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A. Mckenzie. Monitoring the effects of deer on plant abundance and diversity in old-growth coastal temperate rainforests, Haida Gwaii, British Columbia. Environmental Sciences. 2009. hal-02592986

HAL Id: hal-02592986

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Monitoring the effects of deer on plant abundance and diversity in old-growth coastal temperate rainforests

Haida Gwaii, British Columbia

Annie McKenzie
Final MFC paper
December 2009

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Acknowledgements

I need to send a big thank you to all the people who helped me with this research and who contributed to making my internship experience in Haida Gwaii truly incredible.

Thank you to Jean-Louis Martin for inviting me to participate in this long-term monitoring deer exclosure project. Christophe Baltzinger and Soizic Lesaout for endless laughs and doughnuts while carrying out field work, and for assisting me with sedge identifications and data analysis. Having the opportunity to visit smaller Islands in Laskeek Bay and Gwaii Hanaas gave me valuable insight into the impacts of deer on understory vegetation, and I need to thank the Laskeek Bay Conservation Society, Parks Canada and the Research Group on Introduced Species (RGIS) for making this possible.

A huge thank you goes out to all the staff at the Haida Gwaii Forest District – Ministry of Forests and Range. I need to thank Len Munt for making this internship possible and for providing me with the unique opportunity to learn about resource management in Haida Gwaii. Thank you to Tyler Peet and Sean Muise for provided me with endless guidance and support throughout my internship. I am also grateful to Berry Wijdeven, Dave Crossley, Colin Richardson and Mark Salzl for taking me into the field with them and to everyone else in the office for being so welcoming. I also need to thank Doug Louis for providing the map for this report and Steph Regi and Celena Faulkner for sending me great deer pictures.

At the University of Toronto, I am grateful to Andy Kenny for making this internship possible and for encouraging me throughout my time in the MFC program. Thank you to Terry Carleton and Jay Malcolm for assisting me with the multivariate analyses and to Tat Smith for his support. I also need to thank Jess Kaknevicius for her advice and help with statistics. A big thank you goes out to my friends Martin Danyluk, Katie Mazer and Alex MacIntosh for their editing assistance and home-cooked meals. Finally, I need to thank my fellow masters of forest conservation students for making the MFC program so enjoyable.

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Abstract

Overabundant deer populations are a major factor affecting forest ecosystem dynamics in many parts of North America. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) were introduced to Haida Gwaii, a remote island archipelago in British Columbia, in the late 19th century. The mild climate, abundant vegetation, absence of predators, low hunting pressure and lack of competing herbivores on Haida Gwaii allowed the deer to flourish and the population exploded. This long-term monitoring experiment studies the effects of Sitka black-tailed deer on the diversity, abundance and reproduction of understory vegetation. In this study 20 deer exclosures were monitored over a period of 12 years from 1997 to 2009 in old growth forests on Graham Island, the largest island of the Haida Gwaii archipelago. The results showed that protection from deer did not have an effect on species richness. However, deer are having a significant impact on the abundance of understory vegetation in the medium height stratum (0.5 m - 1.5 m) and they are shifting the community composition towards less palatable species. The plant species most affected by deer browsing were bunchberry (*Cornus unalaschkensis*) and fern-leaved goldthread (*Coptis aspleniifolia*), and these are important forage species for Sitka black-tailed deer in their natural habitat in Alaska. Deer are also having an impact on plant reproduction, as a significantly higher proportion of flowers and fruits were found inside the exclosures. More research is needed to understand the impacts of deer on understory vegetation and therefore this study provides practical recommendations for improving this long-term monitoring experiment as well as recommendations for future research.

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1 Background

The explosion of deer populations, in the absence of natural predators, has become a major factor affecting forest ecosystem dynamics in many parts of North America (Sullivan et al. 1990, McShea et al. 1997) and Europe (Baines et al. 1994, Gill 1999). These population explosions can be triggered by natural processes or result from imbalances caused by human activities, such as species introductions (Vila et al. 2004). Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) were introduced to Haida Gwaii, a remote island archipelago in British Columbia, in the late 19th century. The deer were purposely introduced by the British Columbia Gaming Commission in 1911 as a source of game for settlers of European descent (RGIS 2009). The mild climate, abundant vegetation, absence of predators, low hunting pressure and lack of competing herbivores on Haida Gwaii allowed the deer to flourish and the population exploded (Martin and Baltzinger 2002). Current deer populations on Haida Gwaii are estimated to range between 113,000 and 250,000 individuals in 8,500 km^2 of available habitat (Martin and Baltzinger 2002). Average population density on larger islands in the archipelago has been estimated at about 13 deer per km^2, which is much higher than the density on the adjacent mainland (Daufresne and Martin 1997). Understanding the ecological role of this introduced and overabundant species in the forests of Haida Gwaii has become an important focus of research and a major concern for local communities and forest managers in recent years.

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2 Literature Review

In the absence of predators, deer can have a strong effect on the structure and composition of forest herb layers, subcanopy and ultimately forest canopies, as they impact tree regeneration (Stroh et al. 2008). Overabundant deer populations have been shown to shift plant community composition from a forest understory dominated by shrubs and herbs to one dominated by ferns and graminoids (Horsley et al. 2003, Stockton et al. 2005, Rooney 2009). This change in community composition reflects a decline in the abundance and diversity of palatable species and an increase in unpalatable, resistant or browse-tolerant species (Kirby 2001, Horsley et al. 2003, Rooney and Waller 2003, Gill and Fuller 2007) In general, studies have indicated that overabundant deer populations decrease plant species diversity, simplify vegetation structure and contribute to the biotic homogenization of forest ground-layer vegetation (Anderson and Katz 1993, Wardle et al. 2001, Coomes et al. 2003, Kraft et al. 2004, Gaston et al. 2006, Rooney 2009). As a consequence, deer exert cascading effects on small mammals, birds and invertebrates by competing directly for resources and by modifying the composition and structure of understory habitats (Flowerdew and Ellwood 2001, Allombert et al. 2005a, Allombert et al. 2005b, Gill and Fuller 2007).

Many studies have evaluated the effects of high population densities of white tailed deer (*Odocoileus virginianus*) on the vegetation of the eastern hardwood forests of North America (Reviewed in Russell 2001). These studies have shown that overabundant populations of white tailed deer reduce the abundance and diversity of woody plants (Alverson et al. 1988, Tilghman 1989, Hobbs 1996, deCalesta 1997, Waller and Alverson 1997, McShea et al. 1997). In some cases deer have caused the extirpation of plant

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species (Whitney, 1984; Rooney and Dress, 1997). Fewer studies have examined the effects of black-tailed deer on the plant communities of the temperate rainforest of North America (Woodward et al. 1994, Daufresne and Martin 1997, Stockton et al. 2005).

Several studies have been carried out to characterize the impacts of the introduced Sitka black-tailed deer on the understory vegetation communities in the temperate rainforest Haida Gwaii (Daufresne and Martin 1997, Engelstoft 2001, Gaston et al. 2006, Martin and Baltzinger 2002, Martin and Daufresne 1999, Pojar et al. 1980, Stockton et al. 2005, Stroh et al 2008). To date, published research has largely been focused on small islands in Laskeek Bay in the south of Haida Gwaii. Selecting islands of similar size but differing in their history of deer browsing, these studies found that deer have important negative impacts on the vegetation structure and composition on these island communities (Stockton et al. 2005). Deer have reduced plant diversity and simplified the forest ecosystems on these small islands. However, deer culls have resulted in the recovery of understory plants and an increase in species diversity (Golumbia 1999, Gaston 2002, Gaston et al. 2006).

Much less is known about the impacts of deer on Graham Island, the largest island in the Haida Gwaii archipelago. A long-term monitoring deer exclosure experiment was set up on Graham Island in 1997 by the Research Group on Introduced Species (RGIS) to monitor the effects of the introduced black-tailed deer on understory vegetation and tree regeneration in old-growth forests. Stroh et al. (2008) published the first study based on this long-term monitoring experiment. Their study revealed that Sitka black tailed deer had a drastic negative impact on western red cedar (*Thuya plicata*) regeneration, however red cedar seedlings did show a significant recovery following deer exclusion. Two unpublished

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studies analyzed the data collected from this long-term monitoring experiment from 1997 to 2005 in order to evaluate the impact of deer on understory vegetation and to test the potential for the recovery of plant species following the prolonged exclusion of deer (Kaknevicius 2008 and Stroh 2008). These studies found that understory vegetation recovery was much slower on Graham Island than on the smaller islands in the south, and the protection from deer did not affect plant species richness. Both of these studies concluded that additional research was needed to understand the dynamics of understory vegetation recovery on Graham Island.

This study extends this research by evaluating the composition and abundance of plant species after an additional four years of deer exclusion in order to determine if there was a continued divergence in species composition and an increase in plant abundance within the exclosures over the long-term. The results of this study are compared with those found by Kaknevicius (2008) and Stroh (2008) and the data collected in 2009 was added to the database for this long-term monitoring experiment. Finally, recommendations for improving this long-term monitoring experiment and for further research are made.

3 Objective

The objective of this study is to determine if Sitka black-tailed deer limit the diversity, abundance and reproduction of understory vegetation below the 1.5m browse limit in old growth forests on Graham Island, Haida Gwaii.

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4 Methodology

4.1 Study Site

Haida Gwaii is a remote island archipelago in British Columbia, situated 80km west of mainland British Columbia and 50 km south of Alaska. Haida Gwaii is the largest archipelago in western Canada at 300 km long, and is composed of two main islands, Graham and Moresby, as well as hundreds of smaller islands (Stroh et al. 2008). The study was carried out on the largest island, Graham Island which is 6,361 km^2, in the northern part of the archipelago.

Haida Gwaii is in the Coastal Western Hemlock (CWH) bioclimatic zone (Banner et al. 1989) and the climate is a cool temperate, oceanic, humid-perhumid type (Pojar 2002). Haida Gwaii has 2,000-4,000 mm of precipitation annually with cool summers and mild winters (Pojar 2002). The Haida Gwaii landscape is largely forested with coastal temperate rainforest. The forest canopy is dominated by Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and western red cedar (Pojar 2002). At higher elevations, mountain hemlock (*Tsuga mertensiana*) and yellow cedar (*Chamaecyparis nootkatensis*) are also present (Pojar 2002). The flora of the Haida Gwaii archipelago is similar to that of southeast Alaska (Banner et al. 1989) however the species richness is lower with 665 vascular plant species compared to 2,300 on the mainland (Douglas et al. 1998).

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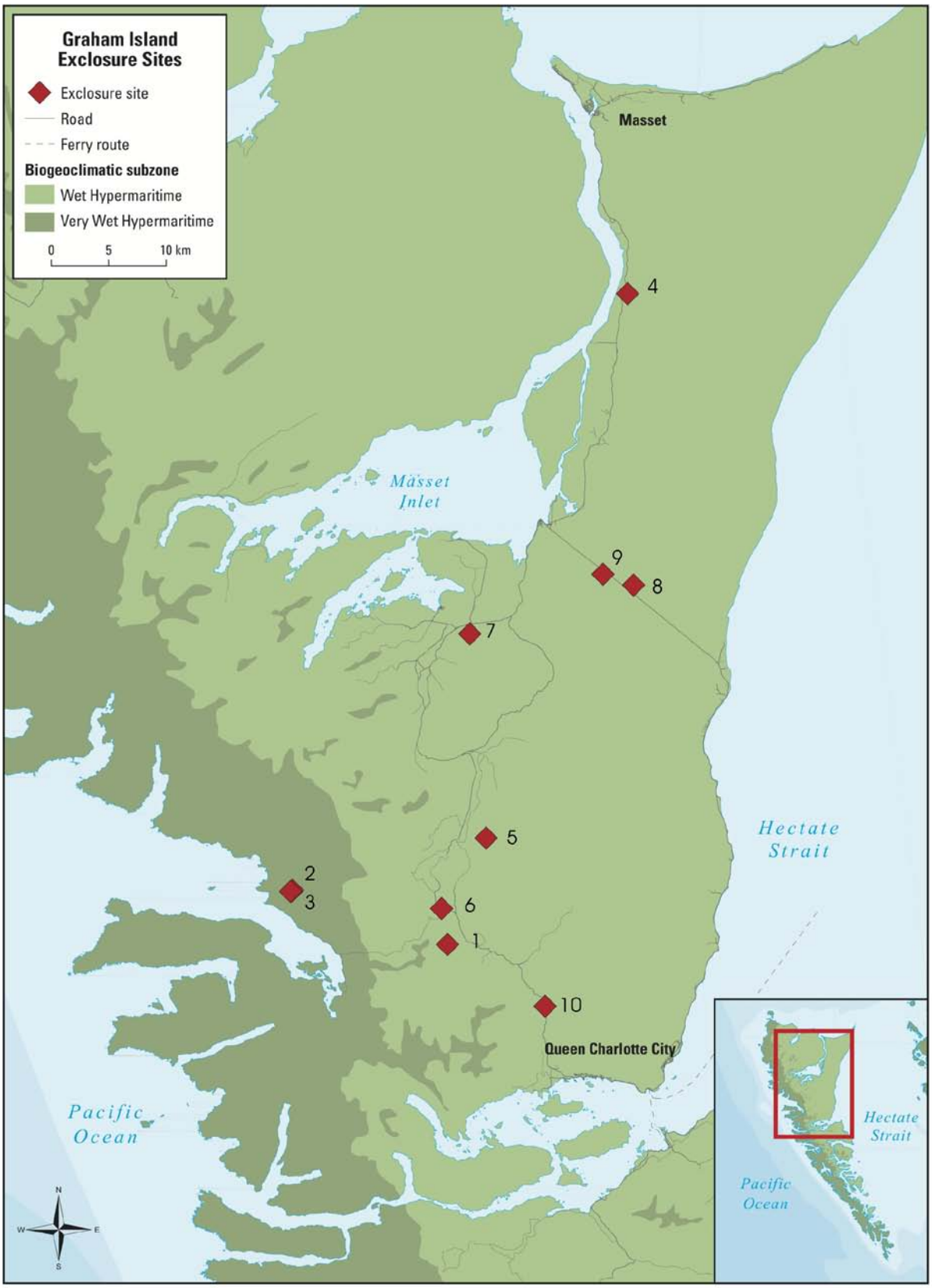

Map produced by Martin Danyluk
Source: BC Ministry of Forests and Range

Figure 1. Location of study sites on Graham Island, Haida Gwaii

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Deer exclosures were set up on Graham Island in 1997 to monitor the long-term impacts of deer on forest understory vegetation and western red cedar regeneration. As this is a long-term monitoring experiment, the experimental design and sampling procedures used in this study were consistent with previous years. The experiment consisted of 10 sites on Graham Island in remnant old-growth forest patches (Figure 1). The names and locations corresponding to the site numbers shown in Figure 1 are found in Appendix III. The sites were initially chosen because they were under mature forest canopy and had an abundance of red cedar seedlings (Stroh et al. 2008). All of the sites are within the Coastal Western bioclimatic zone. Two of the sites are in the Very Wet Hypermaritime subunit, as shown in Figure 1.

Every site contained two square deer exclosures that measured 25 m^2. Each deer exclosure plot was paired with an unfenced control plot. The control plots were circular, with a radius of 2.82 m and a total area of 25 m^2. The center of the control plot was located 10 m from the center of the exclosure. Field sampling was carried out from July 3rd to July 14th 2009. Previous data used in this study was collected in the fall of 1997, 2000, 2005 and 2009.

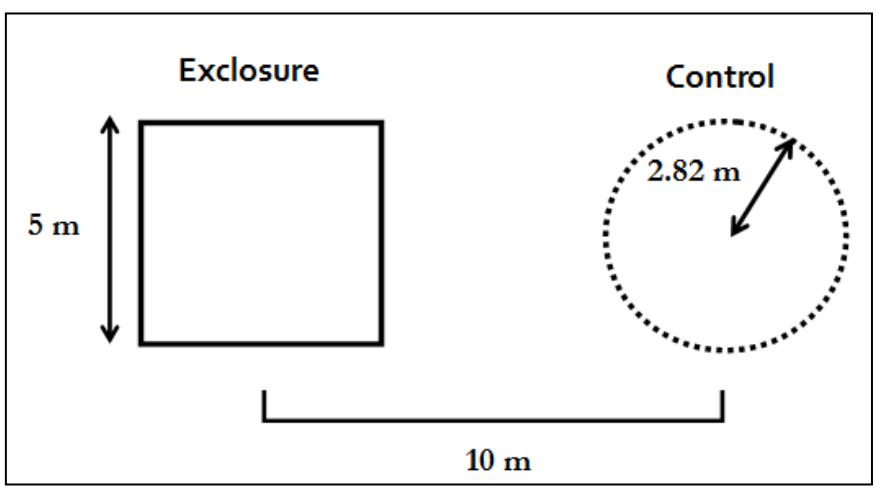

Figure 2. Experimental design showing paired exclosure and control plot

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To measure the abundance and diversity of the understory vegetation, all the plants in the exclosures and control plots were identified to the species level according to Pojar and MacKinnon (1994). Grasses and sedges were identified according to Douglas et al. (2001) to the species level. The percent cover of each plant species was estimated in all exclosures and control plots. The percent cover was measured in eight different height classes. For simplification, the height class data will be classified into 3 categories for the statistical analyses: 0-0.5 m, 0.5-1.5 m and 1.5-4.0 m. The first two categories are below the browse line which was identified at 1.5m by Martin and Daufresne (1999) and is shown in Figure 3. This method of measuring the abundance and diversity of understory vegetation is consistent with previous studies that collected data for this long-term monitoring experiment (Stroh et al. 2008, Stroh 2008, Kaknevicius 2008).

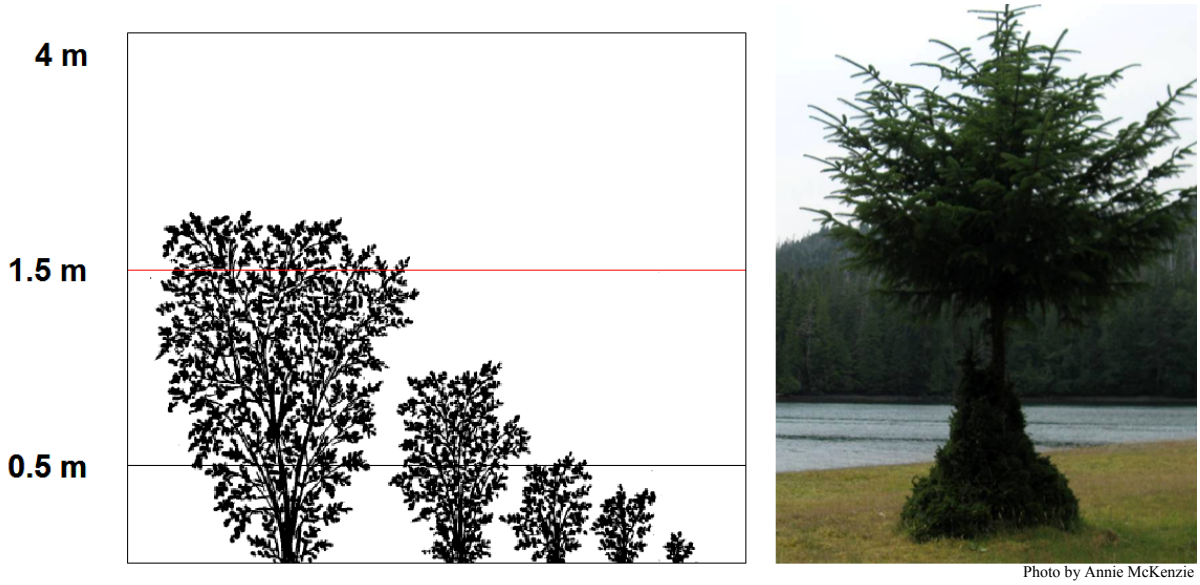

Photo by Annie McKenzie

Figure 3. Illustrations of the 1.5 m browse limit (diagram from: Martin and Daufresne 1997).

To study the impact of deer on ground cover, the percent cover of various substrates was estimated, including wood, rock, lichen, moss, root, litter, bare soil and

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grass. The total canopy cover was also estimated from the center of each exclosure and control plot.

Additional data was collected in 2009 that was not collected in previous years. The presence or absence of reproductive structures (flowers and fruits) was recorded in the exclosures and control plots for all species. The presence or absence of deer browse damage was also recorded for all the species in the control plots.

4.2 Data Analysis

4.2.1 Species richness

To calculate species richness, the total number of species found in the exclosures and the control plots was counted for all four years (1997, 2000, 2005 and 2009). The number of species only found in the exclosures, in the control plots, and in both the exclosures and the control plots was recorded. The species observed in 2009 were then compared with the British Columbia list of plant species at risk (B.C. Ministry of Environment n.d.) to determine if any of them were threatened or endangered on Haida Gwaii.

4.2.2 Understory plant abundance

A Before-After Control Paired (BACIP) test was used to compare the changes in average total percent cover of all understory vegetation in the exclosures and control plots from 1997 (before they were established) to 2009 (12 years after the exclosures were established). To do this, the average total percent cover of vegetation in the exclosures was subtracted from the average total percent cover of vegetation in the

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control plots for 1997 and 2009. The mean differences between exclosures and controls in 1997 and 2009 were compared using a two-sample paired t-test for means (Smith 2002). The following formula was used for the BACIP test:

Equation 1: $\mathbf{Dik = XiCj - XiIk = \mu + \eta i + \varepsilon ik}$

μ = the mean difference between control and impact

ηi = the change in difference from before to after

εik = the error associated with the difference (Smith 2002).

In addition to comparing the changes in average total percent cover, the BACIP test was also used to compare changes in average understory cover within the three height strata and to compare changes in average total cover for various species groups (trees, shrubs, ferns, herbs and graminoids). Finally, BACIP tests were performed on an individual species basis to evaluate whether individual species responses to the exclosure treatment were significant.

4.2.3 Vegetation Community Composition

To prepare the data for statistical analyses, a species table matrix was created for all species and all years. As there were two paired plots per site, the average total percent cover of each species was calculated for the two exclosures and the two control plots at each site. This was carried out for the data in 1997, 2000, 2005 and 2009. The table was organized so that species were columns and rows represented the treatments (exclosure vs. control plot), within plots, within years. This species matrix was used for all of the multivariate analyses. In addition to the species data table, a design matrix of incidences was constructed indicating the membership in plots, year of survey and treatment effect.

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The average percent cover of each species was also calculated for all 10 sites in 1997, 2000, 2005 and 2009 both in the exclosures and the control plots, to gain a better understanding of the overall abundance of each species. The graphs in Appendix II illustrate the total average percent cover for each species in the exclosures and control plots in 2009.

Multivariate analyses

Several multivariate analyses were performed to gain a better understanding of the effect of the exclosures on community composition. Because the primary interest focused on the exclosure effects, and to a lesser extent on yearly variation, the effects of plot variation were partialled out of the multivariate analyses.

A partial principal components analysis (PPCA) was carried out on the species data table described earlier, from which the plot effects were removed as covariates. In the analysis, the data were centered by species with no prior normalization (Leps and Smilauer 2003). To emphasize the species that contributed most to treatment differences (the differences between the exclosures and the control plots), a partial redundancy analysis (PRDA) was conducted using the same options as for the PPCA described above, but with the treatment used as constraining environmental variables (Leps and Smilauer 2003). Another PRDA was conducted as above, but with years included as covariates in order to evaluate the significance of the treatment effect. Two tests were conducted, one on untransformed data, and one on log-transformed data.

4.2.4 Plant Reproduction

A likelihood-ratio chi-square test was used to test the null hypothesis that the proportion of plots with plants with reproductive structures (fruits and flowers) is the

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same for exclosures and control plots. This test was performed for each species that had reproductive structures in more than 5 plots. To carry out this test, a 3x2 contingency table was constructed for each species. The first column contained the position (exclosure or control), the second column contained the presence of reproductive structures (yes or no) and the last column contained the total number of plots. If the expected count in any of the cells was less than 5, a Fisher's exact test was used instead of the likelihood ratio chi-square test.

4.2.5 Ground Cover and Canopy Cover

The BACIP design was also used to compare changes in the differences in moss and litter cover between 1997 and 2009, as well as changes in the differences in average canopy cover between the exclosures and control plots at each site.

All statistical analyses were performed using Statistical Analysis Software (Version 9) (SAS Institute Inc. 2000) and CANOCO (version 4.5) (ter Braak and Smilauer 2002) with a significance test of P=0.05.

5 Results

5.1 Species richness

The total species richness in the exclosures and control plots, as well as the number of species unique and common to the exclosures and control plots are shown in table 1. The total number of species has almost doubled between 1997 and 2009 both in the exclosures and control plots. However, there is no significant difference between the number of species in the exclosures and the control plots in 2009. Therefore, the exclosure treatment did not have an effect on species richness.

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In 2009, there were six species of plants that were unique to the exclosures. All of these species were dicots with perennial growth habits. Of these species, five were herbs including deer-cabbage (*Nephrophyllidium crista-galli*), pearly everlasting (*Anaphalis margaritacea*), western rattlesnake-root (*Prenanthes alata*), small bedstraw (*Galium trifidum*) and round-leaved sundew (*Drosera rotundifolia*). The sixth species, one-sided wintergreen (*Orthilia secunda*), was a sub-shrub.

None of the species found within the exclosures or control plots in 2009 were listed as species at risk on Haida Gwaii. Both Sitka spruce and pacific crabapple (*Malus fusca*) were recorded in the exclosures and control plots at site 18 (Mayer Lake), and this is characterized as a rare plant community on Haida Gwaii (HG SLUA 2007).

Table 1. Species richness in four sampling years

Year	Unique species in exclosure	Unique species in control plots	Species in exclosure and control plots	Total Species
1997	7	2	17	26
2000	2	3	24	29
2005	7	2	33	42
2009	6	4	35	45

5.2 Understory plant abundance

The average abundances of all species with a percent cover greater than 0.5% in the exclosures and the control plots are shown in table 2 in decreasing order of total average abundances in 2009. The three most abundant tree species were western hemlock, western red cedar and Sitka spruce. The most abundant shrub species were *Vaccinium sp.*, salal (*Gaultheria shallon*) and false azalea (*Menziesia ferruginea*). The three most abundant herb species were bunchberry (*Cornus unalaschkensis*), skunk cabbage (*Lysichiton americanum*) and fern-leaved goldthread (*Coptis aspleniifolia*).

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These results are consistent with the understory vegetation that is characteristic of the Coastal Western Hemlock biogeoclimatic zone (Pojar et al. n.d.). A complete list of average total abundances for all plant species in the four sampling years is found in Appendix I.

Table 2. Mean percent cover of plant species in four sampling years

			1997		2000		2005		2009	
Species name	**Scientific names**	**Code**	**Exclo**	**Cont**	**Exclo**	**Cont**	**Exclo**	**Cont**	**Exclo**	**Cont**
western hemlock	*Tsuga heterophylla*	WEHE	34.6	35	37.1	45	15	13	12	9.4
Vaccinium sp.	*Vaccinium sp.*	VACC	41.3	38	34.2	34	18	15	13	5.4
salal	*Gaultheria shallon*	SALA	14.4	18	21.4	24	13	19	7.8	6.4
western red cedar	*Thuja plicata*	RECE	4.3	4.9	6.4	4.4	4.4	2.7	3.3	4.2
false azalea	*Menziesia ferruginea*	FAAZ	10.7	13	11	10	7.2	3.5	4.7	2.7
bunchberry	*Cornus unalaschkensis*	BUBE	1.9	1	5	0.8	13	1.4	4.4	0.7
skunk cabbage	*Lysichiton americanum*	SKCA	1.3	0.6	1	0.2	5.4	0.1	4	0.3
Sitka sedge	*Carex sitchensis*	SISE	2.1	2.8	2	1.3	3	2.5	2	0.8
fern-leaved goldthread	*Coptis aspleniifolia*	GOTH	0.2	0.1	1.5	0.6	5.4	0.3	1.9	0.5
mountain hemlock	*Tsuga mertensiana*	MOHE	0	0	0	0	0.3	0.3	0.9	1
heart-leaved twayblade	*Listera cordata*	HLTW	0	0	0.1	0.2	0.3	0.8	0.8	1
Sitka spruce	*Picea sitchensis*	SISP	1.7	4.3	2.1	5	1.7	1.9	0.9	0.8
deer fern	*Blechnum spicant*	DEFE	0.5	0.5	0.6	0.5	1.6	0.7	1.1	0.5
carex sp.	*Carex sp.*	SEDGE	0	0	0	0.4	1.4	1.7	1.2	0.4
grass spp.	*Poaceae sp.*	GRASS	6.1	0.6	3.7	0.8	1.1	0.7	0.7	0.7
western yew	*Taxus brevifolia*	WEYE	0.6	0.8	0.8	1.1	0.4	0.9	0.3	1
false lily-of-the-valley	*Maianthemum dilatatum*	FALV	0.1	0	0.3	0.3	0.6	0.4	0.6	0.5
five-leaved bramble	*Rubus pedatus*	FIBR	0.2	0.1	0.3	0.3	0.9	1	0.6	0.3

Note: Only species with an average percent cover of 0.5% or more in exclosures and control plots are shown. Species in decreasing order of mean percent cover in 2009.

The changes in average understory vegetation percent cover in the exclosures and control plots over 12 years in the three height classes is shown in Figure 4. The BACIP tests revealed that the change (exclosure - control plot) in average percent cover of all understory vegetation between 1997 and 2009 was not statistically significant for the lowest height strata (0 m – 0.5 m) and the highest height stratum (1.5 m – 4 m). However, the change in percent cover in the middle height stratum (0.5 m to 1.5 m) between 1997 and 2009 was statistically significant (P=0.0027). The average percent cover of

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understory vegetation increased in the exclosures from 1997 to 2009, while it decreased in the control plots. The protection from deer therefore had a positive effect on the vegetation in the medium height class, which is below the browse line.

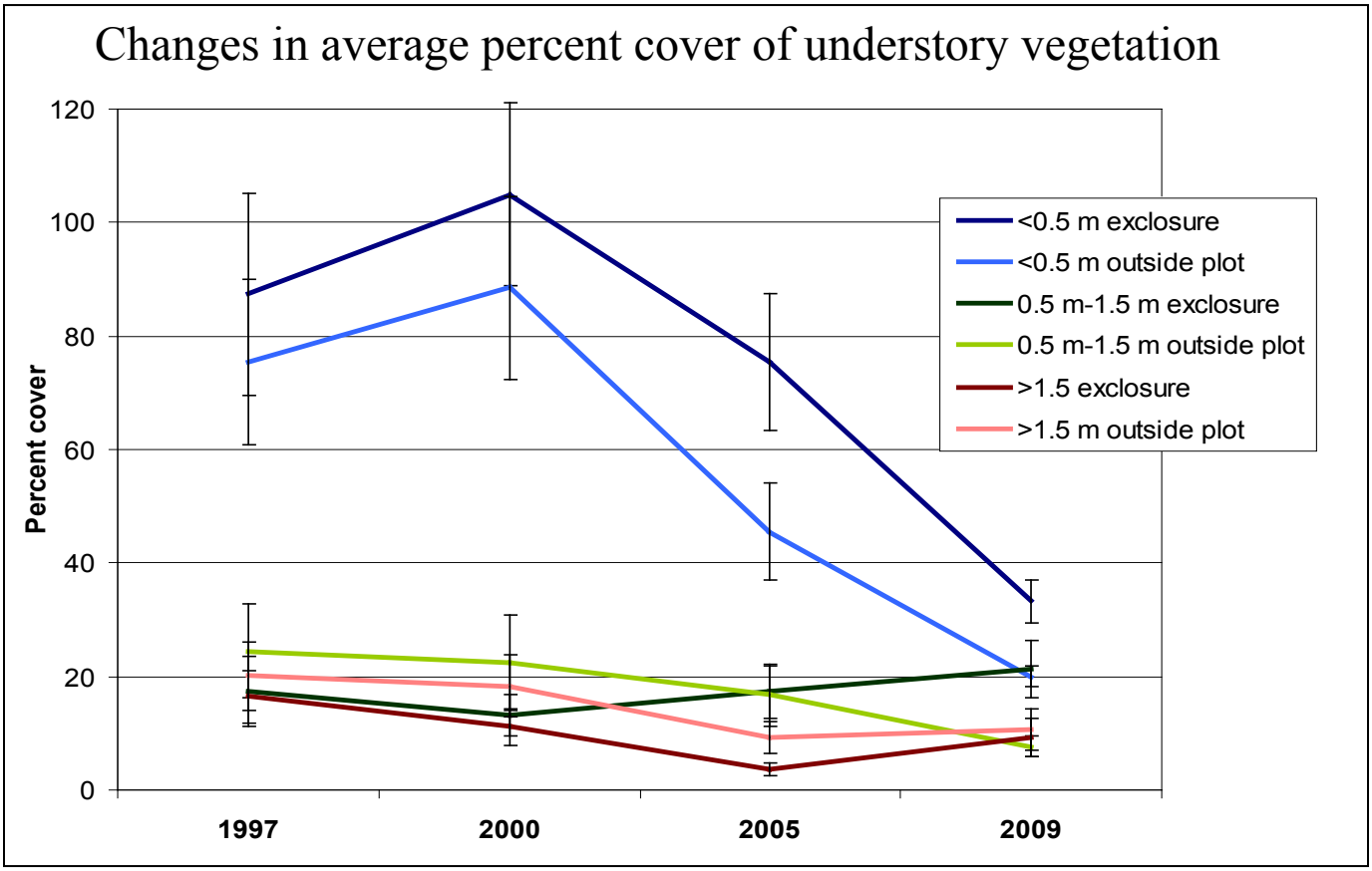

Figure 4. Changes in average percent cover of understory vegetation

When the BACIP tests were used to compare changes in average total cover for all of the species groups (trees, shrubs, herbs, ferns and graminoids), none of the results were statistically significant. Therefore, the protection from deer had no effect on the average vegetation cover grouped by species type. When BACIP tests were performed on each individual species, the change in average percent cover from 1997 to 2009 was statistically significant for bunchberry (P=0.0149) and marginally significant for fern-leaved goldthread (P=0.0549). Both of these species increased in abundance inside the

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exclosures. These results are consistent with those found by Kaknevicius (2008), however there was no significant increase in skunk cabbage between 1997 and 2009, while there was in 2005 (Kaknevicius 2008). This could be a result of seasonal differences in sampling times. Figures 5 and 7 illustrate the changes in percent cover of bunchberry and fern-leaved goldthread over the four sampling years. The error bars represent standard error.

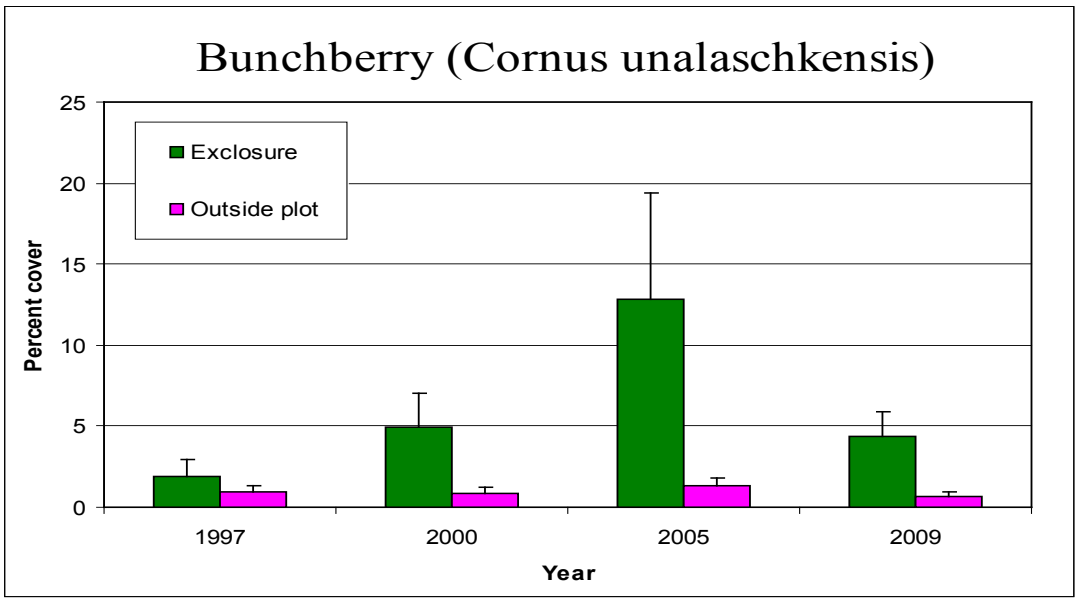

Figure 5. Changes in average percent cover of bunchberry over time

Photos by Annie McKenzie

Figure 6. Photographs of bunchberry plants in exclosures

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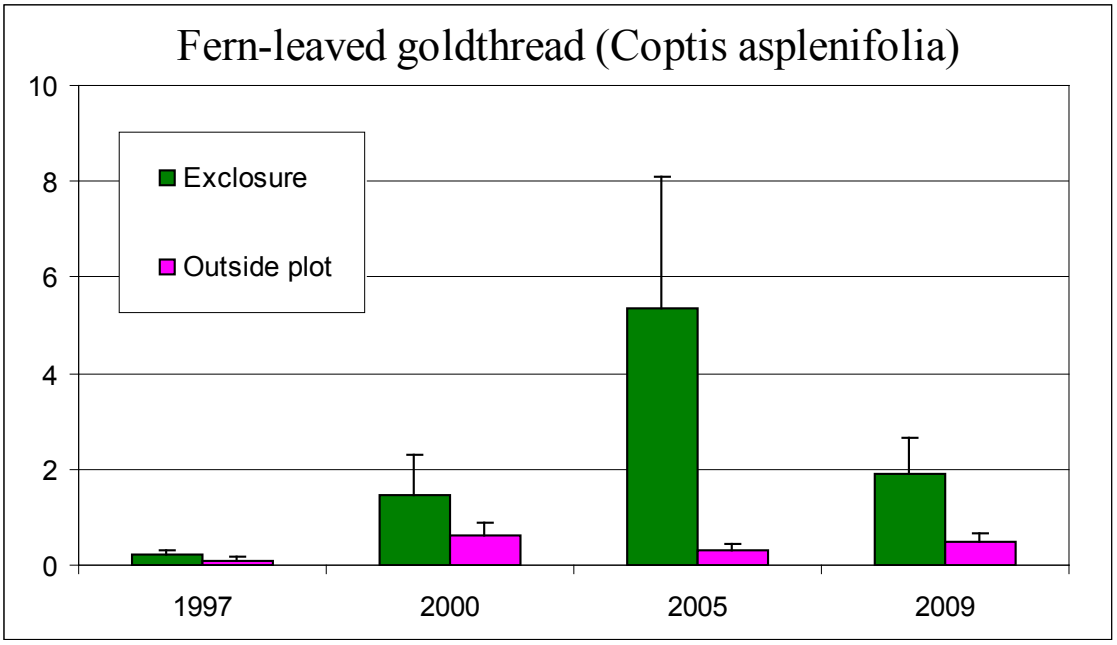

Figure 7. Changes in average percent cover of fern-leaved goldthread over time

Photos by E-flora BC

Figure 8. Photographs of fern-leaved goldthread (E-flora BC 2009)

5.3 Vegetation Community Composition

The results of the PRDA with plot effects removed as covariates showed that the exclosure treatment was significant (P=0.0002) when the data was log-transformed, however it was not significant (P= 0.3534) when the data was not log-transformed. The

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differences between excluded and non-excluded plots are therefore not to be found within the most abundant species. The results of the PPCA analysis, where plot effects were removed as covariates, are shown in the ordination diagrams in Figure 9 and Figure 10. Figure 9 illustrates that axis 2 (vertical axis) represents the treatment effect, which accounts for 15.4% of the within-plot variation in species composition. Figure 10 illustrates that Axis 1 (horizontal axis) represents the year effect, which accounts for 26.4% of the within-plot variation in community composition. This ordination diagram clearly shows the divergence in species composition between the exclosures and the control plots over time.

The results of the PRDA with treatment used as constraining environmental variables emphasized the species that contributed most to the treatment differences (the differences between the exclosures and the control plots). The species ordination diagram in Figure 11 illustrates these differences. The four letter codes represent species (see Appendix I for a list of corresponding species names). The species to the right of the diagram were more closely associated with exclosures, while species falling to the left of the diagram were more closely associated with control plots. The species that were the most closely associated with the exclosures, in order of importance were bunchberry, skunk cabbage, fern-leaved goldthread, deer fern (*Blechnum spicant*) and deer-cabbage. These results suggest that these species are sensitive to deer browsing. The species that were most associated with control plots, in order of importance were heart-leaved twayblade (*Listera cordata),* Labrador tea (*Ledum groenlandicum*)*,* Sitka spruce, red alder (*Alnus rubra*) and western bog-laurel (*Kalmia microphylla*).

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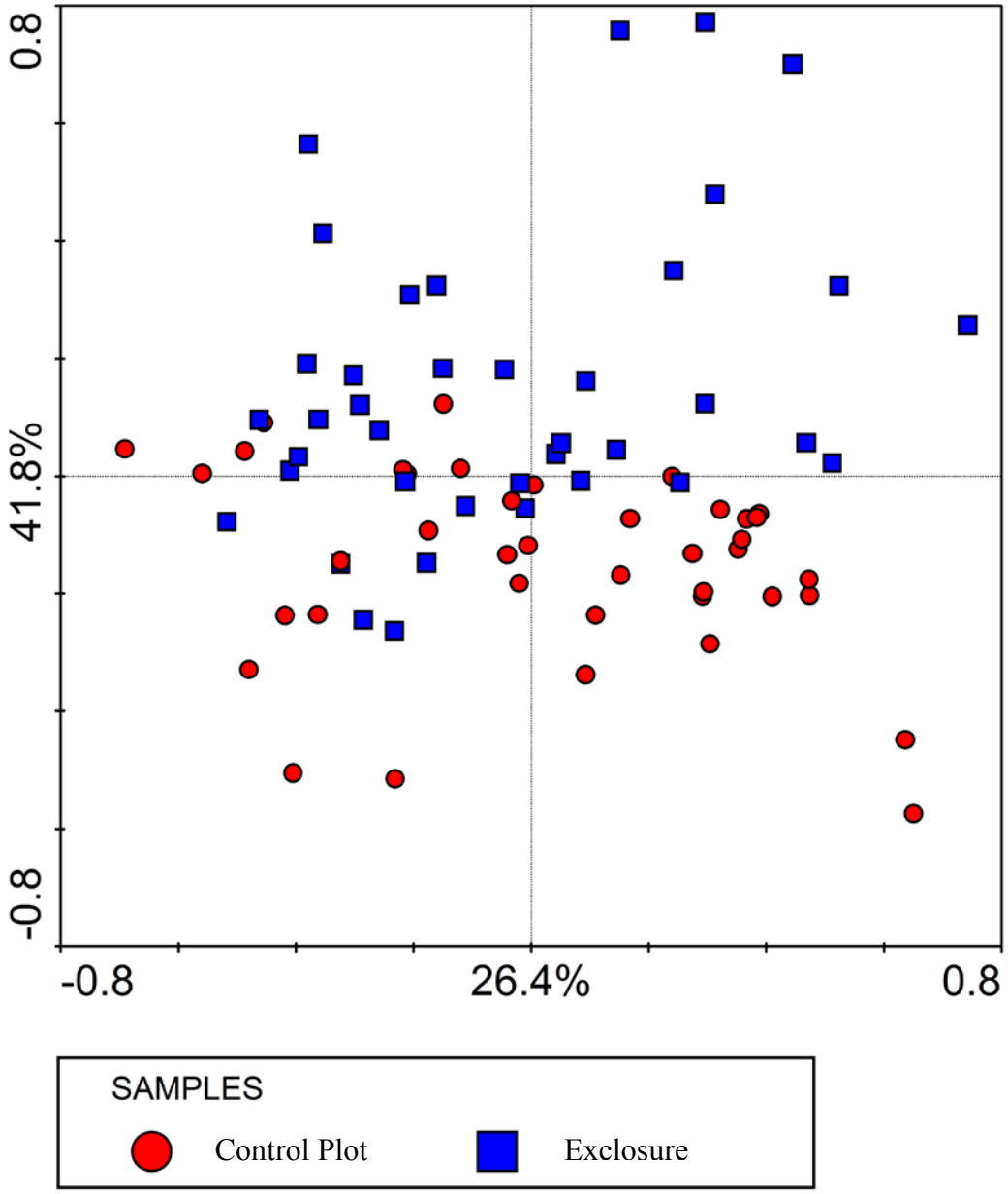

Figure 9. Samples ordination diagram showing the results of the partial principal components analysis (PPCA) from which the plot effects were removed as covariates. The samples are classified according to treatment.

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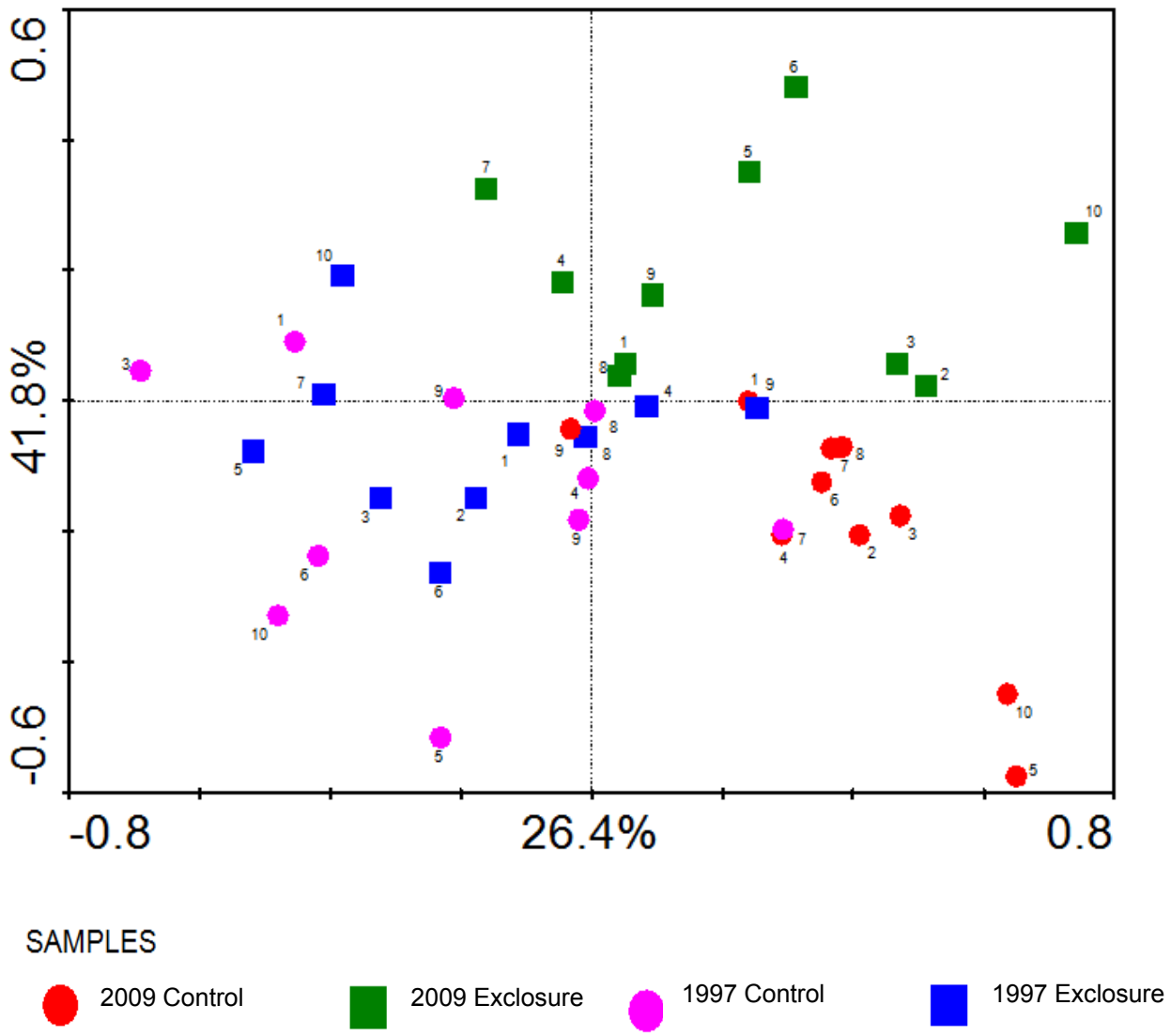

Figure 10. Samples ordination diagram showing the results of the partial principal components analysis (PPCA) from which the plot effects were removed as covariates.

Note: The samples are classified according to treatment and years. The results from 2000 and 2005 were excluded from this diagram in order to highlight the divergence in species composition over time. The numbers in the diagram correspond to the site numbers shown in Figure 1.

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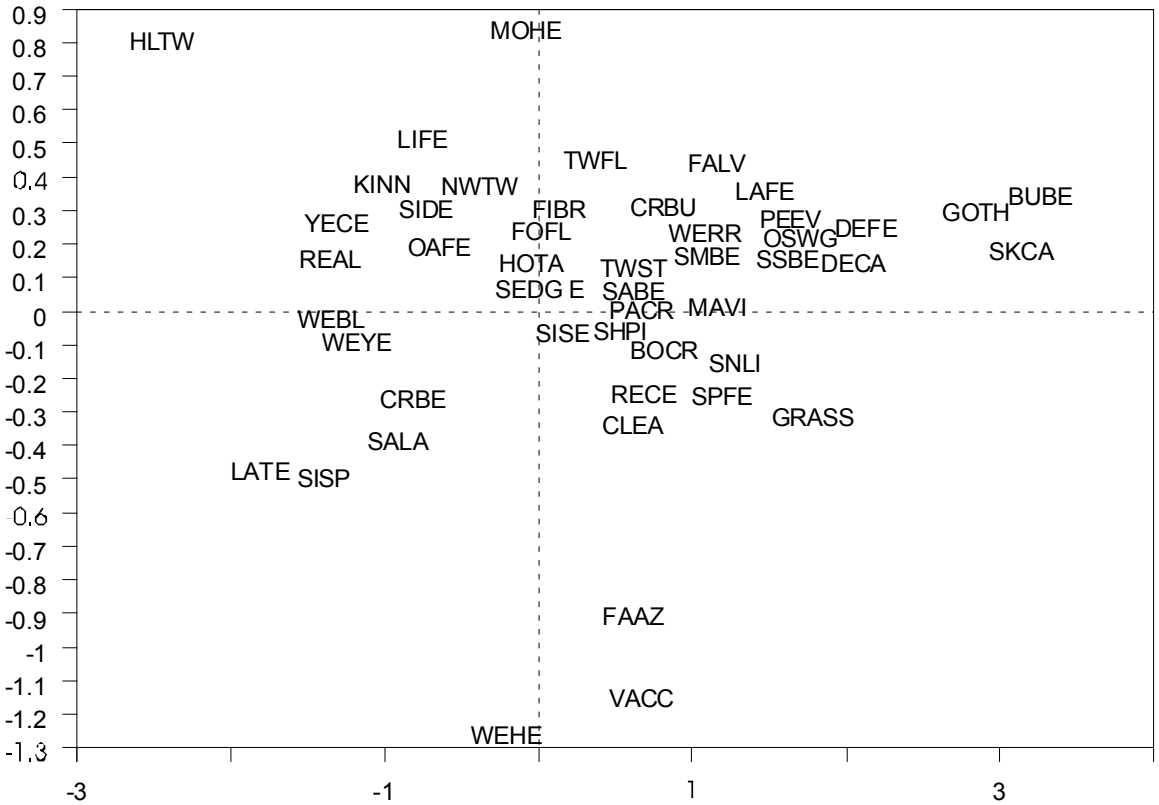

Figure 11. Species ordination diagram for partial redundancy analysis (PRDA) with treatment used as constraining environmental variables.

Note: The four letter codes represent species (see Appendix I), and the species to the right of the diagram were more associated with exclosures, while species falling to the left of the diagram were more closely associated with control plots.

5.4 Plant Reproduction

The proportion of exclosures and control plots with plants with flowers or fruit are shown in Figure 12 for each species. The null hypothesis that stated that the proportion of fruits and flowers is the same in the exclosures and control plots was rejected when Chi-square tests were performed for bunchberry, and *Vaccinium sp*. The proportion of plots with flowering plants was significantly higher in the exclosures than the control plots (χ^2=7.9142, d.f. = 1, P=0.0049) and the same was true for *Vaccinium sp*. (χ^2=5.8122, d.f. = 1, P=0.0159). The fisher's exact test also revealed that the proportion

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of plots with flowering plants of fern-leaved goldthread was significantly higher in the exclosures than in the control plots (P=0.0152). There was no statistically significant difference in the proportion of flowers or fruit between the exclosures and control plots for all other species. However, the species that were found to be more closely associated with the exclosures in the ordination diagram in Figure 11 generally had a higher proportion of flowers or fruits within the exclosures than the control plots. Deer cabbage was only observed at one site in 2009, therefore the results were not included in the chi-square analysis. However, at this site many of the Deer cabbage plants inside the exclosure were in flower, while the plants in the control plot did not have any flowers.

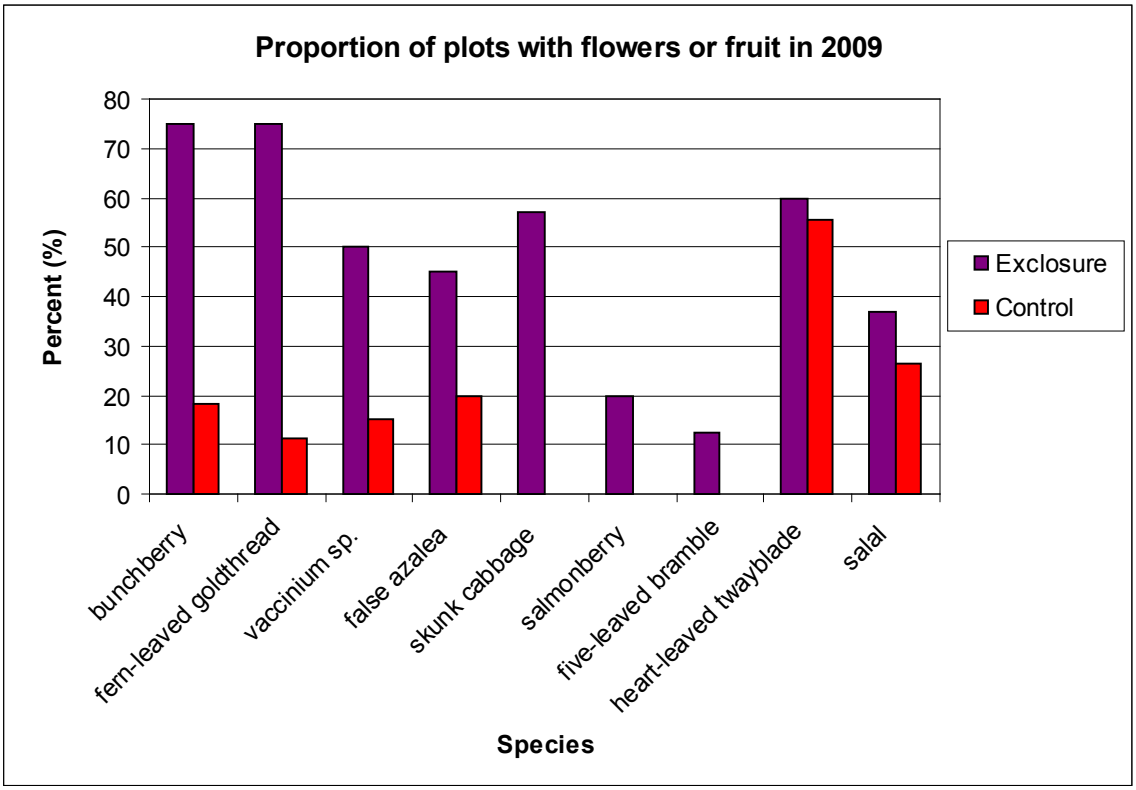

Figure 12. The proportion of plots containing plants with reproductive structures (flowers or fruit) in 2009.

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5.5 Overstory Canopy Cover and Ground Cover

Most of the ground cover did not change significantly between 1997 and 2009. However, the results of the BACIP test showed that the differences in changes in moss cover in the exclosures and the control plots was significant between 1997 and 2009 (P=0.0441). The change in average percent cover of moss is shown in Figure 13 (the error bars represent standard error). The average percent cover of moss increased in the control plots, and decreased in the exclosures. There were no statistically significant differences between the change in litter cover or canopy cover between 1997 and 2009.

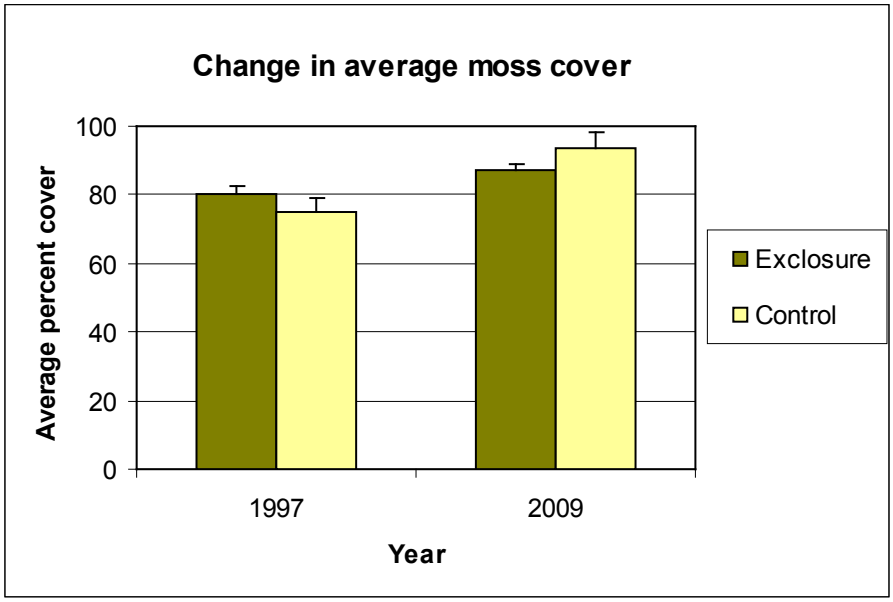

Figure 13. Change in average percent cover of moss in exclosures and control plots

6 Discussion

6.1 Impact of deer on plant species richness

Decreased plant diversity has been recorded for many forest ecosystems affected by moderate to high deer densities (Anderson and Katz 1993, Woodward et al. 1994, deCalesta 1997, Gill and Beardall 2001). However, Stockton et al. (2005) points out that

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these studies generally occurred in contexts where other factors, such as logging, may have played a role in emerging species richness patterns. The results of this study showed that deer do not have a significant impact on understory plant species richness, which confirms the results that Kaknevicius (2008) and Stroh (2008) found for the data in 2005. These results are consistent with other deer exclosure experiments which have shown that overall species richness shows little response to protection from deer browsing (Kraft et al. 2004, Nomiya et al. 2002).

Several authors have put forth hypotheses to explain these results. Nomiya et al. (2002) found that environmental heterogeneity, soil variables and natural disturbances have a stronger effect on overall species richness than deer browsing. Stroh (2008) points out that the impact of deer on species richness will be largely dependent on deer densities. At intermediate densities, deer can increase species richness by consuming competitively dominant plant species (Hester et al. 2000, Suzuki et al. 2008). However, at very high densities, only browse-tolerant species will be able to persist, and some species will be eliminated (Stroh 2008). It may be that high deer densities on Graham Island eliminated certain species from the study sites before the exclosures were established, or it could also be that intermediate deer densities have maximized species richness on Graham Island by consuming competitively dominant plant species. Additional studies on deer density gradients and population dynamics would need to be carried out on Graham Island to understand how deer densities affect the total number of plant species in these old-growth forests.

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Although deer did not have a significant impact on the total number of understory plant species, a considerably large proportion (over 20%) of the species were unique to either the exclosures or control plots. However, because this 20% is almost equally distributed between the exclosures and control plots, it does not seem to indicate a change in species composition. The small size of the sample plots ($25m^2$) meant that the appearance of a species in an exclosure, but not in a paired control plot could simply be due to chance. Many of these species, such as pearly everlasting, were only present in trace amounts and were only found in one exclosure or control plot. Species richness in both the exclosures and the control plots increased over the 12 year study period, but this is likely because of an increase in observer's expertise.

6.2 Impact of deer on plant abundance

In general, the understory plants in the study sites were mostly long-lived, slow-growing species that are common in the old-growth forests of Haida Gwaii. The average percent cover of all species was fairly low in both the exclosures and the control plots. Previous studies on Haida Gwaii have noted that deer feed on understory vegetation mainly between 0 m and 1.5 m above the ground, and this creates a visible browse line in the vegetation (as shown in Figure 3). Kaknevicius (2008) did not find any significant differences in overall average percent cover in any of the three height strata for the data in 2005. However, after four more years of deer exclusion, the medium height stratum (0.5 m to 1.5 m) is finally significantly higher in the exclosures. This confirms the hypothesis that deer have a direct negative impact on the vegetation below the 1.5 m browse limit. The upper height stratum could be indirectly affected by deer browsing, as browsing in the medium stratum could limit the recruitment into the highest height

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stratum (Stroh 2008), however this was not evident in our results. It is likely that a much longer time-frame is needed to be able to detect the indirect changes in the highest height stratum as a result of deer browsing.

A decreased abundance of vegetation in the medium height class of old-growth forest understories has important negative ecological, social, cultural and economic impacts. These impacts are discussed in detail in the report by Kaknevicius (2008). It is important to note that the impact of deer on the abundance of understory vegetation below the browse line is likely higher in areas that are further from roads and hunters. As all of the study sites were located near roads and were accessible to hunters, browsing stress was likely lower than in more remote areas. For example, Martin and Baltzinger (2002) showed that red cedar regeneration was much higher in areas where deer were exposed to hunting. They attributed this to the fact that hunting changes deer behaviour (deer spend less time browsing and more time looking around for hunters), rather than the actual reduction in deer numbers.

6.3 Impact of deer on plant community composition

The results of the multivariate analyses in this study clearly showed that there was a divergence in species composition in the exclosures and the control plots. Differences in species composition between exclosures and control plots have also been noted by several other authors (Casabon and Pothier 2008, Anderson and Katz 1993, Gill and Beardall 2001, Morecroft et al. 2001.) These authors point out that at high deer densities, palatable species that are preferred by deer grow scarce or disappear and are replaced by less sought after species (deCalesta 1997, Reyes and Vasseur 2003, Rooney and Waller

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2003, Kraft et al. 2004, Casabon and Pothier 2008, Rooney 2009). Similar results were found in this study.

The species that were the most closely associated with the exclosures, such as bunchberry, skunk cabbage, fern-leaved goldthread, deer fern and deer-cabbage, are all important forage species for Sitka black-tailed deer and have high nutritional value (Hanley and McKendrick 1983). The species that were most associated with the control plots such as heart-leaved twayblade and Labrador tea are known to be low in digestibility for deer (Hanley and McKendrick 1983). The results of the PPCA therefore seem to show a divergence in community composition based on the palatability of the understory plant species.

A study on the diet composition of Sitka black-tailed deer in Southeast Alaska revealed that bunchberry was the most important forage species, representing approximately 29% of their diet (Kirchhoff and Larsen 1998). This is reflected in our results, as bunchberry was the species most affected by the protection from deer and showed a significant positive increase in abundance from 1997 to 2009 within the exclosures. Kirchhoff and Larsen (1998) found that red huckleberry (*Vaccinium parviflorum*) composed 13% of deer diets in Southeastern Alaska, followed by western red cedar at 9% and skunk cabbage at 5%. Although the PPCA analysis showed that *Vaccinium sp*., western red cedar and skunk cabbage were associated with the exclosures in our study, these species did not show significant increases in abundances from 1997 to 2009. The fact that our experiment did not reveal any significant impact on the abundance of Red huckleberry could be due to the fact that *Vaccinium sp*. was only identified to the genus level. Kirchhoff and Larsen (1998) showed that although red

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huckleberry was a preferred forage species of Sitka black-tailed deer, other species of *Vaccinium* (such as early blueberry (*Vaccinium ovalifolium*) and Alaska blueberry *(Vaccinium alaskaense*)) only contributed minor components to deer diets, despite being the most abundant and widely available browse species in the area. In order to quantify the impact of Sitka black-tailed deer on Red huckleberry on Graham Island, *Vaccinium* would need to be identified to the species level.

Although western red cedar did not show a significant increase in total average abundance inside the exclosures in this study, previous results of this long-term monitoring experiment have shown that deer browsing had a drastic and negative effect on both red cedar survival and the number of leafed shoots per individual (Stroh et al. 2008). It appears that the measurements of plant morphology used by Stroh et al. (2008) such as measurements of individual height, number of leafed shoots, number of stems and seedling survival are more sensitive indicators of deer browsing than community measurements such as richness and cover.

6.4 Impact of deer on plant reproduction

Plant reproduction is another sensitive indicator of the impacts of deer browsing. The results of this study showed that bunchberry, fern-leaved goldthread and *Vaccinium sp*. all had significantly higher proportions of plants with fruits or flowers inside the exclosures than in the control plots. Although the other plants did not show statistically significant differences, all species had higher proportions of flowers inside the exclosures than in the control plots. In fact, skunk cabbage, salmonberry (*Rubus spectabilis*), five-leaved bramble (*Rubus pedatus*) and deer cabbage were never found flowering in any of the control plots. heart-leaved twayblade and salal had almost equal proportions of

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flowers in the exclosures and the control plots, and this is consistent with the fact that they are not easily digestible by deer, and are likely resistant to deer browsing (Kirchhoff and Larsen 1998). Stockton et al. (2005) found that salal was one of the only shrubs that remained on small islands in the south of Haida Gwaii that were heavily impacted by deer browsing (Stockton et al. 2005). Although these results give some indication of the effects of deer on understory plant reproduction, individual plant measurements (such as the number of plants in flower, and the number of flowers per plant) would likely reveal more pronounced differences between the exclosures and the control plots.

6.5 Changes in ground cover and canopy cover

The results of this study showed that the average percent cover of moss increased significantly in the control plots, while it decreased in the exclosures from 1997 to 2009. Mosses are known to have little nutritional value to deer, and therefore mosses can out-compete plants that are sensitive to deer browsing (Hanley and McKendrick 1983). As the successful establishment of understory plants and tree seedlings is dependent on the quality and type of ground cover (Kumar and Shibata 2007), an increase in moss cover could inhibit the establishment of some species. Kaknevicius (2008) hypothesized that changes in overstory conditions could play an important role in determining the composition and abundance of understory vegetation communities, however our results did not support this hypothesis, as there was no significant change in canopy cover between 1997 and 2009.

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7 Recommendations

7.1 Practical recommendations

Although we are beginning to see differences in plant communities following 12 years of deer exclusion, the richness and cover of flora in the understory will continue to change, and long term monitoring for more than 20 years could reveal different patterns for species richness and percent cover, therefore this experiment should be continued. The results of this study showed that plant morphology and reproductive structures appear to be sensitive indicators of deer browsing, and these measurements could be included in this long-term monitoring experiment. This is especially important for species that are sensitive to deer browsing such as bunchberry and Fern-leaved gold thread. As some of the variation in the long-term data could be a result of differences in observer expertise, it would be beneficial to maintain observer continuity in this experiment over the long-term.

As mentioned earlier, several groups of plants in this long-term monitoring experiment were not identified to the species level, including grasses, sedges and *Vaccinium* species. In order to gain a complete picture of the plant community composition in these study sites, it is important to identify all the plants to the species level. The Haida Gwaii Forest District could facilitate this by creating a plant herbarium for Haida Gwaii in cooperation with the Haida Gwaii Museum. This would be an extremely useful tool not only for this long-term monitoring experiment, but also for assisting other researchers and local community members in identifying the plants of Haida Gwaii. I would also recommend that the exclosures continue to be used as an

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educational tool for local students and communities. Finally, several of the exclosures were damaged by fallen trees, and these exclosures need to be repaired if this experiment is to continue over the long-term.

7.2 Recommendations for future research

Although this research illustrates the impact of deer on common understory plant species, it does not show how deer are affecting threatened or endangered species, as these species were not present in any of the study sites. Furthermore, many species which are culturally significant to the Haida, such as Devil's club (*Oplopanax horridus*) and known to be susceptible to deer browsing were not present in the study sites. This could be an indication that these species have already disappeared from many of the old-growth forests on Haida Gwaii. Additional research could focus specifically on the impacts of deer on culturally significant, endemic or endangered and threatened plant species.

Deer browsing has important impacts on the understory vegetation in the temperate rainforests of Haida Gwaii, however industrial logging, as defined by large scale clear-cut harvesting and extensive road development, has also had profound effects on forest ecosystems. Deer research could be greatly enriched by accounting for the dramatically altered landscape that exists around the remaining old-growth forests. Although several studies have looked at the impact of deer browsing on the regeneration of tree seedlings in second-growth and clear-cut stands (eg. Martin and Baltzinger 2002), less is known about the combined impacts of deer browsing and logging on forest understory plants. As the province of British Columbia moves towards ecosystem based forest management, I would argue that a better understanding of the interaction between forest harvest and deer is critical to maintaining and managing biodiversity in managed

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forests, not only for tree species but for all understory plants. I therefore recommend that deer herbivory should be studied and managed in the context of current and past forest management practices in Haida Gwaii.

8 Conclusion

In conclusion, deer on Graham Island are having a significant impact on the abundance of understory vegetation in the medium height class (0.5 m – 1.5 m) and they are shifting the community composition of understory vegetation towards less palatable species. The plant species that were most affected by deer browse on Graham Island were important forage species for Sitka black-tailed deer in their natural habitat in Alaska (Kirchhoff and Larsen 1998). Deer seem to be preferentially browsing nutrient rich forbs rather than less palatable species, and this is an indication that deer populations on Graham Island have likely not reached their ecological carrying capacity. This is in contrast to the impacts of deer on smaller islands in Laskeek bay, where the entire shrub and herb layers of the understory vegetation have been eliminated and less palatable species such as Sitka spruce are heavily browsed. More research is needed to better understand the impacts of deer on understory vegetation in the old-growth forests of Haida Gwaii.

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Appendix I. Average total percent cover of all species

Table showing the average percent cover of all species in all four sampling years, in the exclosures (Exclo) and in the control plots (Cont).

Species name	Code	Scientific names	1997		2000		2005		2009	
			Exclo	Cont	Exclo	Cont	Exclo	Cont	Exclo	Cont
bog cranberry	BOCR	*Oxycoccus oxycoccos*	0.10	0.03	0.00	0.00	0.00	0.00	0.00	0.00
bunchberry	BUBE	*Cornus unalaschkensis*	1.88	0.95	4.95	0.83	12.85	1.35	4.40	0.70
cleavers	CLEA	*Galium aparine*	0.00	0.00	0.50	0.20	0.00	0.00	0.00	0.00
crowberry	CRBE	*Empetrum nigrum*	0.00	0.00	0.10	0.05	0.00	0.10	0.00	0.03
creeping buttercup	CRBU	*Ranunculus repens*	0.00	0.00	0.00	0.00	0.13	0.08	0.10	0.03
deer-cabbage	DECA	*Nephrophyllidium crista-galli*	0.10	0.00	0.20	0.03	0.40	0.08	0.15	0.00
deer fern	DEFE	*Blechnum spicant*	0.48	0.50	0.58	0.50	1.58	0.65	1.13	0.53
false azalea	FAAZ	*Menziesia ferruginea*	10.73	12.98	11.03	9.95	7.23	3.53	4.73	2.68
false lily-of-the-valley	FALV	*Maianthemum dilatatum*	0.10	0.00	0.30	0.25	0.58	0.38	0.58	0.45
five-leaved bramble	FIBR	*Rubus pedatus*	0.15	0.10	0.30	0.33	0.90	1.03	0.55	0.28
fir clubmoss	FICL	*Lycopodium selago*	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00
foamflower	FOFL	*Tiarella trifoliata*	0.00	0.00	0.00	0.05	0.13	0.20	0.23	0.08
fern-leaved goldthread	GOTH	*Coptis aspleniifolia*	0.20	0.10	1.48	0.60	5.38	0.33	1.90	0.48
grass spp.	GRASS	*Poaceae sp.*	6.05	0.63	3.65	0.75	1.10	0.70	0.70	0.68
heart-leaved twayblade	HLTW	*Listera cordata*	0.00	0.00	0.08	0.15	0.25	0.83	0.83	1.00
common horsetail	HOTA	*Equisetum arvense*	0.00	0.00	0.35	0.15	0.73	1.03	0.25	0.10
kinnikinnick	KINN	*Arctostaphylos uva-ursi*	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.20
lady fern	LAFE	*Athyrium filix-femina*	0.03	0.00	0.00	0.00	0.38	0.08	0.28	0.13
Labrador tea	LATE	*Ledum groenlandicum*	0.00	0.40	0.23	0.35	0.10	0.30	0.00	0.10
licorice fern	LIFE	*Polypodium glycyrrhiza*	0.00	0.00	0.00	0.03	0.05	0.08	0.10	0.13
marsh violet	MAVI	*Viola palustris*	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
mountain hemlock	MOHE	*Tsuga mertensiana*	0.00	0.00	0.00	0.00	0.33	0.25	0.93	0.98
northwestern twayblade	NWTW	*Listera caurina*	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.10
oak fern	OAFE	*Gymnocarpium dryopteris*	0.10	0.10	0.00	0.00	0.15	0.18	0.10	0.20
one-sided wintergreen	OSWG	*Orthilia secunda*	0.00	0.00	0.00	0.00	0.08	0.00	0.08	0.00
pacific crabapple	PACR	*Malus fusca*	0.00	0.00	0.00	0.00	0.28	0.15	0.13	0.10
pearly everlasting	PEEV	*Anaphalis margaritacea*	0.00	0.00	0.00	0.00	0.03	0.00	0.05	0.00
purple-leaved willowherb	PUWI	*Epilobium ciliatum*	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00
red alder	REAL	*Alnus rubra*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
western red cedar	RECE	*Thuja plicata*	4.33	4.88	6.40	4.38	4.35	2.68	3.33	4.18
round-leaved sundew	RLSU	*Drosera rotundifolia*	0.13	0.00	0.00	0.00	0.05	0.00	0.05	0.00
salmonberry	SABE	*Rubus spectabilis*	0.00	0.18	0.20	0.15	0.18	0.13	0.40	0.05
salal	SALA	*Gaultheria shallon*	14.43	18.38	21.43	23.55	12.65	19.33	7.75	6.43
carex sp.	SEDGE	*Carex sp.*	0.00	0.00	0.00	0.35	1.35	1.65	1.23	0.43
shore pine	SHPI	*Pinus contorta*	0.00	0.00	0.05	0.05	0.30	0.20	0.15	0.13
single delight	SIDE	*Moneses uniflora*	0.00	0.00	0.03	0.00	0.00	0.05	0.05	0.08
Sitka sedge	SISE	*Carex sitchensis*	2.05	2.80	1.95	1.25	3.00	2.45	2.00	0.83
Sitka spruce	SISP	*Picea sitchensis*	1.70	4.25	2.13	4.95	1.70	1.90	0.93	0.75
skunk cabbage	SKCA	*Lysichiton americanum*	1.25	0.55	0.98	0.20	5.38	0.13	4.00	0.25
small bedstraw	SMBE	*Galium trifidum*	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
snake liverwort	SNLI	*Conocephalum conicum*	0.25	0.00	0.00	0.00	0.00	0.00	0.05	0.03

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Species name	Code	Scientific names	1997		2000		2005		2009	
			Exclo	Cont	Exclo	Cont	Exclo	Cont	Exclo	Cont
spiny wood fern	SPFE	*Dryopteris expansa*	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00
sweet-scented bedstraw	SSBE	*Galium triflorum*	0.15	0.00	0.00	0.00	0.15	0.08	0.20	0.05
twinflower	TWFL	*Linnaea borealis*	0.00	0.00	0.00	0.00	0.08	0.05	0.10	0.08
twistedstalk	TWST	*Streptopus sp.*	0.20	0.10	0.03	0.03	0.15	0.08	0.08	0.13
Vaccinium sp.	VACC	*Vaccinium sp.*	41.28	37.68	34.18	33.85	18.25	15.10	13.30	5.43
wall Lettuce	WALE	*Lactuca muralis*	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00
western bog-laurel	WEBL	*Kalmia microphylla*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
western hemlock	WEHE	*Tsuga heterophylla*	34.60	34.73	37.08	45.25	15.43	12.45	12.23	9.35
western rattlesnake-root	WERR	*Prenanthes alata*	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00
western yew	WEYE	*Taxus brevifolia*	0.60	0.75	0.75	1.13	0.38	0.93	0.28	1.03
yellow cedar	YECE	*Chamaecyparis nootkatensis*	0.40	0.00	0.00	0.00	0.15	3.13	0.10	0.13

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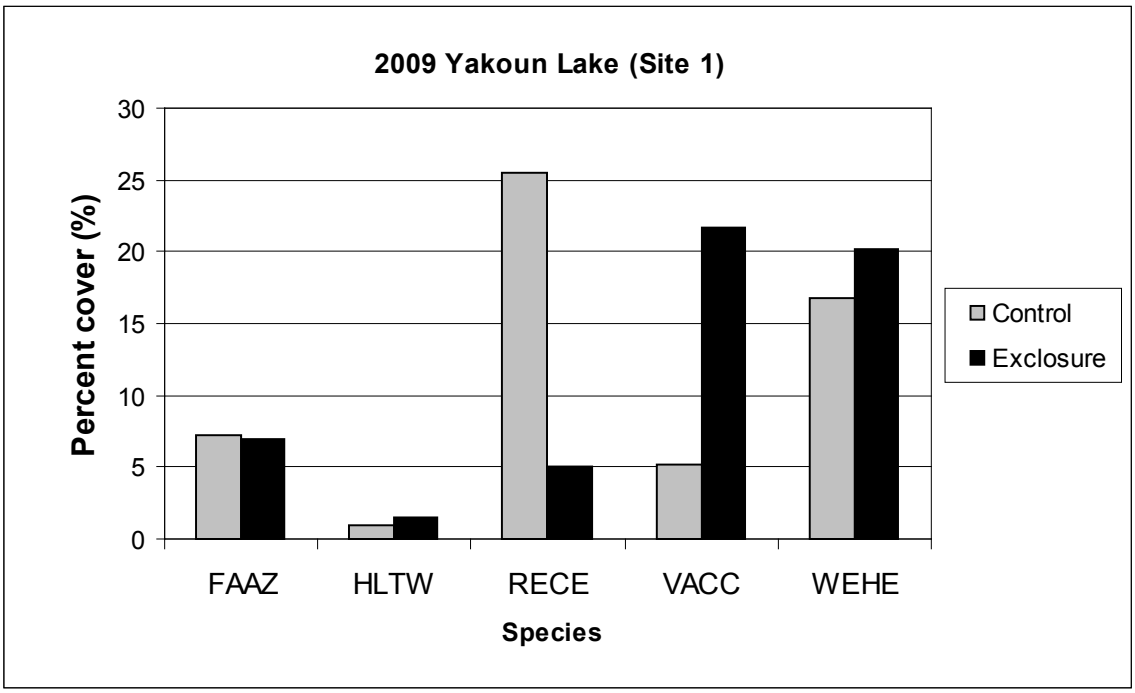
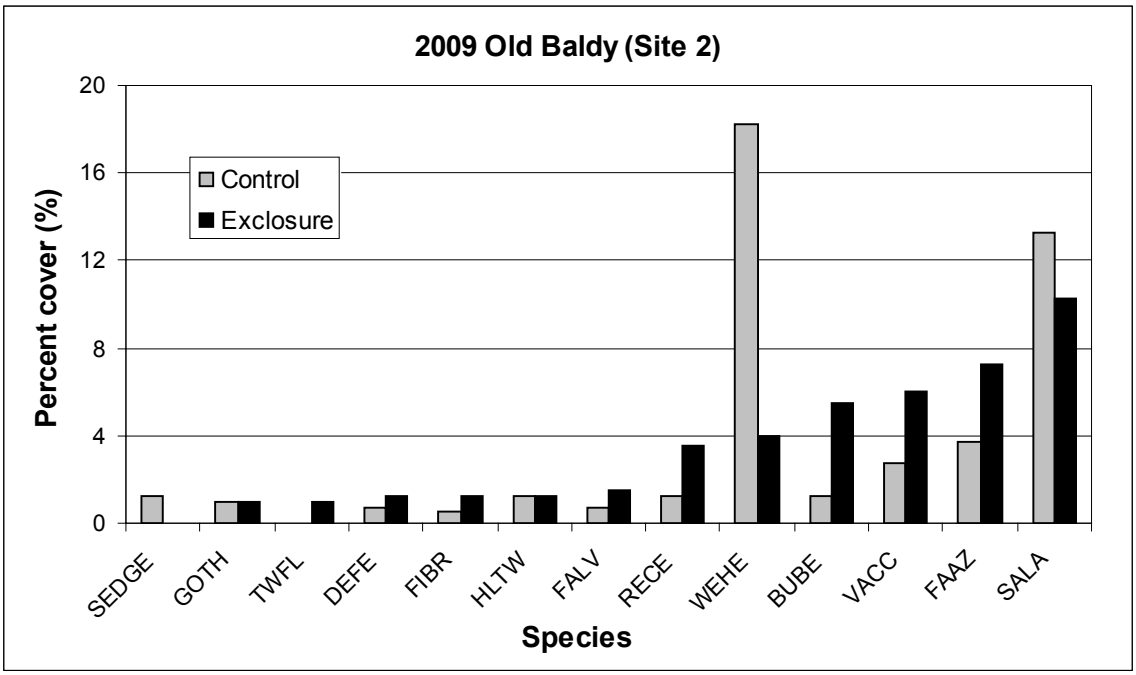
Appendix II. Graphs showing the average percent cover of each species at each site in 2009 in the exclosures and the control plots.

Note: Only species with more than 0.5% cover were included in the graphs. The average percent cover was calculated by calculating the sum of the percent cover in all height strata and then taking the average of the two exclosures and control plots at each site.





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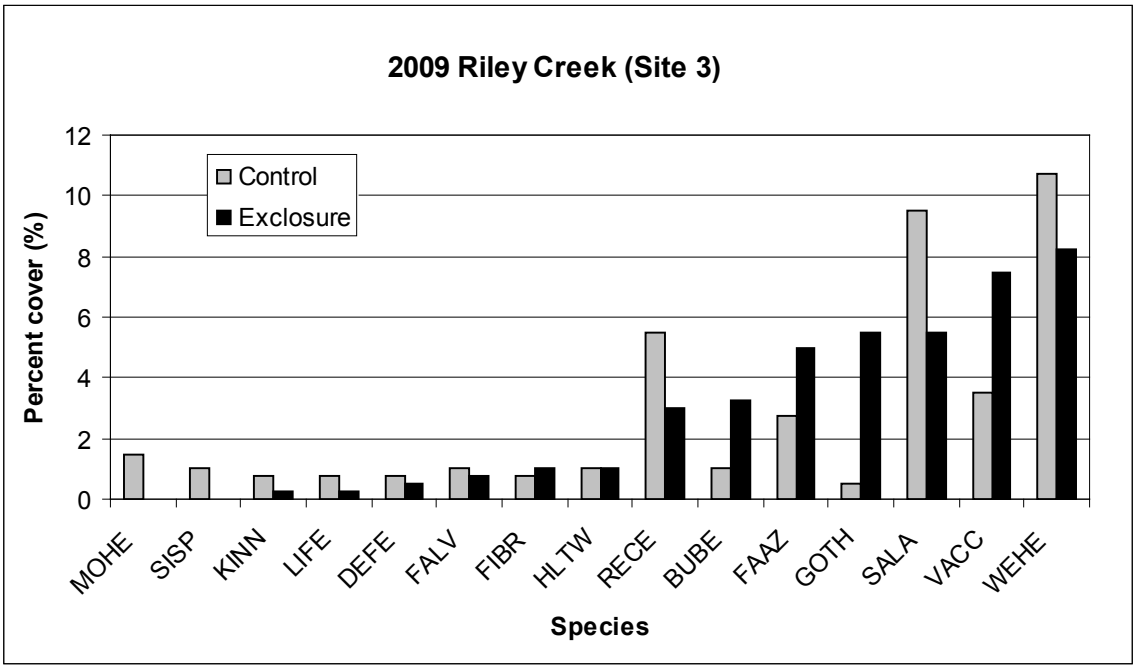

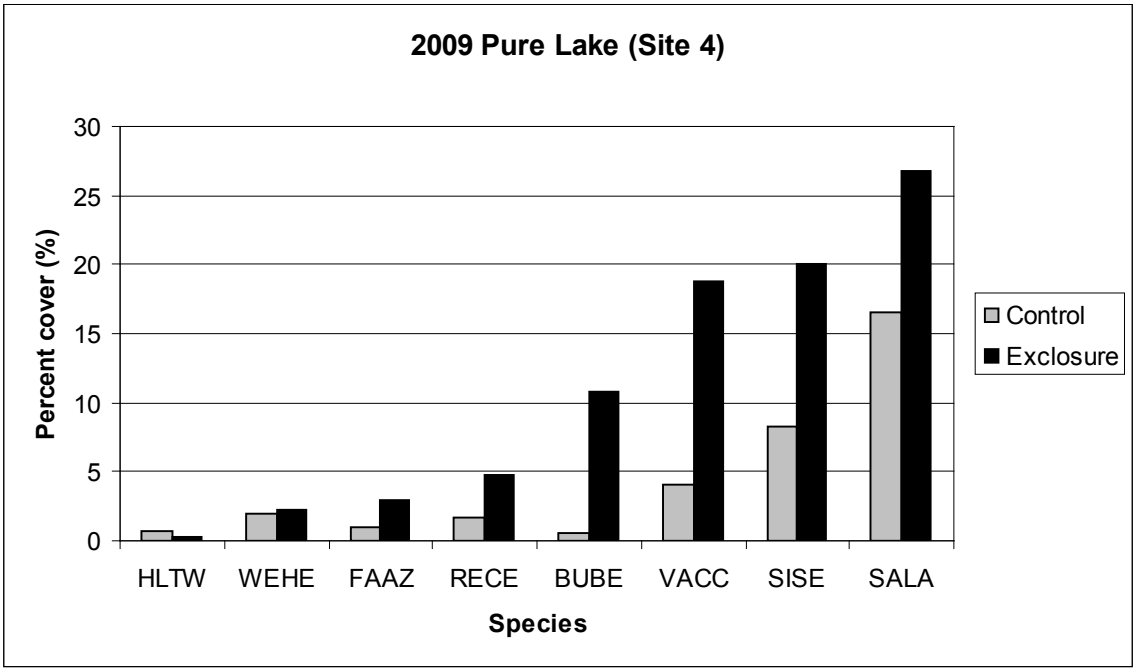

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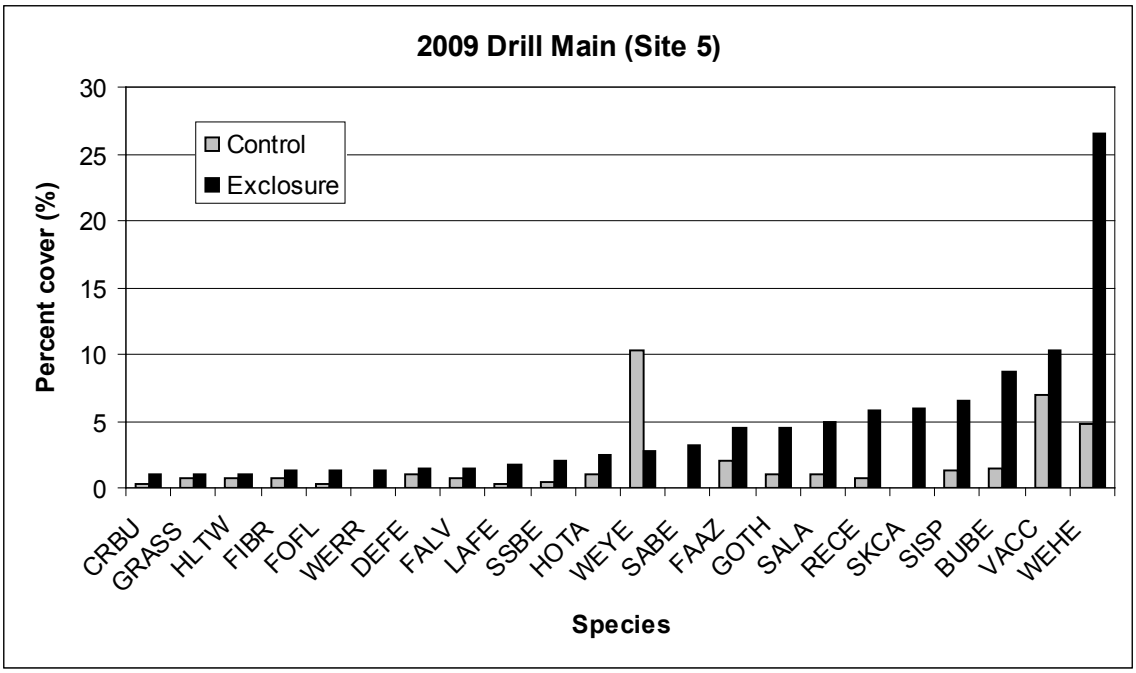

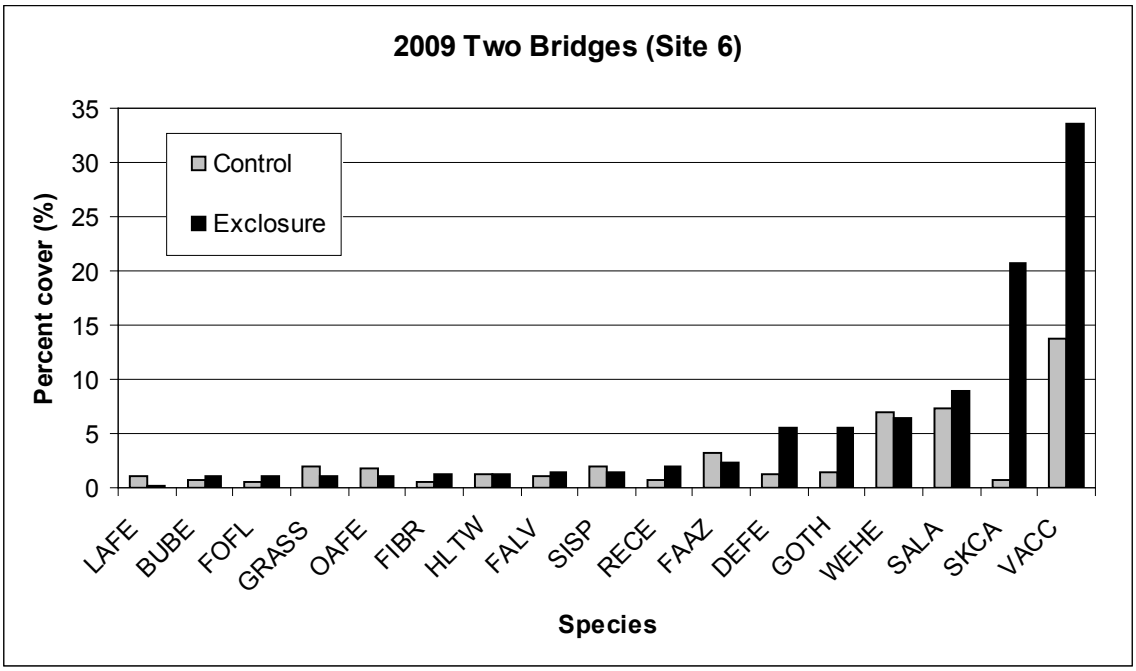

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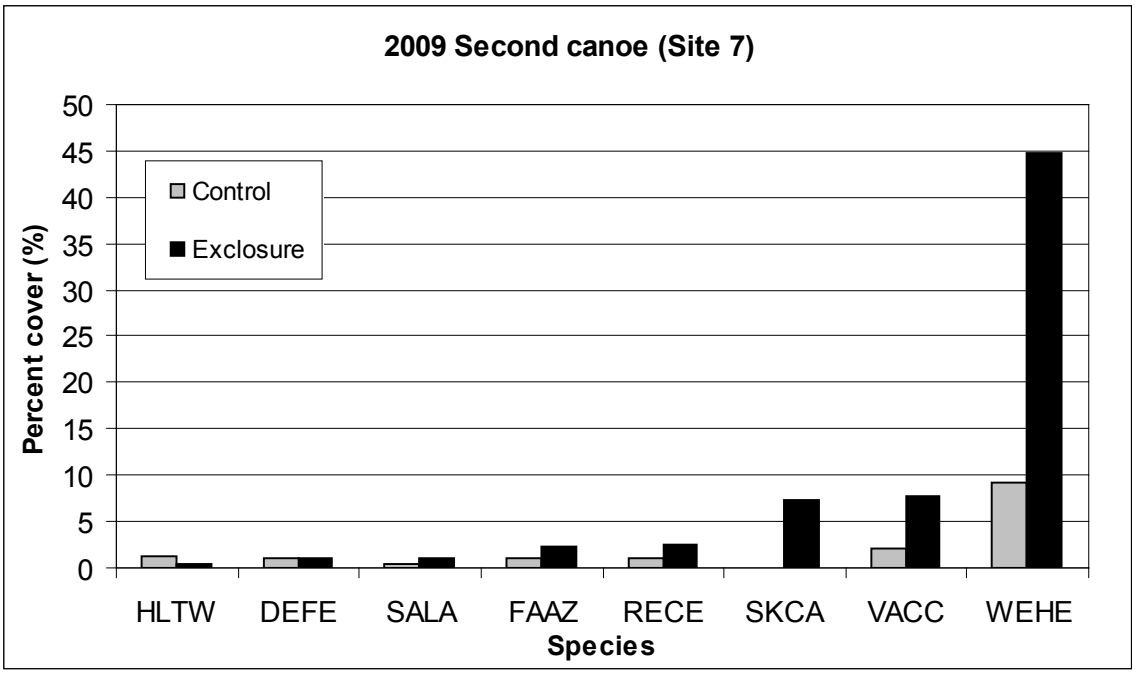

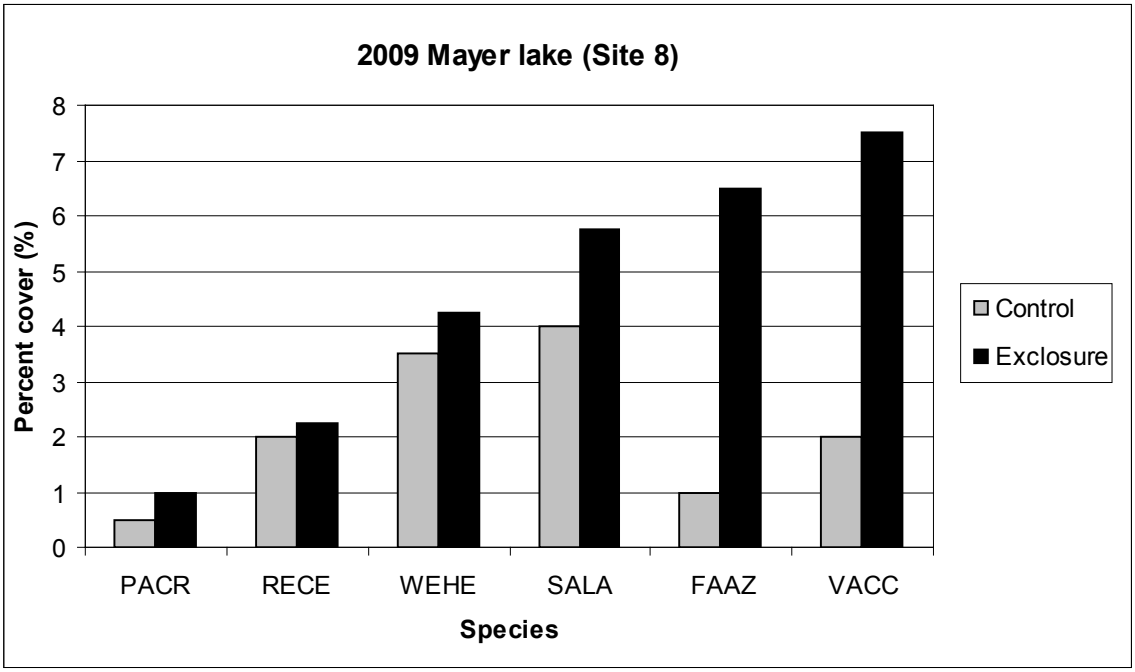

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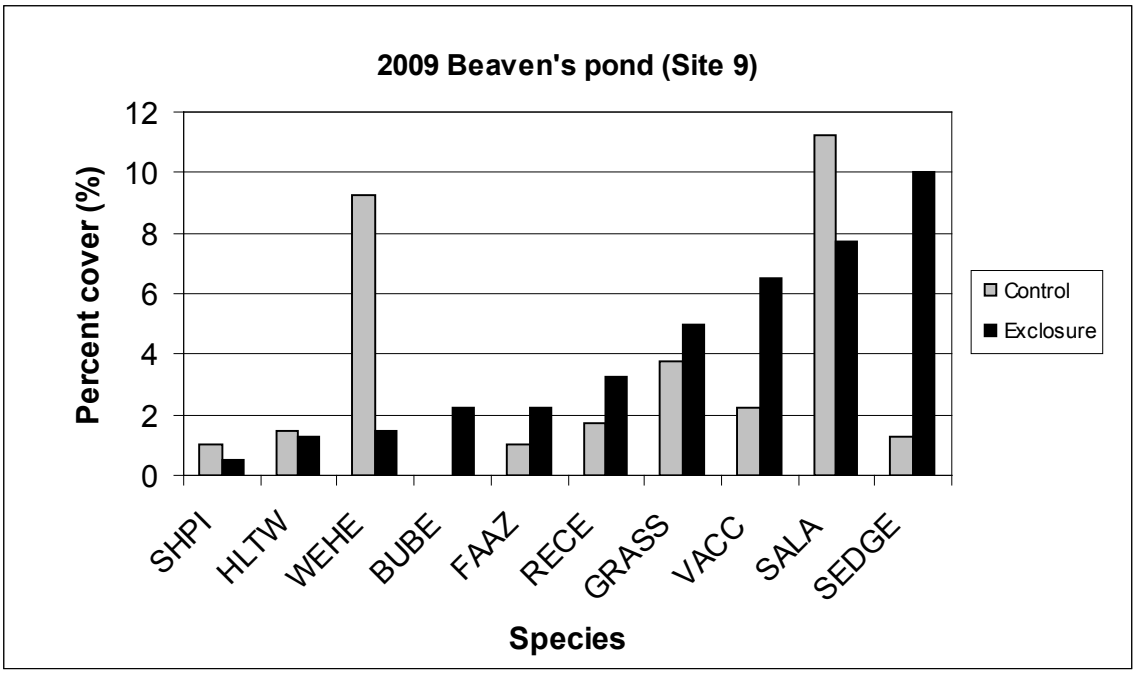

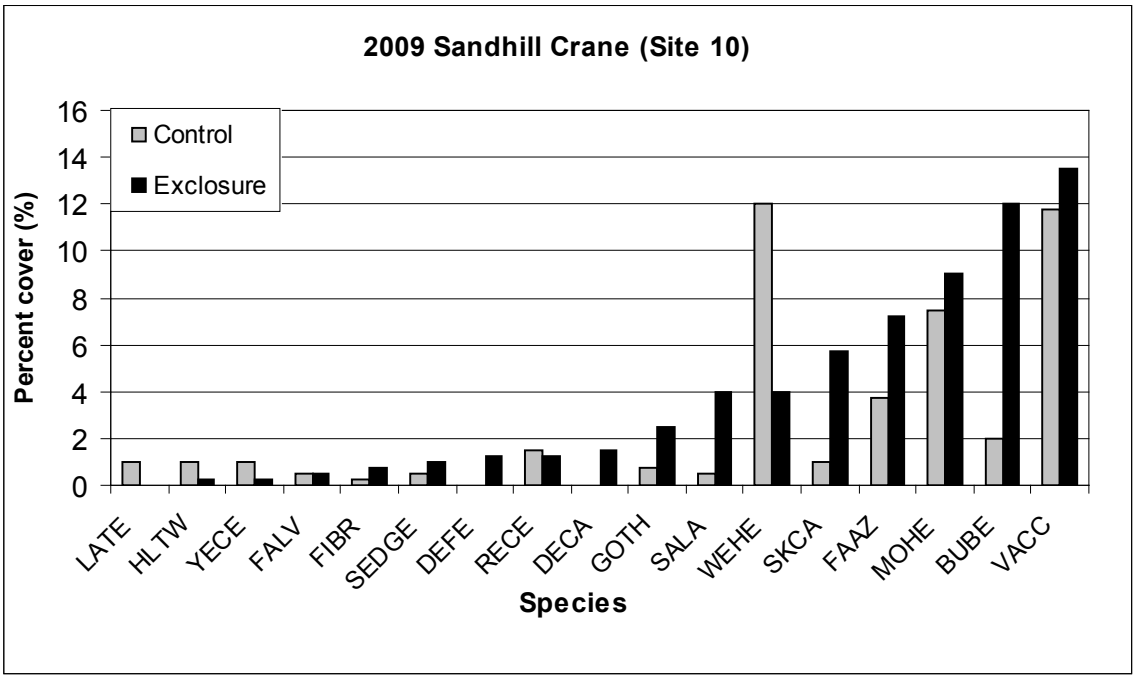

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Appendix III. Site numbers, names and locations of exclosures on Graham Island.

Site number	Site name	Latitude	Longitude
1	Yakoun Lake	53,35335	-132,2806722
2	Old Badly	53,3901297	-132,4861549
3	Riley Creek	53,3892	-132,488156
4	Pure Lake	53,8685286	-132,0826333
5	Drill Main	53,4381149	-132,2365977
6	Two Bridges	53,3813111	-132,2904794
7	Second Canoe	53,5969711	-132,2703616
8	Mayer Lake	53,6407543	-132,05812
9	Beavens Pond	53,6482512	-132,0988329
10	Sandhill Crane	53,3085456	-132,1497464

Note: Although there are two exclosures at each site, the GPS coordinates were only included for the first exclosure, as they are close together.

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