreline habitat of islands with deer >50 years (Tables 1, 2). In presence of deer such plants had no chance of flowering and producing seeds.

In western coastal forests, shrubs provide a large and important component of deer forage throughout

the year (Bunnell 1990). Because the nutrient availability of woody plants changes with the seasons, deer switch from species to species as the year progresses (Wallmo 1981). Rubus species provide important spring forage, while huckleberry provides important winter forage (Cowan 1945; Bunnell 1990). Salal does not digest well on its own, but makes up an important component of both summer and winter diets when eaten with arboreal lichens (Bunnell 1990).

Grasses

The cover of the most common grasses (Table 1) decreased with the duration of deer presence. Deer are generally thought to avoid grasses, sedges, and rushes. However, black-tailed deer heavily utilize many grasses in spring and summer (Bunnell 1990). Sedges were heavily utilized by Columbia black-tailed deer in some habitats on Vancouver Island but were hardly used in others (Cowan 1945). In our data, reduced cover of red fescue resulted primarily from reduced size rather than reduced numbers and, although the absolute abundance of red fescue decreased when browsing history increased, it comprised a large proportion of the total cover of grasses remaining in the understorey. One species, Nootka reedgrass, followed a guild II pattern but had substantially higher cover in the 0–50 cm vegetation layer on islands with deer <20 years. The low cover on the islands with deer >50 years may partly reflect habitat availability, as Nootka reedgrass is associated with lightly-wooded, exposed areas (Gaston et al. 2006), which are less prevalent on these islands.

Forbs

The abundance of most forbs decreased dramatically in presence of deer (guild I pattern mostly). Forb species provide most of the summer forage for deer (McCaffery et al. 1974). Preferred species such as fireweed are easily digestible and rich in energy (Bunnell 1990). They are highly susceptible to repeated browsing and their abundance is reduced at high deer densities (Miller et al. 1992; Rooney 1997; Rooney and Dress 1997; Augustine et al. 1998; Rooney 2001; Moser and Schütz 2006; Waller 2008).

Ferns

The two fern species retained in the analysis followed a guild I pattern, with sword fern being able to maintain some cover on islands with deer <20 years. Ferns are a heavily used food source for black-tailed deer in western forests (Cowan 1945; Pojar et al. 1980; Bunnell 1990). The fronds of deer fern, *Blechnum spicant*, and the rhizomes of shield fern are important winter food. The fiddle-heads of bracken fern are important spring food (Cowan 1945; Bunnell 1990; Gillingham et al. 2000). On the islands without deer sword fern occurred as many densely packed large individuals (over 1 m tall) in limited areas on both cliffs and flats. On the islands with deer <20 years, they maintained substantial cover but were heavily browsed where accessible, at times retaining only a few fronds, none of them new growth. Subsequent to the observations used for this analysis, sword fern was virtually eliminated from West Skedans Island (one of our two <20 year sites) by 2007, about 20 years from deer arrival (pers. obs.). On islands with deer >50 years, they occurred only in inaccessible areas (mainly cliffs) and were entirely missing from the vegetation plots.

In eastern North America ferns are considered low preference food for white-tailed deer, *Odocoileus virginianus*, with selective browsing contributing to the formation of fern glades (mostly hay-scented fern, *Dennstaedtia punctilobula*, and New York fern, *Thelypteris noveboracensis*) (Horsley and Marquis 1983; Waller 2008. Nurseries advertise intermediate shield fern, *Dryopteris intermedia*, sword fern and lady fern as deer resistant plants (Deer-resistant landscape nursery 2000). This may illustrate the deer response under conditions of intermediate browse pressure.

Top-down within and between vegetation simplification by deer

When synthesized through a Principal Component Analysis, deer browsing appeared to cause a dramatic simplification of both shoreline and interior plant communities and to erase differences in species composition between them. The well marked within- and between-community diversity observed on islands without deer was replaced by a ubiquitous simplified species assemblage consisting of grasses and young conifers (mainly Sitka spruce) on islands

with deer >50 years. Based on our results, this simplification started with the rapid elimination or reduction of the most sensitive segments of the communities: those dominated by forbs and shrubs other than salal and, to some extent, red huckleberry *Vaccinium parvifolium*.

Herbivory and plant resistance

The effect of herbivores on a given plant species will depend on its palatability and on its ability to withstand tissue loss (Huston 1979; Augustine and McNaughton 1998). The relative importance of these factors will vary with herbivore pressure. With low densities of deer and high forage availability, the most preferred plant species experience the highest level of tissue loss. With moderate densities, plant species composition is often greatly affected by selective foraging and differential recovery (Tilghman 1989; McInnes et al. 1992). As deer density, and/or length of browsing history, increase, selectivity decreases because availability of preferred forage is greatly reduced (Augustine and McNaughton 1998), the proportion of the plant removed increases, and the ability of the plant to sustain tissue loss can be quickly exhausted (Burt 1943). In our study, constitutive physical defenses such as the thorns, spines, and prickles of black gooseberry, *Ribes lacustre*, and Nootka rose, *Rosa nutkana*, provided little protection from the long-term effects of deer. The heavily armed devil's club, *Oplopanax horridus*, (not present at our study site) also has been greatly reduced over much of Haida Gwaii since the arrival of deer (Pojar et al. 1980; Pojar 1999). Similarly, chemical defenses did little to prevent the demise of redcedar regeneration in mature forests (Vourc'h et al. 2002; Stroh et al. 2008).

Among the few features that seemed to temporarily reduce sensitivity to browsing on Haida Gwaii were physical barriers. Dense thickets of salal offered protection to new growth and to various plants for a few years before being eliminated on islands with > 50 years of deer browsing. The sharp mature needles of Sitka spruce appeared to be effective in protecting a fraction of new growth each year. This resulted in a densely branched shape further protecting the tissue growing inside. A few individuals of shade-tolerant species, such as western redcedar, were able to grow within such thickets. In graminoid species good protection was provided by the basal

position of the meristem tissue and by the cover of old foliage (Coughenour 1985). The ability of salal and red huckleberry to produce stems tall enough and rigid enough to put some foliage and seeds out of reach of deer enabled them to survive the arrival of deer and to sustain browsing for decades, before dying from lack of replacement of the aging stems (Vila et al. 2004b; Vila and Martin 2008). However, the only permanent protection was afforded by complete inaccessibility to deer on cliff faces, stumps or snags (Stockton et al. 2001).

On islands with deer >50 years, plant species assemblage composition, both within ecotopes and at the scale of the landscape, was the result of the ability of a few plants such as young Sitka spruce and Western hemlock and some grasses to withstand herbivory.

Deer effect on other trophic levels

Reduction in species density, cover/abundance, and diversity in plants as the duration of deer presence increased found a clear echo in the pattern of dramatic reduction of ground layer vegetation invertebrates, and song birds, and with variation in rate or shape of response among taxa or between ecotopes within taxa. Litter insects were an exception. Species density and specimen abundance were highest on islands with deer for >50 years. This was due to the increase in occurrence and abundance of a few weevil and millipede species. Suominen (1999) and Allombert et al. (2005a) have already emphasized that, contrary to most other taxa analyzed, the response of ground-dwelling invertebrates to deer browsing is more complex and does not follow a systematic negative trend. Some studies (Greenwald et al. 2008) have over-emphasized such results (possibly in part as a consequence of sampling biases). But the fact that some species or even species groups do react positively, or at least correlate positively with deer presence, should not mask the overall trend of biodiversity loss that results from a cascade of effects triggered by prolonged browsing by ungulates in the absence of their predators.

Top-down and bottom-up consequences of unchecked ungulate browsing on biodiversity

Beyond the reduction in plant cover and species density with increasing length of deer presence

already documented by Stockton et al. (2005) for these islands, we show here how a high abundance of large ungulates will, over a few decades, not only greatly simplify the vegetation within a habitat but also, at the scale of the landscape, reduce differences between habitats. Although the speed of this simplification can be locally sensitive to the presence of particular plant species, the ultimate result will be similar whatever the nature of the starting point. This dramatic process of biotic homogenization (McKinney and Lockwood 1999) is precisely what has been suggested for eastern forests with high deer populations (Rooney et al. 2004, and review in Côté et al. 2004), and is suspected in areas of Europe that have already experienced decades of high browsing pressure (Gill and Fuller 2007). In our case, an explicit demonstration was possible because we had access to reference forests that had never been exposed to browsing by deer and that had remained free of major human disturbance. Structural and species diversity in both the shoreline and interior communities were highest in the absence of deer. We found no evidence of native plant species resistant enough to deer browsing to allow them to take advantage of the massive reduction in plant biomass and vegetation cover caused by deer. There were many losers in this process but no real winners (McKinney and Lockwood 1999). Our results contrast with what has been shown to occur in many non-forest ecosystems (Keddy 2005), perhaps because human alteration to these insular systems have been small and, in particular they lack a diverse pool of non native species (Gaston et al. 2006). The lack of positive effects of browsing on diversity could result from a high instantaneous rate of biomass removal by deer that prevents the recovery of the preferred plant species once they are affected, and from limited initial gains by the least preferred species. Our results unambiguously emphasize that, in the absence of external control on the herbivore, the physical or chemical defences of most native plants were unable to prevent the dramatic reduction in plant biomass and plant species diversity below 1.5 m. In this system, when herbivores became established in the absence of predators, the result was extreme simplification of the vegetation.

On the time scale that we are dealing with here, somewhere between 50 and 100 years, the main impact on biodiversity has been on the understorey

vegetation and on its dependent birds and insects. The impact was greater on shoreline than on interior vegetation because the shoreline was initially more diverse. For understory arthropods, trends matched those of the vegetation fairly closely, perhaps because insects are more closely tied to specific plant species. A multivariate analysis of changes in these arthropod communities (Allombert et al. 2005a, b) reveals the same pattern of simplification and homogenization between ecotopes than the one shown here for the vegetation. For birds, the opening out of the understory on islands with deer <20 years was associated with a peak in species richness, indicating that we may be seeing some initially positive effect of disturbance by deer. However, for islands with prolonged deer browsing understory bird species were greatly reduced, with consequent reductions in richness and diversity. Because of their range sizes we could not distinguish shoreline and interior effects for birds, but, among the species recorded, only the Song Sparrow *Melospiza melodia* can be regarded as shoreline-associated (Arcese et al. 2002), so differences between ecotopes seems unlikely.

Projecting current trends into the future, we can predict further changes in biodiversity, with the gradual elimination of western redcedar and red alder as canopy elements, possibly affecting insect and bird species composition. However, many of the most drastic changes were caused in less than 20 years of browsing. Further change should be much slower than the adjustments seen to date.

Our results should encourage managers to pay serious attention to the ecological consequences of deer populations unrestrained by predators. In contrast to our simplified island situation, mainland situations offer more potential complexity. There, the effects of ungulate on mainland forest ecosystems will depend on constraints imposed by the presence of predators and/or hunters (Brown et al. 1999). Understanding how this complexity allows the maintenance of a more diverse flora will be critical to the design of land management strategies capable of preventing forest oversimplification by unchecked deer populations. Our results also pose the question of what temperate forest looked like before centuries of intensive browse pressure by domestic and, more recently, wild ungulates affected them in the absence of predators.

Acknowledgments This is a publication from the Research Group on Introduced Species (RGIS). Funding was provided by the Canada—British Columbia South Moresby Forest Replacement Account (SMFRA); contract # SMFRA99DQC-002, SMFRA Project 24.2, “Pattern of Western Red Cedar Regeneration,” and by Forest Renewal British Columbia (FRBC), research award: PA97335-BRE and by the International Program of Scientific Collaboration (PICS 389) from the Centre National de la Recherche Scientifique (CNRS) and the French Ministry of Foreign Affairs. The Canadian Wildlife Service of Environment Canada and the Laskeek Bay Conservation Society (LBSCS) provided logistical support. The Archipelago Management Board (AMB) and the B.C. Department of Lands, Forests and Parks provided research permits. Special thanks to Liann Bobechko, Rob Kelly, Isabel Buttler, Ian Fuhr, Denis Chrétien, Nadine Wilson, Céline Boutin, Todd Golumbia, Sean Sharpe, Jim Pojar, Don Waller, and Barb Rowsell our project coordinator, for help and insight.

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