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Species-area relationships and the impact of deer-browse in the complex phytogeography of the Haida Gwaii archipelago (Queen Charlotte Islands), British Columbia[1]

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Abstract: We studied the biogeography of vascular plants on 10 islands in Laskeek Bay, Haida Gwaii (Queen Charlotte Islands), British Columbia. The islands varied in size from 4.5 to 395 ha and experienced a range of different browse pressures from introduced black-tailed deer (*Odocoileus hemionus*). We examined how island size interacted with browse pressure in determining the total species counts for individual islands. Numbers of plant species recorded increased with island area. The regression exponent for the log–log plot of species number on island area was 0.18, at the lower end of the range for such exponents. Many species absent from islands < 25 ha in area were characteristic of forest interiors, and consequently part of the increase in richness on larger islands probably was the result of increased forest interior area. Among the islands < 25 ha in area, the normal species–area and species–isolation relationships were reversed, with smaller, more isolated islands supporting more plant species than larger islands and, for a given area, more isolated islands supporting more species than less isolated ones. This reversal of the normal trend appears to be the result of deer browsing. Small, isolated islands were the only islands without deer and were richer, especially in wildflowers, than the larger, less isolated islands. On large islands, total species complement remained as predicted by area because the effect of deer was mitigated by the presence of deer-free refugia on cliffs and in isolated gullies. We conclude that deer are a major factor structuring the island plant communities and that continued protection of island habitats from introduced deer is essential to maintain the native flora of Haida Gwaii.
Keywords: deer browsing, Haida Gwaii, introduced species, island biogeography, species richness, vegetation.

Résumé : Nous avons étudié la biogéographie des plantes vasculaires de dix îles de la baie Laskeek, Haida Gwaii (îles de la Reine-Charlotte), Colombie-Britannique. Les îles étudiées dont la superficie variait de 4.5 à 395 ha subissaient différentes pressions de broutement de la part du cerf mulet introduit (*Odocoileus hemionus*). Nous avons examiné comment l'interaction entre la superficie de l'île et la pression de broutement influençait le nombre total d'espèces présentes sur une île. Le nombre d'espèces de plantes augmentait avec la superficie de l'île. Dans un graphique log-log du nombre d'espèces en fonction de la superficie de l'île, l'exposant de la régression était 0,18, ce qui se situe dans les valeurs les plus basses pour ce type d'exposant. Plusieurs des espèces absentes des îles de moins de 25 ha étaient caractéristiques de l'intérieur des forêts et par conséquent l'augmentation de la richesse en espèces dans les îles plus grandes était en partie due à l'augmentation de la superficie des forêts. Parmi les îles de moins de 25 ha, les relations espèces-superficie de l'habitat et espèces-isolement de l'habitat étaient inverses de ce qu'on voit normalement. Les îles plus petites et plus isolées supportaient plus d'espèces de plantes que les îles plus grandes et pour une même superficie, les îles plus isolées supportaient plus d'espèces que celles moins isolées. Ce renversement de la tendances normale semble être dû au broutement par le cerf. En effet, les petites îles isolées étaient les seules où le cerf était absent et elles étaient plus riches en espèces particulièrement en fleurs sauvages que les îles plus grandes et moins isolées. Sur les grandes îles, le total d'espèces était tel que prédit par la superficie parce que l'effet du cerf était mitigé par la présence de refuges libres de cerf sur des parois et dans des ravins isolés. Nous concluons que le cerf est un facteur principal structurant les communautés de plantes des îles et qu'il est essentiel de maintenir la protection des habitats des îles contre l'introduction du cerf afin de préserver la flore indigène de Haida Gwaii.
Mots-clés : biogéographie d'îles, broutement par le cerf, espèces introduites, Haida Gwaii, richesse en espèces, végétation.

Nomenclature: Wallmo, 1981; Pojar & Mackinnon, 1994.

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Introduction

Island biogeography has been the subject of substantial theoretical work, especially relating to the determinants of species richness (McArthur & Wilson, 1963; 1967; Diamond & May, 1981). The species–area relationship within island groups forms a special case of the general species–area relationship that can be observed when areas of varying size are sampled, whereby, all else being equal, species number is an increasing function of sample area (Preston, 1962; McGuinness, 1984; Lomolino, 2000).

The general shape of island species–area log–log curves is such that, on a large scale, they assume a sigmoidal pattern, with a range at the low end of island size where the slope of the curve is shallow, a zone of intermediate island size where it is steep and a zone at the large end of the size range where it levels off because island biotas are complete with respect to potential colonists. The reduction in slope of the island species–area curve at the lower end is known as the small island effect (SIE) and is greatest in isolated archipelagos or for species with low dispersal abilities (Lomolino & Weiser, 2001). Most investigations of island species–area relationships have concentrated on the intermediate size range, roughly from 0.01 to 1000 km^2 (Lomolino & Weiser, 2001).

The Haida Gwaii archipelago (Queen Charlotte Islands), British Columbia consists of over 350 islands 50–130 km off the mainland coast (Figure 1) that have been isolated from continental North America since the last glaciation *ca* 10,000 y ago. The islands vary in size from less than 1 ha up to the largest, Graham and Moresby, which together are more than 9000 km^2. The majority of the islands are clustered very closely together, with only a small proportion being more than 1 km from any other island, thus allowing high rates of colonization between islands (McArthur & Wilson, 1963). Like other isolated island groups, Haida Gwaii provides an excellent opportunity to examine ecological and biogeographical theories about the role of dispersal and community interactions in determining community structure (MacArthur & Wilson, 1963; 1967; Moors, 1985; Moody, 2000).

As part of a project to assess the impact of introduced deer on island ecosystems, we collected and identified vascular plants on a suite of islands in Laskeek Bay, on the east coast of the archipelago. This area includes the most physically remote islands of the group, those that are furthest offshore from the large islands (those > 1000 ha in area). The impacts of introduced black-tailed deer (*Odocoileus hemionus*) on the vegetation of these islands has already been described on the basis of studies using uniform plot sampling methods (Stockton, 2003; Stockton *et al.,* 2005; Gaston *et al.,* 2006). In this paper, we use the complete species counts for the islands to deduce distribution patterns relating to island size and deer impact.

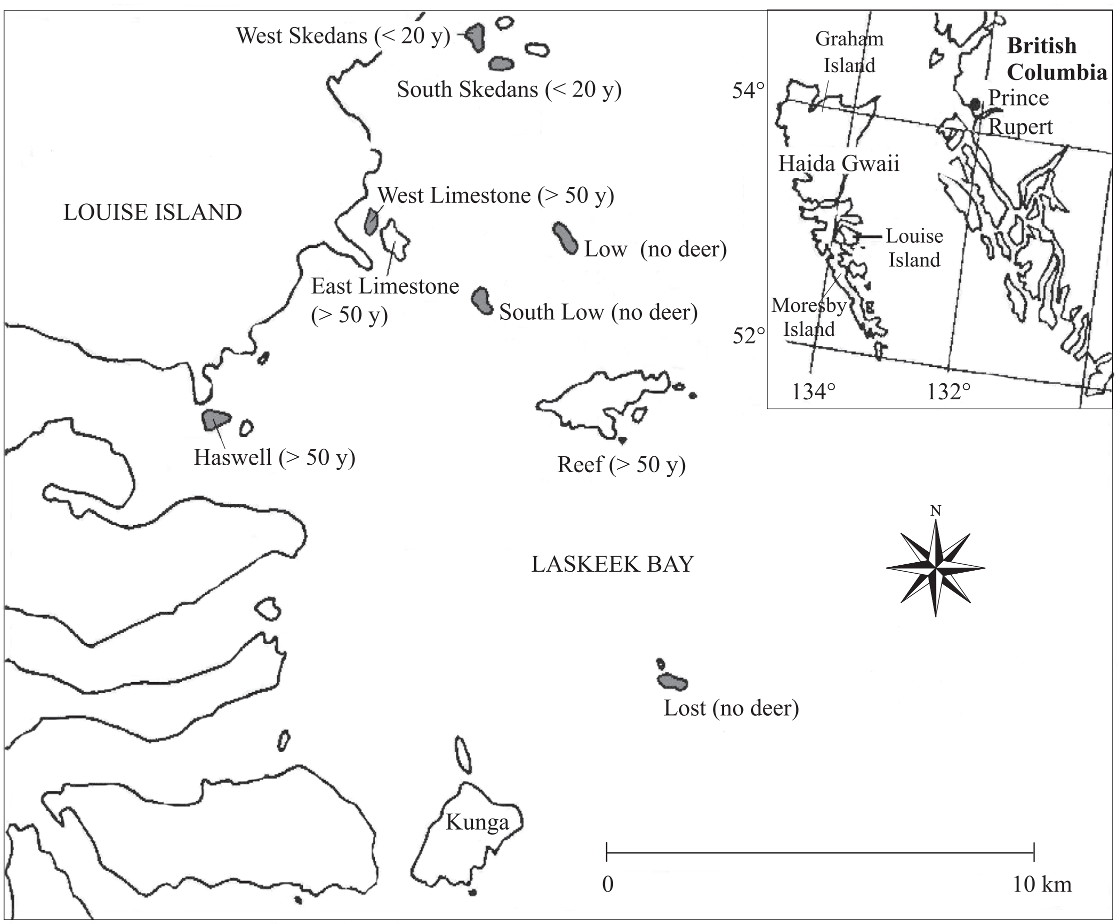

FIGURE 1. Map of Laskeek Bay showing the location of islands mentioned. Small islands (< 25 ha) are shaded.

Study area

Laskeek Bay is situated on the east side of Haida Gwaii, flanking the large Louise and Moresby islands and extending from Cumshewa Inlet south to Lyell Island. It contains numerous reefs, islets, and islands, of which 15 support vegetation that includes trees. We studied 10 of these, ranging in size from the largest, Kunga (353 ha, maximum elevation 200 m), down to South Low (4.5 ha, maximum elevation 15 m). Lost Islands, a group of three small islets barely separated at low tide, are here treated as a single island.

The climate is cool-temperate and humid, characterized by year-round rainfall, often heavy in fall and winter. Summers are cool and frequently cloudy. Strong winds are an important feature of the weather. Mean annual temperatures at Sandspit, just north of Laskeek Bay, range from mean minima and maxima of 0.7 and 5.6 °C in January to 12.1 and 17.9 °C in August (based on 1971–2000 data provided by Environment Canada). Rainfall at the same station, which probably approximates rainfall on the outermost islands of Laskeek Bay averaged 1398 mm.

The vascular plants of Haida Gwaii have been well described previously (Calder & Taylor, 1968; Pojar & Broadhead, 1984; Taylor, 1989; Ogilvie, 1994; Pojar, 2005). Most studies of the botany have concentrated on the larger islands, where significant relief creates a diversity of habitats within the unifying coastal temperate rainforest biome. The archipelago supports about 665 species of indigenous and naturalized vascular plants (Lomer & Douglas, 1999), a number that is steadily increasing as a result of invasions by exotics (Pojar, 2005). This compares with over 2300 vascular plant species on the adjacent mainland (Douglas, Straley & Meidinger, 1998).

The ecology of the Laskeek Bay islands has been described by Stockton (2003), Stockton *et al.* (2005), and Gaston *et al.* (2006). The vegetation of the larger islands is temperate coniferous forest, dominated by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*). Varying amounts of western redcedar (*Thuja plicata*) and shore (lodgepole) pine (*Pinus contorta*) also occur. None of the 10 islands studied has been commercially logged, and all maintain primary forest cover. The islands we studied were too small and rugged to support significant wetlands or streams. Consequently, we could collect little information on those ecosystems. Small areas of non-forest habitat occur along shorelines, especially where they are exposed to the southeast, the prevailing direction of storm winds. Those areas support either a diverse sward of forbs and low shrubs or a rather uniform tussock grass meadow of Nootka reedgrass (*Calamagrostis nootkaensis*).

Black-tailed deer, red squirrels (*Tamiasciurus hudsonicus*), and raccoons (*Procyon lotor*), all introduced into the Haida Gwaii archipelago in the past 120 y, occur on some islands in Laskeek Bay. The deer have had an important impact on the vegetation of all islands that they have reached (Pojar & Banner, 1984; Pojar, 1999; Stockton, 2003; Gaston *et al.,* 2006). Estimates of the duration of deer presence on the different islands in Laskeek Bay have been made from comparative analyses of shrub stem age structures and the dating of fraying scars (Vila *et al.,* 2004a,b) South Low, Low, and Lost islands show no sign of deer, past or present. West and South Skedans islands showed evidence of deer for less than 20 y. Reef, Kunga, East and West Limestone, and Haswell islands all showed evidence of deer presence for 50 or more years.

East and West Limestone islands, West and South Skedans islands, and South Low and Low islands are protected in a British Columbia Wildlife Management Area. Kunga Island and Lost Islands fall within the perimeter of Gwaii Haanas National Park Reserve and Haida Heritage Site. Reef and Haswell islands are British Columbia crown land.

Methods

Vegetation surveys on the study islands were carried out as part of a project to monitor the impact of introduced deer and the vegetation recovery following culling of the deer population on Reef Island (see Stockton *et al.,* 2005; Gaston *et al.,* 2006). All islands were surveyed extensively for vascular plants by 2–5 people during June of 1997–2001. The surveys included intensive searches of circular plots 10 m (shoreline) and 25 m (interior) in diameter, randomly spaced throughout the large islands (Reef, 23 interior and 15 shoreline; Kunga, 20 interior and 10 shoreline; and East Limestone, 10 interior and 10 shoreline). On smaller islands we searched ten 10-m-radius circular plots along the shoreline (10 to 15 m from the high-tide line) and five 10-m-radius circular plots within the forest interior (at least 50 m from the forest edge and at least 50 m from one another; Stockton *et al.,* 2005). As well, we made extensive surveys throughout the islands, amounting to 2–20 person-d per island (depending on island size) to locate additional plant species. Care was taken to visit all parts of each island and to locate and inspect wetlands, cliffs, and south-facing slopes. The intensity of non-plot surveys was similar for all islands except for Kunga Island, where visits were of shorter duration (2–5 d annually) and involved only two people and East Limestone, where biologists were based from April to July in all years. The latter island was proposed as an Ecological Reserve in 1979 because of rare species not found elsewhere in Haida Gwaii (Roemer & Pojar, 1979; Ogilvie & Roemer, 1984). Opportunistic surveys for rare plants on East Limestone Island 1990–1996 and extensive searches each summer from 1997 onward were undertaken to monitor this community (Smith & Buttler, 1999; Smith, 2003). Identifications were made with the help of Hitchcock and Cronquist (1973) and Pojar and Mackinnon (1994). Voucher specimens of all species were preserved and identifications made or confirmed by staff at the Central Experimental Farm, Ottawa.

For analysis, we divided the vascular plants into five types: trees, shrubs, wildflowers (non-woody plants with showy flowers), graminoids (grasses, sedges, and rushes), and ferns and allies (including clubmosses), following the classification of Pojar and Mackinnon (1994). Island area was measured as the area above high tide, and remoteness was measured as the distance to the nearest island of > 1000 ha: in practice either Moresby or Louise island. For some analyses, we compare the three largest islands (Reef, East Limestone and Kunga; all > 40 ha) with the smaller islands (Haswell, West Limestone, Low, South Low, Lost, and West and South Skedans; all < 25 ha). Because of the known negative effect of deer browsing on species richness, we distinguished among three types of islands: those where deer or deer-sign have never been reported (deer-free, DF); those where deer have been present for < 20 y (moderately deer-affected, MDA); and those where deer have been present for > 50 y (heavily deer-affected, HDA). These assignments were based on dendrochronological analysis by Vila *et al.* (2004a,b)

Relationships between species richness and island area were modelled using the General Linear/Non-linear Models module of Statistica 6.1 (StatSoft, 2003), setting model building to "best subsets", using a log link function and assuming a normal distribution. The minimum Akaike Information Criterion (AIC) was used to select the best model among those incorporating island area and deer browse category. Because the effect of island area appeared to differ between islands < 25 ha in area and larger islands, we compared the slopes of these relationships using the homogeneity of slopes module of the General Regression Procedure. For comparison with other studies, relationships between species richness and island area are shown as log–log plots (Diamond & May, 1981).

To compare the plant communities on different islands we calculated similarity coefficients (S):

$$S = 2N_{ij} / (N_i + N_j)$$

where N_i = number of species on island i, N_j = number of species on island j, and N_{ij} = number of species present on both islands. To compare similarity indices among pairs of islands for different plant types and different categories of deer presence/absence we used a factorial ANOVA from the GLM procedure. We divided our paired comparisons into three categories: those between a pair of islands without deer (DF comparisons), those between a pair of islands with deer (DA comparisons), and those between an island with deer and one without (DF/DA comparisons).

Although we deal with several independent variables (island area, isolation, deer browse effects, size categories) our sample size was insufficient to run a full model to test all main effects and interactions. Moreover, some variables were inextricably confounded (all islands without deer were remote, all large islands were heavily affected by deer). Consequently, we proceeded in a hierarchical manner, dealing first with the effect of island area, which has a different relationship to species richness on large and small islands, then dealing with deer effects among small islands only. All models and statistical tests were run using Statistica 6.1 (StatSoft, 2003)

Results

SPECIES RICHNESS

We located 171 species of vascular plants on the study islands of which 5% were trees, 14% shrubs, 56% wildflowers, 16% graminoids, and 9% ferns and allies (Table I, Appendix I). All of the species we identified had been previously recorded in the archipelago. Twelve species were not native to Haida Gwaii: nine wildflowers and three grasses. The potato (*Solanum tuberosum*), found only on Reef Island and almost certainly introduced for cultivation by the Haida people (Meilleur, 2001) was omitted from further analyses.

The largest number of species was recorded for Reef Island, the second largest island (136 spp., 79% of the Laskeek Bay total), and the lowest number was recorded for West Limestone Island, an inshore island, heavily deer-affected, with dense forest canopy (47 spp., 27% of the total). The largest islands (Reef, Kunga, and East Limestone), together comprising 685 ha, supported 95% of the species recorded. The five small offshore islands, together comprising 35 ha, supported 86 species (50% of the total).

TABLE I. Area, deer presence/absence, and counts of vascular plant species for the 10 study islands in Laskeek Bay, Haida Gwaii, with a comparison of combined values for all large and all small islands.

Species	Abbreviations	Area (ha)	Deer (y)	Trees	Shrubs	Wildflowers	Grasses	Ferns	Totals
All islands				9	24	95	27	16	171
1. Reef Island	REE	249	> 50[1]	6	20	75	22	13	136
2. East Limestone Island	ELI	41	> 50	6	17	63	10	7	103
3. Kunga Island	KUN	395	> 50	7	21	52	18	10	108
Larger islands combined (1-3)				9	24	86	26	16	162
% of all island total				100	100	90.5	96.3	100	94.7
4. Haswell Island	HAS	13.3	> 50	6	9	21	9	4	49
5. West Limestone Island	WLI	16.0	> 50	5	11	19	9	3	47
6. West Skedans Island	WSK	8.2	< 20	5	11	32	8	3	59
7. South Skedans Island	SSK	5.6	< 20	5	8	24	12	4	53
8. South Low Island	SLO	4.5	No deer	4	15	36	10	4	69
9. Low Island	LOW	9.6	No deer	5	11	29	9	4	58
10. Lost Island	LOS	7.3	No deer	4	11	30	10	5	60
Small offshore islands combined (6-10)		35.2		5	15	48	13	5	86
% of all island total				55.6	62.5	50.5	48.1	31.3	50.3

[1]A cull of deer on Reef Island began in 1997, but as of 2004 there were still a small number of deer present.

EFFECT OF ISLAND AREA

As expected, numbers of species recorded increased with island area (Figure 2). The trend was significant for all five plant groups (Table II). However, for islands < 25 ha, all groups except trees showed a negative correlation with island area, significant for wildflowers (Table II). The slope of the relationship for all islands differed significantly from that for the small islands only (interaction term in the separate slopes model $F = 13.27$, $P < 0.001$). Despite the difference in species–area relationships between large and small islands, the species count for all small offshore islands combined (86) was very close to the number predicted for their combined area by the regression for all islands (Figure 2). The exponent of the log–log relationship for all islands was 0.18, within the observed range for such relationships (May, 1981).

The reduced species complement of the smaller islands was not a random sample of the flora: it was especially lacking in elements associated with the forest interior. Among species found only on the large islands were three trees (yellow cedar [*Chamaecyparis nootkatensis*], bitter cherry [*Prunus emarginata*], and western yew [*Taxus brevifolia*]; 33% of total), four shrubs (17%), 18 wildflowers (19%), nine grasses (33%) and six ferns (40%). Only 31% of ferns occurred on the combined small offshore islands, compared with 62% of shrubs, 51% of wildflowers, and 48% of grasses.

Among species missing from all five small offshore islands were the shrubs *Cornus stolonifera* and *Aruncus dioicus,* the wildflowers *Cornus canadensis, Clintonia uniflora*, *Boschniakia hookeri*, *Corallorhiza maculata, Hypopitys monotropa, Polemonium pulcherrimum,* and *Isopyrum savilei*, four species of ferns, and all three species of clubmosses. All of these species, except for one clubmoss, are characteristic of shady forest interior situations. In addition, six out of the 12 non-native species were found only on the large islands. The grass *Aira praecox* was the only non-native species found on any of the three deer-free islands, although both *Senecio sylvaticus* and *Cirsium vulgare* were found on all other islands. Of the seven species found only on small offshore islands, one was the shrub *Sorbus sitchensis* and six were wildflowers (*Honkenya peploides*, *Ligusticum scoticum, Saxifraga caespitosa*, *Grindelia integrifolia*, *Hieracium triste*, *Viccia cracca*). All are characteristic of meadows or forest edges (Pojar & Mackinnon, 1994).

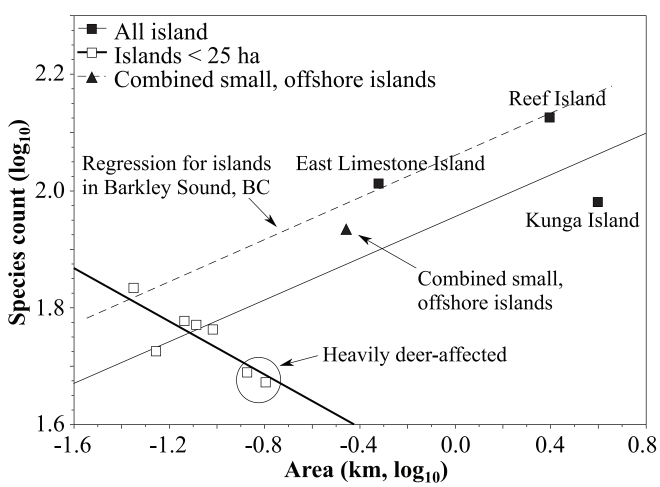

FIGURE 2. Relationship of species richness ($\log_{10}$ number of spp.) to island area ($\log_{10}$ km) for the study islands. Regression equation for all islands: species recorded = 1.96 + 0.18×$\log_{10}$ island area; for small islands only, species number = 1.50 –0.23×$\log_{10}$ island area. The dashed line shows the corresponding regression for islands in Barkley Sound, on the west coast of Vancouver Island, British Columbia (Cody *et al.,* 2002; regression slope = 2.05 + 0.17×$\log_{10}$ island area).

EFFECTS OF DEER

Among islands smaller than 25 ha, species richness was strongly affected by deer browse history (Figure 3). Moreover, the heavily deer-affected islands were larger than others in this sample (Figure 2). In an analysis of covariance for deer browse history controlling for island area, the best-fit model based on the AIC criterion incorporated both independent variables ($\log_{10}$ area, Wald Statistic = 4.63, $P = 0.03$; browse history, Wald Statistic = 8.33, $P = 0.02$). Duncan critical range tests showed species richness to be significantly higher on deer-free islands than on heavily deer-affected islands ($P = 0.03$), with moderately deer-affected islands being intermediate and not significantly different from either category.

TABLE II. Results of correlation analyses for numbers of species of different plant types in relation to island area ($\log_{10}$, ha). * = $P < 0.05$; ** = $P < 0.01$.

	Correlations coefficients	
Plant type	All islands ($n = 10$)	Islands < 25 ha ($n = 7$)
Trees	0.88**	0.66
Shrubs	0.85**	-0.37
Wildflowers	0.80**	-0.76*
Grasses	0.83**	-0.58
Ferns	0.91**	-0.26
All species	0.81**	-0.81*

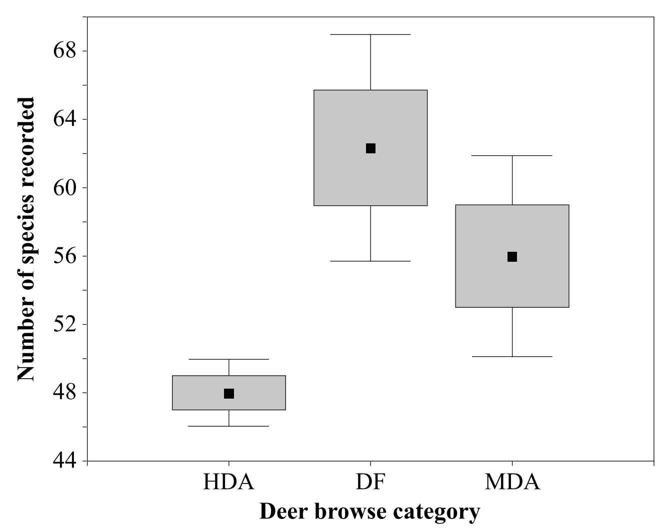

FIGURE 3. Mean (black box) ± 1 SE (grey box) and ± 1.96 SE (error bars) numbers of plant species recorded on small islands (< 25 ha), comparing different deer browse histories. HAD = heavily deer-affected, MDA = moderately deer-affected, DF = deer-free.

The highest numbers of shrub and wildflower species (15 and 36 species) were recorded on the smallest island, the deer-free South Low Island, while the lowest numbers of wildflowers occurred on the two largest islands, Haswell and West Limestone (21 and 19 species, respectively), both heavily deer-affected.

Species found on at least two deer-free islands but on none of the smaller islands with deer were the shrub *Rubus parviflorus* and the wildflowers *Heracleum lanatum, Barbarea orthoceros, Claytonia sibirica*, and *Tellima grandiflora*. Species missing from the heavily deer-affected small islands (Haswell, West Limestone) but found on other small islands were all wildflowers: *Sedum divergens, Epilobium angustifolium, Fragaria chiloensis* and *Mimulus guttatus*. A comparison of all the small islands (< 25 ha) shows that wildflowers were the group most affected by deer (Figure 4). Heavily deer-affected islands supported a mean of 20.0 ± 1.0 (SE) wildflower species, whereas those only moderately affected or without deer supported 30.2 ± 2.0 species ($t_5 = 3.07$, $P = 0.03$).

Although the moderately deer-affected islands were similar in species richness to deer-free islands, they showed substantial effects of deer browsing in the form of dead and dying shrubs, especially *Vaccinium parvifolia, Symphoricarpos albus*, and the fern *Polystichum munitum*. This die-back proceeded visibly during the period of the study, so that few *Polystichum munitum* (a large fern forming clumps including several years' growth) remained alive by 2003.

Similarity among islands

Similarity indices for inter-island comparisons were generally greater among islands with similar deer impacts. The mean similarity index was highest for comparisons among the three deer-free islands (0.85 ± 0.02; mean ± SD), lower for comparisons among deer-affected islands (both moderately and heavily affected; 0.69 ± 0.07), and least for comparisons between deer-affected and deer-free islands (0.60 ± 0.02). A factorial ANOVA for similarity indices in relation to vegetation type and island group (DF pairs, DA pairs, or DA/DF pairs) showed that differences were significant for both independent variables (vegetation type $F_4 = 20.41$, $P < 0.001$; island pairing, $F_2 = 17.57$, $P < 0.001$; adjusted $R^2 = 0.71$, $F_{14, 60} = 13.80$, $P < 0.001$). In addition, similarity indices showed a significant interaction between plant group and the type of islands being compared ($F_8 = 4.50$, $P < 0.001$). Similarities between island groups were greatest for trees and shrubs and lowest for wildflowers, results supported by earlier comparisons. For all island groups, the similarity among deer-free islands was greater than for deer-affected islands for all vegetation types except trees (Figure 5).

Discussion

Species–area relationship

Our observations demonstrate that, among the range of island size represented in Laskeek Bay (4–400 ha), the effect of island size on the numbers of species on each

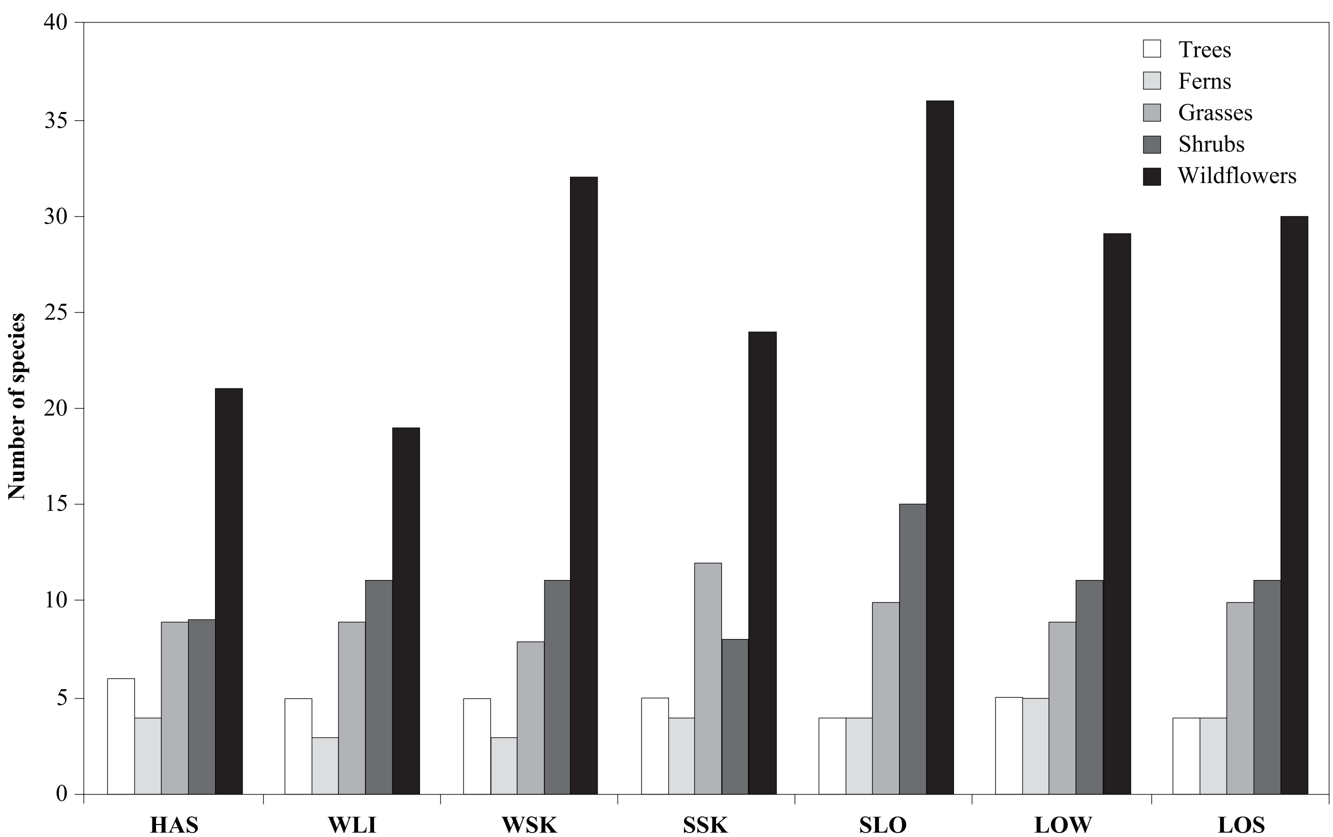

Figure 4. Numbers of plant species recorded, by plant group, for the small islands (< 25 ha). HAS = Haswell, WLI = West Limestone, WSK = West Skedans, SSK = South Skedans, SLO = South Low, LOW = Low, LOS = Lost.

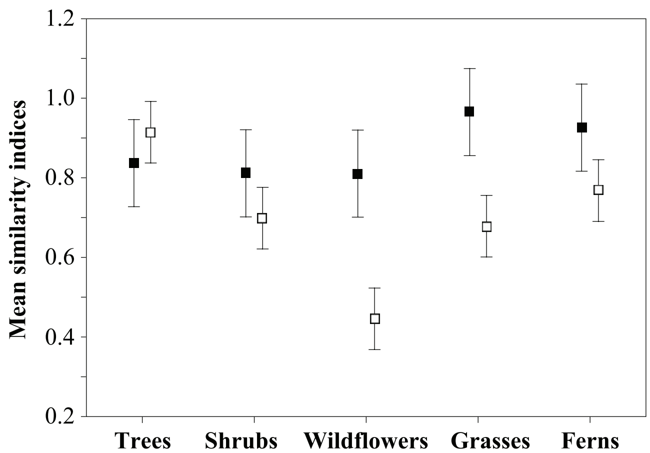

FIGURE 5. Mean indices of similarity among deer-free islands (solid squares) and among deer-free and deer-affected island pairings (open squares). Vertical bars represent 95% confidence intervals. Deer-free islands showed greater similarity with one another than with islands affected by deer for all groups except trees.

island falls along the well-established pattern of increasing diversity with island size (Lomolino, 2000). Increase in species with area operates mainly through an increase in forest interior species on the larger islands. Shrubs and wildflowers characteristic of shorelines and forest edges were well represented on the smallest islands, but those species characteristic of forest interior were often lacking.

The log–log relationship of species number to island area for all islands gave an exponent value of 0.18, close to the lower boundary of those observed for species groups over the range of island size involved (Diamond & May, 1981) and very close to that observed for ecologically similar islands in Barkley Sound, on the west coast of Vancouver Island, Canada (Cody *et al.,* 2002). The intercept value was higher for Barkley Sound, predicting about 20 more species for an island of 100 ha. This corresponds to the more diverse flora of Vancouver Island compared to Haida Gwaii. Both of these island groups comprise islands that are relatively close together, allowing easy inter-island dispersal and effectively removing the influence of island isolation. The slope of the relationship for Laskeek Bay predicts a total count for Haida Gwaii (area 9830 km^2) of 477 species, lower than, but comparable with, the known count of 665 species.

Several factors suggest that our sample probably was not affected by the small island effect (SIE). First, the smallest island in our sample was larger than the upper limit for the SIE estimated for 80% of vegetation studies listed by Lomolino and Weiser (2001). Second, most island groups exhibiting SIE involve species counts of less than 10, whereas our lowest island count was 47 species (West Limestone Island). Third, the total species complement estimated for Haida Gwaii by our regression, although lower than that observed, was not greatly different. Last, save for one small offshore island group (Lost Islands), the study area was not spatially isolated from neighbouring, larger islands, thus making colonization and dispersal possible for most plant species recorded. Given that SIE was unlikely to have operated in our island sample, we need an alternative explanation for the significantly different species–area relationship found among islands < 25 ha in area.

DEER BROWSING EFFECTS

The effect of deer browsing on plant diversity in the archipelago has been demonstrated by Stockton *et al.* (2005). Structural simplification and a reduction in diversity, particularly in ground and shrub layers, is a typical result of deer introductions to areas without native predators (Côté *et al.,* 2004; Chouinard & Filion, 2005). In the case of the Laskeek Bay islands, a massive reduction in plant cover in shrub and ground layers has been accompanied by a severe reduction in the diversity of species in study plots on deer-affected islands. The negative effect of deer on species richness was most obvious when species counts on the small islands were compared to island area. For this sample, the species–area relationship was the reverse of that observed for the entire sample of islands. Through the effect of deer browsing, species richness was highest on the most remote of the small islands, which were also deer-free, and lowest on the least remote, which were heavily deer-affected. This is a reversal of the relationship predicted by island biogeographic theory (MacArthur & Wilson, 1967). Deer-affected islands were especially lacking in wildflowers.

Our results suggest that the number of species found on moderately deer-affected islands was more similar to those recorded on deer-free islands than to those islands heavily affected by deer (Figure 3). However, Stockton *et al.* (2005), who compared species richness based on the mean number of species recorded in standardized sample plots, found the opposite effect (*i.e.,* that mean number of species per plot on moderately deer-affected islands was more similar to numbers on heavily deer-affected islands than to those on deer-free islands (Stockton *et al.,* 2005). The contradiction between these results arises because although not yet extirpated, those species strongly affected by deer have become rarer on the moderately deer-affected islands.

Although heavily deer-affected, East Limestone Island supported more species (103) than predicted by its 41-ha area (92 species) and substantially more than the five small offshore islands (86 species), which had an aggregate area almost as large. As its name suggests, East Limestone Island lies on a limestone outcrop that not only affects soil chemistry, thereby supporting a unique plant community (Roemer & Pojar, 1979), but also affords numerous refuges for plants in the form of steep cliffs and limestone karst features that keep them out of reach of deer.

On the larger islands, especially Reef Island, we found most of the species recorded in Laskeek Bay. However, species strongly affected by deer (*e.g.,* those absent from the small, heavily deer-affected islands) were confined on large islands to cliff faces, out of reach of the deer. There is some indication from our results that colonization by non-native species was more likely on deer-affected islands, although the absence of non-natives from the deer-free islands could also be because of their isolation. Deer browse or disturbance contributes to alternative stable ecosystem states (Côté *et al.,* 2004) and may facilitate introductions of non-native flora (Pojar, 1999).

At Reef Island, a small valley on the south coast was completely inaccessible to deer, being surrounded by steep cliffs on the landward side. This valley supported luxuriant stands of *Sambucus racemosa*, *Rubus spectabilis*, *Heracleum lanatum*, *Claytonia sibirica*, *Aquilegia formosa,* and *Tellima grandiflora*. This list includes several species found on deer-free islands but not on other small islands. Without this valley and the deer-free refugia provided by cliff ledges, it is likely that the number of species on Reef Island would have been substantially lower.

FLORAL SIMILARITY

The pattern of similarity indices between different island groups suggests that small deer-free islands were the most alike in vegetation composition. Their plant communities presumably were typical of undisturbed islands. Similarity was lowest when deer-free and deer-affected islands were compared, results that support other studies that concluded that deer play a major role in structuring plant communities on Haida Gwaii (Pojar, 1999; Gaston *et al.,* 2006). The greater similarity among deer-affected islands, although complicated by greater size variation within this sample, suggests that the flora of these islands is converging towards a suite of deer-resistant species, including some introduced to the archipelago. The moderately deer-affected islands are in transition from one equilibrium state to another.

Conclusion

Our results demonstrate that the usual effects of island size and isolation on diversity are reversed among the small islands in Laskeek Bay. Because the smallest, most isolated islands have avoided colonization by deer, they continue to support plants extirpated from deer-affected islands of similar size. The same species persist on larger islands because those islands are large enough to have diverse terrain and a higher chance of refuges created by cliffs and gullies.

The persistence of deer-free refugia is very important in providing the only surviving evidence of what the flora of Haida Gwaii might have looked like prior to deer introductions. Some of the small, isolated deer-free islands support insects and other invertebrates not found elsewhere in the archipelago (Allombert, Stockton & Martin, 2005a), as well as higher densities of birds than seen on deer-affected islands (Allombert, Gaston & Martin, 2005b). Continued protection of these outlying islands and immediate removal of any deer attempting to colonize them is essential to maintaining these fragments of pre-existing Haida Gwaii ecosystems.

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Appendix I. Plant species identified on the islands of Laskeek Bay, 1997-2005.

	Reef	East Limestone	Kunga	Haswell	West Limestone	West Skedans	South Skedans	South Low	Low	Lost
Trees										
Alnus rubra	1	1	1	1	1	1	1	1	1	1
Chamaecyparis nootkatensis		1								
Malus fusca	1	1	1	1	1	1	1	1	1	
Picea sitchensis	1	1	1	1	1	1	1	1	1	1
Pinus contorta var. *contorta*	1			1						
Prunus emarginata			1							
Taxus brevifolia			1							
Thuja plicata	1	1	1	1	1	1	1		1	1
Tsuga heterophylla	1	1	1	1	1	1	1	1	1	1
Shrubs										
Alnus crispa ssp. *sinuata*	1	1	1	1	1	1	1	1	1	
Amelanchier alnifolia	1	1	1	1	1			1		1
Arctostaphylos uva-ursi	1	1	1	1		1		1		1
Aruncus dioicus	1		1							
Cornus canadensis	1									
Cornus stolonifera			1							
Gaultheria shallon	1	1	1	1	1	1	1	1	1	1
Lonicera involucrata	1	1	1	1		1	1	1	1	1
Menziesia ferruginea	1	1	1	1						
Oplopanax horridus			1							
Prunus stolonifera			1							
Ribes bracteosum	1		1							
Ribes lacustre	1	1	1		1			1		
Ribes laxiflorum	1	1	1		1	1	1	1	1	1
Rosa nutkana	1	1	1		1	1		1	1	1
Rubus parviflorus	1	1	1					1	1	1
Rubus spectabilis	1	1	1	1	1	1	1	1	1	1
Salix scouleriana	1	1	1	1	1	1	1	1	1	1
Salix sitchensis	1	1								
Sambucus racemosa ssp. *pubens*	1	1	1		1	1	1	1	1	
Sorbus sitchensis								1		
Symphoricarpos albus	1	1	1		1	1		1	1	1
Vaccinium alaskaense	1	1	1							
Vaccinium parvifolium	1	1	1	1	1	1	1	1	1	1
Wildflowers										
Achillea millefolium	1	1	1	1	1	1	1	1	1	1
Ambrosia chamissonis	1					1				
Anaphalis margaritacea	1									
Anemone multifida		1								
Angelica lucida	1	1	1	1				1	1	1
Aquilegia formosa	1	1	1		1			1	1	1
Arabis hirsuta	1	1	1					1		
Arceuthobium campylopodum	1									
Arnica spp.		1								
Aster subspicatus	1	1	1			1	1	1		1
Barbarea orthoceras			1					1		1
Boschniakia hookeri	1									
Calypso bulbosa	1	1	1							
Campanula rotundifolia	1	1	1		1	1	1	1	1	1
Cardamine occidentalis	1		1							
Cardamine oligasperma	1	1	1							
Castilleja unalaschcensis	1	1				1		1	1	
Cerastium arvense	1	1	1	1	1	1		1		
Chimaphila menziesii	1	1		1						
Cirsium arvense	1	1	1							
Cirsium edule	1	1	1							
Cirsium vulgare	1	1	1	1	1	1	1			
Claytonia sibirica	1	1	1					1	1	1
Clintonia uniflora		1								
Cochlearia officinalis	1									
Collinsia parviflora	1	1						1		
Conioselinum pacificum	1	1	1	1	1	1	1	1	1	1
Corallorhiza maculata ssp. *mertensiana*	1	1	1	1						
Dodecatheon pulchellum		1	1		1			1		
Draba hyperborea	1	1	1			1	1		1	
Epilobium angustifolium	1	1	1			1	1	1	1	1

APPENDIX I. Continued.

	Reef	East Limestone	Kunga	Haswell	West Limestone	West Skedans	South Skedans	South Low	Low	Lost
Epilobium ciliatum	1	1	1			1		1	1	
Fauria crista-galli	1									
Fragaria chiloensis	1	1	1			1	1	1	1	1
Fritillaria camschatcensis	1	1	1	1		1	1	1	1	1
Galium aparine	1	1	1					1	1	1
Galium trifidum	1	1	1							
Galium triflorum	1	1	1		1	1	1			
Gentiana platypetala		1								
Geranium richardsonii		1								
Gnaphalium uliginosum	1		1	1	1					
Goodyera oblongifolia	1	1							1	
Grindelia integrifolia							1			
Heracleum lanatum	1	1						1	1	1
Heuchera chlorantha	1	1								
Hieracium triste						1				
Honkenya peploides								1		1
Hypochaeris radicata			1							
Hypopitys monotropa	1									
Lactuca muralis	1	1	1							
Lathyrus japonicus	1					1		1		1
Ligusticum scoticum								1		
Listera caurina	1	1	1	1						
Listera cordata	1	1	1	1						
Lloydia serotina										
Lupinus nootkatensis	1			1					1	1
Lysichiton americanum	1	1								
Maianthemum dilatatum	1	1	1	1	1	1	1	1	1	1
Mentha arvensis		1	1							
Mimulus guttatus	1	1	1			1	1	1	1	1
Minuartia tenella		1								
Moneses uniflora	1	1	1			1				
Montia parvifolia	1	1	1	1	1					
Oenanthe sarmentosa	1	1								
Pinguicula vulgaris										
Plantago maritima ssp. *juncoides*	1	1	1	1	1	1	1	1	1	1
Plectritis congesta	1					1		1	1	1
Polemonium pulcherrimum		1								
Potentilla villosa	1	1	1	1	1	1	1	1	1	1
Prenanthes alata	1	1	1	1	1	1	1	1	1	1
Prunella vulgaris		1								
Ranunculus occidentalis	1	1	1				1	1	1	1
Ranunculus repens	1									
Ranunculus uncinatus	1									
Rumex crispus	1	1				1	1		1	
Sagina maxima	1	1	1	1	1	1	1	1	1	1
Saxifraga caespitosa								1		
Saxifraga ferruginea	1	1	1	1		1		1	1	1
Sedum divergens	1	1	1			1	1	1	1	1
Senecio sylvaticus	1	1	1	1	1	1	1			
Sisyrinchium littorale	1	1				1		1	1	1
Solanum tuberosum	1									
Solidago canadensis	1									
Sonchus asper	1		1							
Stachys cooleyae	1									
Stellaria crispa	1	1	1		1	1	1			1
Streptopus amplexifolius	1		1							
Taraxacum officinale	1				1	1	1			
Tellima grandiflora	1	1	1					1		1
Tiarella trifoliata	1	1	1							
Urtica dioica	1	1	1							
Veronica beccabunga ssp. *americana*	1	1								
Vicia cracca							1			
Vicia gigantea	1		1	1	1	1		1	1	1
Viola spp.	1		1							
GRASSES, SEDGES AND RUSHES										
Carex deweyana	1	1	1		1		1			
Carex gmelinii	1		1							
Carex lyngbyei	1									

APPENDIX I. Concluded.

	Reef	East Limestone	Kunga	Haswell	West Limestone	Skedans	West Skedans	South Low	South Low	Lost
Carex mertensia	1			1						
Carex sitchensis	1			1			1	1		1
Aira praecox	1	1	1	1		1	1	1	1	1
Aira caryophyllea			1							
Bromus sitchensis	1					1		1	1	1
Calamagrostis nutkaensis	1		1	1	1	1	1	1	1	1
Cinna latifolia	1									
Deschampsia elongata	1	1								
Elymus glaucus	1		1							
Elymus mollis	1	1	1		1	1	1	1	1	1
Festuca occidentalis	1		1							
Festuca rubra	1	1	1	1	1	1	1	1	1	1
Festuca subulata	1	1	1		1		1			
Hordeum brachyantherum	1		1		1	1	1	1	1	1
Holcus lanatus			1							
Melica subulata			1							
Poa sp.		1								
Puccinellia nutkaensis				1	1	1	1	1	1	1
Juncus arcticus	1	1	1	1			1	1	1	1
Juncus effusus	1		1							
Juncus falcatus	1									
Luzula multiflora	1	1	1	1	1	1	1	1	1	1
Luzula parviflora	1	1	1	1	1		1			
Luzula piperi	1		1							
FERNS										
Adiantum pedatum	1	1	1							
Asplenium trichomanes		1								
Blechnum spicant	1	1	1							
Dryopteris expansa	1	1	1	1	1	1	1			1
Gymnocarpium dryopteris	1									
Equisetum spp.	1		1							
Lycopodium clavatum			1							
Lycopodium selago	1									
Lycopodium annotinum			1							
Athyrium filix-femina	1	1	1	1				1	1	1
Cryptogramma crispa	1									
Polypodium glycyrrhiza	1	1	1	1	1	1	1	1	1	1
Polystichum munitum	1	1	1	1	1	1	1	1	1	1
Pteridium aquilinum	1						1	1	1	1
Selaginella wallacei	1		1							
Thelypteris phegopteris	1									