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THE EFFECT OF INTRODUCED SITKA BLACK-TAILED DEER, *ODOCOILEUS HEMIONUS SITKENSIS* MERRIAM, ON THE FOREST UNDERSTOREY PLANT COMMUNITIES OF HAIDA GWAII, BRITISH COLUMBIA: PATTERN, PROCESS, AND RECOVERY

IMPACT DE L'INTRODUCTION DU CERF-À-QUEUE NOIRE *ODOCOILEUS HEMIONUS SITKENSIS* SUR LES COMMUNAUTÉS DE PLANTES DU SOUS-ÉTAGE FORESTIER DE HAIDA GWAII, COLOMBIE BRITANNIQUE : MODÈLE, PROCESSUS, RÉTABLISSEMENT

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Abstract

The introduction of Sitka black-tailed deer, *Odocoileus hemionus sitkensis* Merriam, to Haida Gwaii (Queen Charlotte Islands, B.C., Canada) in the late 19th century provides a valuable opportunity to understand the long-term effects of deer populations on the vegetation of the North American temperate rain forest. We conducted two island-based experiments to investigate the effect of Sitka black-tailed deer on the forest understorey vegetation of this archipelago. In the first experiment we used a set of seven small islands (<15 ha) with different browsing histories (more than 50 years of deer presence, less than 20 years of deer presence, and no evidence of any deer presence) to test the effects of deer on plant cover, species richness and community composition. Browsing history was inversely proportional to both vegetation cover and plant species richness. Modification of the forest understorey plant communities followed a series of steps towards a greatly simplified community of plants possessing mechanisms to keep developing plant tissue inaccessible to deer. In the second experiment we utilized the cull of Sitka black-tailed deer from two large islands (295 ha and 170 ha) to investigate the release of forest plant communities from deer browsing. Using a paired-island approach, deer were culled on two experimental islands but remained on three adjacent control islands. Clear increases in species richness and cover as well as changes in the community composition of the forest understorey of experimental islands in the five years following the initiation of culls suggested a quick return to the forest understorey communities thought to exist before deer modification. However, failure of key shrub species to establish, coupled with the development of closed canopy stands of Sitka spruce, *Picea sitchensis*, suggests possible alternate stable-states for some communities.

Résumé

L'introduction du cerf-à-queue noire Sitka *Odocoileus hemionus sitkensis* sur Haida Gwaii (Iles de la Reine-Charlotte) à la fin du 19ème siècle nous permet de comprendre les effets à long terme des populations de cerfs sur la végétation de la forêt tempéré de l'Amérique du Nord. Nous avons mené deux expériences sur l'île destinées à analyser l'impact du cerf à queue noire sur la végétation du sous-étage forestier de cet archipel. La première expérience a été conduite sur un groupe de sept petites îles (<15 ha), qui se différenciaient au niveau de leur histoire de grands herbivores exploitant les forêt s (plus de 50 ans de présence de cerfs, moins de 20 ans de présence de cerfs et aucun signe de présence de cerfs) pour évaluer les effets du cerf sur le couvert végétal dans trois domaines: couvert végétal, diversité d'espèces et composition des communautés. L'histoire de broutage de la forêt par l'herbivore est inversement proportionnelle à la fois à la richesse du couvert végétal et à la diversité des espèces de plantes. Des modifications dans les communautés de plantes du sous-étage ont développé une série d'adaptation par étapes aboutissant à une communauté de plantes considérablement simplifiée s'étant dotée des mécanismes particuliers destinés à rendre inaccessible leur jeune tissu végétal au broutage des cerfs. Dans la deuxième expérience, nous avons profité de l'abattage de cerf à queue noire pour analyser le soulagement des communautés de plantes par rapport au broutage des cerfs. Une méthode comparative sur cinq îles d'histoire différente a été utilisée: sur deux d'entre elles, les cerfs avaient été abattus; sur les trois autres (îles expérimentales), la population de cerfs avait été maintenue (îles de référence) Sur les îles expérimentales, dans les cinq années suivant l'abattage, l'augmentation importante dans la diversité d'espèces et la densité du couvert végétal ainsi que des modifications dans la composition des communautés du sous-étage suggèrent un retour rapide aux communautés du sous-étage censées avoir existées avant la présence des cerfs. Cependant, l'absence notoire de certaines espèces principales de buissons et le développement concomitant chez l'épicéa Sitka, *Picea sitchensis,* de groupements à voûte fermée suggèrent que pour quelques communautés, il existe un état alternatif de stabilité.

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Contributions and Collaborators

The first chapter in this thesis was written as an article for publication with collaboration from Sylvain Allombert[1], Jean-Louis Martin[1] and Anthony J. Gaston[2]. Interior plots used in this study were originally established by Sylvain Allombert in 1999. These plots were sampled in 2000 with the assistance of Research Group on Introduced Species[3], RGIS, research assistant, Liann Bobechko, using the protocol described in chapter one. Statistical analysis of the data (GLMM) was performed with the assistance of Jean-Louis Martin. Collaboration on the text of various drafts of this article occurred between Jean-Louis Martin, Anthony J. Gaston and Stephen A. Stockton from 2000 to 2003.

The second chapter of this thesis was also written as an article for publication. Collaboration on the text of various drafts of this article occurred between Jean-Louis Martin, Anthony J. Gaston, and Stephen A. Stockton in 2003.

The third chapter of this thesis was again written as an article for publication. Collaboration on the text of various drafts of this article occurred between Anthony J. Gaston and Stephen A. Stockton in 2002 and 2003. Permanent plots used in this study were originally established by Jean-Louis Martin in 1995. Sampling of vegetation in 1997 and 1998 was conducted by Anthony J. Gaston and RGIS research assistants, Robert Kelly and Isabel Buttler. Sampling of vegetation in 1999 was done with the assistance of RGIS research assistants, Isabel Buttler and Liann L. Bobechko. Sampling of vegetation in 2000 and 2001 was done with the assistance of RGIS research assistant, Liann Bobechko. Exclosures were erected by RGIS research assistants, Robert Kelly and Isabel Buttler in 1998.

Appendix five consists of a research note submitted to the *Canadian Field-Naturalist*, authored by Stephen A. Stockton, Liann Bobechko, Isabel Buttler, and Joanna L. Smith[4]. Observations in this note were made with the help of Liann Bobechko and built on previous observations in the same region by Isabel Buttler and Joanna L. Smith.

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Contents

Figures

Chapter 1

Chapter 1 continued

Chapter 2

Chapter 2 continued

Chapter 3

Chapter 3 continued

Chapter 3 continued

Chapter 3 continued

Appendices

Tables

Chapter 1

Chapter 2

Chapter 2 continued

Chapter 3

Chapter 3 continued

General Introduction

Over the past century, deer populations have greatly increased in North America, Europe and around the world (Alverson et al. 1988, Stewart and Burrows 1989, Warren 1991, Shimoda et al. 1994, McCabe and McCabe 1997, McShea et al. 1997, Gill 1999, Nomiya et al. 2003). As populations have grown, deer have been implicated as key species in the modification of many forest ecosystems (Sullivan et al. 1990, Diamond 1992, Hester et al. 1991, Baines et al. 1994, Waller and Alverson 1997, Rooney 2001).

The modification of eastern forests in North America by white-tailed deer, *Odocoileus virginanus*, has been extensive and well documented (Frelich and Lorimer 1985, Alverson et al. 1988, Tilghman 1989, Waller and Alverson 1997, McShea et al. 1997). In eastern forests, deer impacts have been influenced by the extirpation of the principal non-human predators, wolves, *Canis lupus* L., and cougars, *Puma concolor* L., and extensive anthropogenic modification of the forests themselves since the 1700s (Braun 1974) improving and expanding the habitat for white-tailed deer (Alverson et al. 1988, Waller and Alverson 1997).

Large-scale changes to the temperate rain forest of North America have occurred mainly in the last century (Schoonmaker et al. 1997, Ricketts et al. 1999) and much of the remaining temperate rain forest, north of 48° N latitude, continues to support viable predator populations (Harbo and Dean 1983, Kirchoff 1991). Consequently, the modification of temperate rain forest by Columbia black-tailed deer, *Odocoileus hemionus columbianus*, and Sitka black-tailed deer, *O. h. sitkensis*, appears to be less widespread relative to eastern forests and has received much less attention (but see Klein 1965, Pojar et al. 1980, Wiggins 1999). However, the continued modification of this

region promises to bring about conditions similar to eastern forests (Ricketts et al. 1999). Over the last century the temperate rain forest has been reduced to only 44% of an estimated original extent of 25 million hectares (Schoonmaker et al. 1997). Proposed conservation plans for the forests of British Columbia aim to maintain viable populations of both deer and their predators while continuing to modify the landscape through forestry, agriculture and road construction (Province of British Columbia 2001). The temperate rain forest of North America is considered a conservation priority, consisting of globally rare habitat requiring immediate protection and extensive restoration (Ricketts et al. 1999). Clarification of the role that deer play in the modification of this forest may be necessary for targeting conservation efforts in this region.

The modification of the temperate rain forest of Haida Gwaii by Sitka black-tailed deer *O. h. sitkensis* provides an unusually clear example of the potential of deer to modify this forest system. Sitka black-tailed deer were introduced intentionally to Haida Gwaii in the late 1800s (Osgood 1901, Munro 1935). Since that time the population has greatly expanded and deer now densely populate all but the most remote islands of the archipelago (Pojar et al. 1980). Three key factors contribute to the pattern of deer modification on this archipelago.

Firstly, deer possess no predators on these islands, with the exception of humans and black bears, *Ursus americanus carlottae*, which occasionally kill young fawns (Pojar et al. 1980). Because of this extremely low predation rate, deer population densities on Haida Gwaii are unusually high for coastal British Columbia (Sharpe 1999).

Secondly, the vegetation and climate of Haida Gwaii is largely similar to that of adjacent Southeast Alaska (Banner et al. 1989) but the flora is relatively impoverished

with only 665 recorded vascular plant species (Lomer and Douglas 1999). The mainland flora consists of over 2300 vascular plant species (Douglas et al. 1998). The emerging pattern of deer modification on Haida Gwaii serves as a simplified model for understanding the more complex systems on the mainland (*sensu* Wallace 1880, 1998)

Thirdly, Sitka black-tailed deer constitute the only large herbivore over most of the archipelago. Three other deer species are either present now or have been present in the past, but only over limited areas. Wapiti, *Cervus elaphus nelsoni*, introduced in the 20th century, presently occurs only in restricted areas of Graham Island (Sean Sharpe pers. comm.). European red deer, *Cervus elaphus elaphus*, introduced in 1920, was entirely eliminated by 1944 and was similarly restricted to Graham Island (Cowan 1989). The only indigenous ungulate, Dawson caribou, *Rangifer tarandus dawsoni*, went extinct in the early 1900s and is also thought to have been restricted to upland habitat on Graham Island (Cowan 1989). Consequently, Sitka black-tailed deer face little to no competition for resources (Sharpe 1999) and identifying the effect of deer browsing proves a relatively easy task (Englestoff 2001).

In order to provide effective management alternatives for this region, an understanding of the deer-forest dynamic needs to be developed (Gaston et al. in press). The three chapters which follow investigate the effect of deer on the vegetation of the forest understorey of Haida Gwaii by measuring the effect of deer on vascular plant diversity, cover and composition, revealing the process that determines this developing pattern and examining the recovery of the deer-modified forest understorey after the removal of deer. The first chapter discusses the first half of the results of a natural experiment (*sensu* Diamond 1983), utilising a set of seven small islands (<16 ha) with

different browsing histories, to determine the pattern of effect of deer on plant cover and species richness in the understorey of forests on Haida Gwaii. The second chapter discusses the second half of the results from this natural experiment, examining the process of deer modification of the forest understorey. This chapter focuses on the differential effect of deer on different plant types, identifying response patterns for each vascular plant species and key morphological attributes. The third chapter discusses the results of a large-scale manipulative experiment, documenting the change in plant cover and species richness, before and for the first five years of an ongoing deer cull on two medium sized islands (295 ha and 170 ha) in Haida Gwaii.

This may be a critical point in time for the conservation of existing biodiversity in the temperate rain forest biome and this study offers to reveal relationships which may be important in guiding conservation efforts. The study also offers to make a potentially significant contribution to ecological theory, both in terms of the understanding of general plant-herbivore dynamics and specific considerations pertaining to the temperate rain forest system. In light of the current understanding of these dynamics and the debate surrounding them (Belsky 1986), such a clear look may be extremely useful to future conservation and management efforts (Gaston et al. in press).

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Chapter 1:

pattern of deer modification

in the forest understorey

1 Abstract

The introduction of *Odocoileus hemionus sitkensis* Merriam (Sitka black-tailed deer) to Haida Gwaii (Queen Charlotte Islands, B.C., Canada) in the late 19th century, provides a valuable opportunity to understand the long-term effects of deer populations on the vegetation of the North American temperate rain forest in the absence of their natural predators wolves, *Canis lupus* L., and cougars, *Puma concolor* L. Using a set of seven small islands with different browsing histories (more than 50 years, less than 20 years, and no deer presence) we tested the long-term effects of uncontrolled deer populations on plant cover and species richness in the understorey of forest interior and forest edge habitats. Browsing history was inversely proportional to both vegetation cover and plant species richness. The difference was most pronounced for the species-rich edge communities and among herb and shrub species. Our results demonstrate that, in the absence of predators, deer have the potential to greatly alter North American coastal forest ecosystems. As forests around the world lose predator species and become increasingly fragmented, our findings provide an important benchmark of how forests can be severely altered by increasing deer populations.

2 Hypothesis

Over time, predator-free deer reduce the cover of vegetation and the plant species richness of the forest understorey.

3 Introduction

Deer populations, unregulated by natural predators, have become a major factor controlling forest ecosystem dynamics in many parts of North America (Sullivan et al. 1990, Diamond 1992) and Europe (Hester et al. 1991, Baines et al. 1994, Gill 1999). As deer overabundance becomes evident in North America (McShea et al. 1997) a clear understanding of the long-term consequences for plant diversity becomes increasingly important.

Many studies have demonstrated the effects of high white-tailed deer, *Odocoileus virginianus* Zimmerman, population densities on the vegetation of the eastern hardwood forests of North America. White-tailed deer have been implicated in the reduced abundance and diversity (Frelich and Lorimer 1985, Alverson et al. 1988, Tilghman 1989, deCalesta 1997a, deCalesta 1997b, Waller and Alverson 1997, McShea and Rappole 2000) and in some instances the extirpation of woody plant species from these forests (Hough 1965, Whitney 1984, Rooney and Dress 1997a). They have been associated with a shift in plant community composition from shrubs and forbs to grasses and ferns (Horsley and Marquis 1983) and the reduced frequency of many plant species listed as threatened or endangered (Miller et al. 1992, Anderson 1994, Rooney and Dress 1997a, Augustine and Frelich 1998). Fewer studies have examined the effects of mule deer, *Odocoileus hemionus* Rafinesque (McArthur et al. 1988, Singer and Renlon 1995), Columbia black-tailed deer, *Odocoileus hemionus columbianus* Richardson (Sullivan et al. 1985, Woodward et al. 1994) or Sitka black-tailed deer, *Odocoileus hemionus sitkensis* Merriam (Klein 1965, Pojar et al. 1980), on western forests, although both

white-tailed and black-tailed deer are known to become overabundant with reduced predation (Leopold 1943, McCullough 1997, Rooney 2001).

Eastern hardwood forests, where deer impacts have in part increased because of the extirpation of the principal non-human predators, wolves, *Canis lupus* L., and cougars, *Puma concolor* L., have undergone extensive modification since the 1700s (Braun 1974), improving and expanding the habitat for white-tailed deer (Waller and Alverson 1997). In contrast, most of the remaining western coastal forest, north of 48° N latitude, continues to support predator populations (Harbo and Dean 1983, Kirchoff 1991). However, coastal western forests have undergone extensive habitat modification of their own in the past century (Schoonmaker et al. 1997, Rickets et al. 1999) and the predator-prey relationship in this region is highly susceptible to habitat modification (Person et al. 1996). Proposed conservation plans aim to maintain viable populations of both deer and their predators (Province of British Columbia 2001), but failure to do so may result in large-scale changes to the vegetation of this region.

The Haida Gwaii archipelago is an anomaly in this region, possessing neither native deer, nor wolves or cougars (Cowan 1989). As such, the introduction of deer to these islands in the late 1800s (Osgood 1901, Munro 1935) provides a rare opportunity to study the effects of predator-free deer in previously unmodified habitat for known durations of time. As deer spread through this archipelago, islands were colonized at different times, providing a *natural laboratory* (*sensu* Diamond 1983, A.R. Wallace in Whittaker 1998) with a gradient of deer effect. We studied one of these island groups, occurring in Laskeek Bay, with similarly sized islands, covered with previously unmodified primary forest, to investigate the long-term effects of predator-free deer browsing on vegetation

cover and plant species richness. The island group consisted of two islands with evidence of deer for more than 50 years, two with evidence of deer for less than 20 years and three with no evidence or history of deer presence (Vila 2002). We tested differences in the cover of vegetation and species richness at different durations of deer presence.

4 Methods

4.1 Study area

The temperate rain forest of North America occurs on the Pacific coast from northern California to Alaska and is chiefly defined by a large oceanic influence, moderate temperatures and heavy, year-round precipitation (Alaback 1990). Over the last century this biome has been reduced to only 44% of an estimated original extent of 25 million hectares, with most of the remaining forest occurring north of 48° N (Schoonmaker et al. 1997). The temperate rain forest of North America is considered a conservation priority, consisting of globally rare habitat requiring immediate protection and extensive restoration (Ricketts et al. 1999).

The Haida Gwaii archipelago (Queen Charlotte Islands) of British Columbia, situated 80 km west of the mainland of British Columbia and 50 km south of the Alexander Archipelago of Alaska, occurs within the perhumid temperate forest zone of the coastal temperate rain forest (Alaback and Pojar 1997) and is the largest and most isolated archipelago on the west coast of Canada. The archipelago contains a significant portion of the remaining temperate rain forest (Alaback and Pojar 1997); over 540,000 hectares of intact temperate rain forest, over 230,000 hectares of it within protected areas (Rickets et al. 1999). The vegetation of these islands is largely similar to that of adjacent

Southeast Alaska (Banner et al. 1989) but the flora is relatively impoverished with only 665 recorded vascular plant species (Lomer and Douglas 1999), including six endemic species and five more endemic infraspecific taxa (Taylor 1989). The mainland flora consists of over 2300 vascular plant species (Douglas et al. 1998). The fauna of the archipelago is also impoverished, relative to the mainland (Rickets et al. 1999), and includes a variety of endemic taxa, including four endemic subspecies of birds (another four subspecies are shared with the mainland and islands in the immediate vicinity) and seven endemic subspecies of mammals (Cowan 1989). However, this region is free of major non-human deer predators (Cowan 1989). Hence, the deliberate introduction of Sitka black-tailed deer to these islands in the late 19th century (Osgood 1901, Munro 1935) created a situation where deer populations, unconstrained by predators, affected large areas of temperate rain forest (Sharpe 1999).

Laskeek Bay is situated on the east coast of Haida Gwaii (Fig. 1) and contains 15 islands of various size and proximity. The seven islands included in our study: Haswell, West Limestone, West Skedans, South Skedans, Low, South Low and Lost, were selected to control, as much as possible, for island area and to include islands affected by deer for three different durations. They are located within 17 km of one another and range in area from 4.5 ha to 16 ha (Table 1). West Limestone Island, West and South Skedans Islands, and South Low and Low Islands are part of a British Columbia Wildlife Management Area while Lost Island falls within the northeastern perimeter of Gwaii Haanas National Park Reserve and Haida Heritage Site. None of the seven has been commercially logged and all maintain primary forest cover.

4.2 Sitka black-tailed deer

In the years following the first introduction of Sitka black-tailed deer to Haida Gwaii, the population expanded greatly and spread naturally, but also with the aid of various individuals and agencies (Munro 1935), until it colonized all but the most remote islands of the archipelago (Pojar 1999). On East Limestone Island (Laskeek Bay, see Fig. 1), the density of deer was determined to be 33.3 deer km^{-2} based on a direct count in the summer months (Daufresne and Martin 1997). On Reef Island, also in Laskeek Bay, 84 deer were culled over five years from 1997 to 2001, revealing a density of over 33 deer km^{-2}. A parallel cull on S'Gaang Gwaii, an island at the southern tip of the archipelago, revealed a density of over 32 deer km^{-2}.

4.3 Evidence of deer presence

Estimation of the duration of deer presence on the different islands in Laskeek Bay (Table 1) was obtained through the comparative analysis of shrub stem age structures and by dating the earliest fraying scars (created by deer rubbing their antlers on trees), through tree ring measurement (Vila 2002, Vila et al. submitted a and b).

Four, 2- by 130-m deer pellet transects (Bennett et al. 1940) were conducted to assess the density of deer pellet groups on each of the seven study islands, as well as on the larger East Limestone Island. To determine the relative deer density on each island, pellet group density was compared to the pellet group density of East Limestone Island where deer density was previously determined through direct count (Daufresne and Martin 1997).

4.4 Habitat types and study plots

We recognized two distinct habitat types on these islands: the forest edge and the forest interior. These differed principally in available light and exposure to wind and salt-spray (Calder and Taylor 1968). The composition of understorey vegetation in the two habitat types was quite different. A greater component of herbaceous species, many with conspicuous flowers, occurred at the forest edge and a larger component of shade-tolerant shrub species occurred in the interior. The transition between these zones usually occurred within 25 m of the high-tide line. Because small islands such as these inherently possess a high edge-to-interior ratio, we sampled each island with ten randomly spaced 10-m radius circular plots along the forest edge (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), sampling 3-10% of each island. All plots were placed at least 50 m from one another. As light availability within the interior was largely a function of canopy cover, we chose interior plot sites to control for differences in light availability between islands. Vegetation did not exceed 400 cm in the forest edge so no such precaution was taken in selecting edge plots.

4.5 Measurement of understorey vegetation

Vascular plant species were identified according to Pojar and MacKinnon (1994), and verified with Hitchcock and Cronquist (1973). The percent cover of each species, as well as the total cover of vegetation in each of three strata, was estimated using standard spot charts (Mueller-Dombois and Ellenberg 1974). Strata (Fig. 2) were set at heights of: 0-50 cm, 50-150 cm, and 150-400 cm. These heights were chosen to highlight the effects of the deer, which are known to feed primarily upon vegetation below 150 cm (Martin and

Daufresne 1999) and to capture and compare different elements of understorey plant communities.

Vegetation sampling and pellet group transects were conducted in 2000, throughout the month of July, the period of maximum cover of herbaceous plants in this region.

4.6 Species richness at multiple scales

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

4.7 Statistical analysis

We used a general linear mixed-model, GLMM (GENMOD procedure of SAS, release 6.09, 1993) to test the effect of deer presence (tested at the level of islands), *habitat* type (edge or interior) and of their interaction on vegetation cover in different strata and on plot species richness. *Islands* were considered a random effect nested in the fixed effect of *browsing history* (three durations of deer browsing). For the analyses of the effects of these explanatory variables on vegetation cover we transformed percent cover values with an arcsine transformation (Sokal and Rolf 1995) and fitted the transformed values to a GLMM with log-link function and a gamma error term. Species counts per plot were fitted to a GLMM with a log link function and a Poisson error term. Chi-squared tests were conducted to test the heterogeneity of island totals and to test for any difference in effect in edge and interior habitat.

5 Results

5.1 Deer density

Current deer density was estimated at greater than 20 deer km^{-2} on all islands with a history of deer presence (Table 1).

5.2 Browsing history and the cover of vegetation

0- to 50-cm stratum – *Browsing history* had a highly significant effect on the cover of vegetation in the first stratum (Table 2). Cover was lowest on the islands with greater than 50 years of deer browsing and greatest on islands with no history of deer browsing (Figs. 3 and 4). There was significant variation in cover between *islands* with the same *browsing history* (Table 2). However, analysis of parameter estimates within the GLMM

showed that this effect was the result of significant variation in cover between islands with greater than 50 years of browsing ($P<0.001$; Figs. 3 and 4). Neither the variation in cover between islands with less than 20 years of browsing nor the variation in cover between islands with no history of deer browsing was significant. Cover of vegetation below 50 cm was significantly different between the forest interior and edge *habitat* types (Table 2). The interaction of *habitat* type with *browsing history* had a significant effect on cover (Table 2). On islands with no history of deer browsing and on islands with over 50 years of deer browsing, vegetation cover in the 0- to 50-cm stratum was slightly greater on average in edge plots (Figs. 3 and 4). On islands with less than 20 years of deer browsing, vegetation cover in the 0- to 50-cm layer was greater on average in interior plots (Figs. 3 and 4).

50- to 150-cm stratum – *Browsing history* also had a highly significant effect on vegetation cover in the second stratum (Table 2). Cover was again lowest on islands with greater than 50 years of deer browsing and greatest on islands with no history of deer browsing (Figs. 5 and 6). We again observed highly significant variation in cover between *islands* with the same *browsing history* (Table 2) and again this observation was explained by a significant effect of *island* on vegetation cover among islands with greater than 50 years of browsing ($P<0.001$; Figs. 5 and 6). *Habitat* type, independent of *browsing history*, had no significant effect on the cover of vegetation in this stratum, however the interaction of *habitat* with *browsing history* was significant (Table 2). On islands with no history of deer browsing and on islands with less than 20 years of deer browsing, cover was much greater in interior plots than in edge plots. In edge plots, the effect of deer browsing on vegetation cover was strong on all islands with deer, whereas

for interior plots the effect of deer browsing was pronounced only on the islands with greater than 50 years of browsing (Figs. 5 and 6).

150- to 400-cm stratum – *Browsing history* had a significant effect on the cover of vegetation in the highest stratum we included in the GLMM (Table 2). In contrast to the two previous strata, there was no significant effect in this stratum of *islands* with the same *browsing h*istory. *Habitat* did have a significant effect in this stratum (Table 2), but the interaction of *habitat* with *browsing history* did not. On islands with no history of deer browsing and on islands with less than 20 years of browsing, cover was again much greater in interior plots than in edge plots. In contrast to the first two strata, a linear effect of *browsing history* on vegetation cover was observed only for forest interior plots (Figs. 7 and 8).

5.3 Browsing history and the cover of different plant types

Herbs – *Browsing history* had a highly significant effect on the cumulative cover of all herbaceous species below 150 cm (Table 3). Herb cover was inversely proportional to the duration of deer presence on islands (Figs. 9 and 10). Although herb cover made up of graminoid species was also inversely proportional to deer duration, with the exception of dunegrass, *Elymus mollis*, graminoids showed a more gradual relationship than other herbs (Fig. 10). Dunegrass occurred in abundance on islands without deer but was virtually eliminated on all other islands. In contrast, cover of the remaining graminoid species showed little difference between islands without deer and islands with less than 20 years of browsing, with grass species constituting much of the herbaceous cover the latter pair of islands (Figs. 9 and 10). *Islands* with the same *browsing history* showed no significant effect on herbaceous cover (Table 3), but *habitat* type did have a

significant effect, as did the interaction of habitat with browsing history (Table 3). On islands with no history of deer and islands with deer for less than 20 years, herbaceous cover was similar in both habitats, while on islands with deer for more than 50 years it was greater at the edge than in the interior (Figs. 9 and 10).

Shrubs – *Browsing history* also had a highly significant effect on the cumulative cover of all shrub species below 150 cm (Table 3). Shrub cover in the understorey was inversely proportional to the duration of deer presence (Figs. 11 and 12). Islands with the same *browsing history* possessed highly significant variation in shrub cover (Table 3). Analysis of parameter estimates within the GLMM showed that this variation was the result of significant variation between islands with greater than 50 years of browsing ($P<0.001$; Figs. 11 and 12). *Habitat* type, independent of *browsing history*, had no significant effect on the cover of shrubs below 150 cm, however the interaction of *habitat* with *browsing history* was highly significant (Table 3). On islands with no deer and on islands with less than 20 years of browsing, shrub cover was greater in the interior than in the edge, but on islands with more than 50 years of deer browsing, shrub cover was lower in the interior than at the edge (Figs. 11 and 12). From 150 to 400 cm, shrub species contributed little cover in the forest edge but substantial cover in the interior on islands with no deer.

The shrub salal, *Gaultheria shallon*, was the most abundant species on all seven islands and constituted much of the cover of shrubs in the interior habitat type, especially on islands with less than 20 years of browsing (Figs. 11 and 12). A highly significant effect of *browsing history* was recorded for the cover of salal below 150 cm (Table 3). The cover of *Salal* below 150 cm was similar on islands with no deer history and on

islands with deer for less than twenty years but was much lower on islands with deer for more than 50 years (Figs. 11 and 12). Variation between islands nested with the same *browsing history* was not significant, but *habitat* type had a highly significant effect, as did the interaction of *habitat* with *browsing history* (Table 3). Like the total cover of shrubs, the cover of salal was greater in the interior than at the edge on islands with no deer and on islands with less than 20 years of browsing, but was lower in the interior than at the edge on islands with more than 50 years of browsing (Figs. 11 and 12).

Trees – Tree cover below 150 cm varied from island to island independent of *browsing history*, which had no significant effect (Table 3). *Habitat* type also had no significant effect. However, the interaction between *habitat* and *browsing hist*ory was significant (Table 3). On islands with no deer and on islands with more than 50 years of browsing, tree cover below 150 cm was greater in the forest edge than in the forest interior. The pattern was opposite for islands with less than 20 years of browsing (Figs. 13 and 14).

5.4 Browsing history and plant species richness

Plot – *Browsing history* had a significant effect on species number per plot, which was lower on average on islands with deer than on islands without (Figs. 15 and 16; GLMM analysis, Table 4). There was no significant variation in species richness between islands with the same *browsing history* (Table 4). However, *habitat type* did have a significant effect on the number of plant species per plot (Table 4); species richness was significantly greater in forest edge plots than in forest interior plots. A significant interaction between *browsing history* and *habitat* was also recorded (Table 4). Analysis of parameter estimates of the GLMM revealed that edge plots had significantly

more species than interior plots on the islands with no history of browsing ($P<0.001$) whereas on islands with deer, species number were similar in edge and interior plots (Figs. 15 and 16).

Island – The total number of species recorded for each island (15 plots) was inversely proportional to the duration of deer presence (Table 5). However, island totals were not significantly different from one another ($\chi^2=2.24$, df=6, $P=0.90$). Variation among islands in the number of species found within each habitat was greater for edge habitat than interior habitat, but the interaction of *islands* with *habitat* at the island scale was not significant ($\chi^2=8.27$, df=6, $P=0.22$). At a regional scale, the total number of species recorded on the three deer-free islands was 71, exactly the same as the number recorded on the four islands with deer. When non-native species were removed from the comparison, 70 native plant species were recorded for deer-free islands and 65 native species were recorded on islands with deer.

From plot to island – Species accumulation for all seven islands rose quickly for sample sizes of one to four plots (Fig. 17). In samples with more than seven plots pooled, species accumulated far more gradually, demonstrating a satisfactory sampling intensity. The accumulation curves developed in three discrete groups in accordance with browsing history. Islands with no history of deer consistently showed the highest estimates of species richness at all scales. Confidence intervals (95%) for islands with no history of deer showed no overlap with other islands, for the entire span of the curve. For sample sizes in excess of 12 plots, confidence intervals for S.Low and Low Islands failed to overlap, however the confidence limits for both islands overlapped those of Lost Island (also with no history of deer) for the entire span. Species accumulation on islands with

less than 20 years of browsing was consistently greater than species accumulation on islands with more than 50 years of browsing, but the confidence intervals overlapped for small sample sizes.

6 Discussion

Within our study, plant cover and plant species richness were inversely proportional to the duration of deer presence. The effect was greatest in the species-rich forest edge and among shrub and herb species. Our results demonstrate that the long-term effect of predator-free deer on forest vegetation brings about an ecological impoverishment of the forest understorey.

6.1 Variation in the pattern

Three factors appeared to contribute to the difference in the cover of vegetation and the cover of shrubs between islands with deer for more than 50 years, (W.Limestone and Haswell islands): current deer density, surface topography, and a thick moss layer.

The difference in current deer density estimates between these islands (Table 1) indicated greater current browsing pressure on W.Limestone Island than on Haswell Island. Although the variation in deer density over long periods of time is unknown for this region, local fluctuations in deer density are common to most deer populations (Schmidt and Gilbert 1978). The difference may have been further affected by the thick moss layer that occurred on Haswell Island, which appeared to provide limited protection to the numerous shrub seedlings that occurred within it (Stockton and Buttler 2001). The difference may also have been partly due to differences in the surface topography of these two islands. Haswell Island possesses many small cliffs and gullies while W.Limestone

Island possesses few. In parts of deer-affected islands, such as cliffs, where access was difficult for deer, we usually observed a lush and rich variety of vegetation, paralleling the understorey found on islands without deer. A similar deer browse signature has been recorded in heavily browsed eastern North American forests where highly preferred species were restricted to the tops of inaccessible boulders (Rooney 1997). As such, local surface topography may play a key role in the conservation of plant species, with small numbers of individuals existing as *relict species* in areas difficult for deer to access (Pojar et al. 1980). Nevertheless, the differences we observed in cover between these islands failed to translate into differences in species richness, suggesting that differences in the current browsing pressure may be a relatively recent phenomenon.

6.2 Communities on the edge

The strong effect of deer we observed in the forest edge was likely influenced by differences in plant composition and by the intense use of edge habitat by deer. On islands without deer, edge plots possessed more species than interior plots but on islands with deer for less than 20 years the difference between edge and interior plots was no longer evident, signaling the removal of a number of plant species from the forest edge. Edge habitat in the coastal temperate forest usually has a larger component of herbaceous vegetation (Calder and Taylor 1968). Herbaceous plants make up the bulk of deer summer diets (McCaffery et al. 1974, Bunnell 1990) and are highly susceptible to repeated browsing (Miller et al. 1992). Because of the availability of high quality forage and the proximity to security and thermal cover inside the forest, edge habitat has traditionally been regarded as beneficial habitat for deer (Leopold 1933) and as such this

habitat type may, at broad scales, be subject to increased herbivory (Alverson et al. 1988).

Vegetation in the interior appeared more resistant to deer modification. In the interior of islands with deer for less than 20 years, extensive patches of salal remained, making up most of the total cover. These patches were often thinned by deer browsing, which allowed light to penetrate to the lowest stratum and produce dense growth throughout. On islands without deer the lowest stratum in the interior was often shaded out and produced little foliage relative to the upper strata. Hence a pattern developed in the interior corresponding with the predictions of the intermediate disturbance hypothesis (Grime 1973). However the increased plant growth resulting from decreased competition for light on islands with deer, did not fully compensate for the vegetation lost through browsing, nor did we observe a concurrent increase in species richness.

6.3 The browse zone

The reduction in vegetation associated with deer is largely targeted to a preferred browse zone and the browse line that delimits this zone often becomes evident when deer are abundant in forests (Rhoads 1997). Species that are restricted to this zone are usually the first to be affected (Waller and Alverson 1997) and are often repeatedly browsed (Miller et al. 1992). Sitka black-tailed deer tend to feed mainly on vegetation between 0 and 150 cm (Bunnell 1990, Daufresne and Martin 1997). Plants above the browse-line are generally only affected indirectly, when young stems are unable to replace older stems (Vila et al. 2001). However, deer can affect even long-lived canopy species by reducing or eliminating recruitment (Alverson et al. 1988, Anderson and Loucks 1979, Anderson and Katz 1993).

Although the effect of deer in Laskeek Bay was limited to the strata below 150 cm at the forest edge, in the interior, vegetation in the 150 to 400 cm stratum was also affected. The effect in this stratum appeared to result from the abundance of shrubs in the interior, which the deer could push over to reach the upper branches. Trees with more rigid stems were generally better able to keep foliage out of reach of the deer.

As the forest understorey is stripped away by deer browsing, an important structural and functional component of the forest is removed. The final product of unconstrained, long-term deer modification of coastal forest appears to be the open cathedral-like forest found over much of Haida Gwaii. These forests consist of tall canopy trees, profuse epiphytes and a thick layer of moss (Calder and Taylor 1968). Noticeably absent from these forests is the dense understorey found in mainland coastal forests where populations of wolves and cougars occur (Pojar et al. 1980).

6.4 Deer-modified plant communities

Unconstrained deer browsing reduces the abundance of some species more than others, creating characteristic deer-modified plant communities. The effect of deer browsing on community composition may be variable in space and time, and compositional changes associated with deer browsing must be considered as the combined effects of diet preference and differential recovery among species (Huston 1979). Nevertheless, in Laskeek Bay, we encountered the same reduced wildflower and shrub abundance recorded in other studies of deer in the temperate rain forest (Woodward et al. 1994, Daufresne and Martin 1997, Pojar 1999). These studies also recorded an increase in the abundance of grass species in deer-modified plant communities while most graminoids in our study showed only small decreases in cover on deer-affected

islands and corresponding increases in dominance relative to most shrub and herb species. On islands with deer for more than 50 years, little cover of vegetation remained in either the edge or interior habitat, but significantly more cover occurred on the shoreline where grasses dominated. The only grass species to depart from this pattern was dunegrass, *Elymus mollis*, which had much lower cover on islands affected by deer than on islands free from deer.

The response of many grasses to defoliation is thought to stem from their unusual morphology, developed through co-evolution with grazing animals (Olff and Ritchie 1998). The position of meristem tissue low to the ground and a high root-to-shoot ratio allows many grass species to escape the loss of expensive meristem tissue when browsed and maintain reserves to regrow rapidly, often spreading laterally and outcompeting other species in the process (McNaughton 1984). Dunegrass, which possesses extensive aboveground structure, remains an exception to this pattern.

Several studies (Hanley and Taber 1980, Daufresne and Martin 1997) suggest that through reduced competition with depleted shrub species, browsing can favour regeneration of tree species such as Douglas-fir, *Pseudotsuga menziesii,* or Sitka spruce. This regeneration can happen despite the delay in growth that results from intense Sitka black-tailed deer browsing (Vila et al. 2001). For other tree species, such as western red cedar, *Thuja plicata*, the browsing of Sitka black-tailed deer has been found to effectively eliminate natural regeneration (Baltzinger and Martin 1998, Pojar 1999). Similarly, the browsing of white-tailed deer has been found to greatly affect the abundance and regeneration of northern white cedar, *Thuja occidentalis* (Little and Somes 1965, Stromayer and Warren 1997, Rooney et al. 2002). In eastern hardwood forests, high

white-tailed deer populations have also significantly reduced regeneration of several other commercial tree species (Marquis 1974, Anderson and Loucks 1979, Alverson et al. 1988, Anderson and Katz 1993). However, in Laskeek Bay, we recorded no effect of deer on trees below 150 cm.

6.5 Measuring what counts

Since McArthur and Wilson (1963) published their model of island biogeography, plant species lists, without reference to cover or biomass, have often been used for island studies (Quin et al.1987). However, failure to take into account the relative frequency and abundance of plant species as well as the potential scale of effect ignores much of what determines the ecological processes within an island. In Laskeek Bay, the similarity in the number of species recorded on the three islands without deer and on the four islands with deer demonstrates that the effect of deer on plant species richness cannot be discerned at such a broad scale. When non-native species were removed from the tally the loss of diversity became only slightly more evident; at the island scale, no significant difference was observed between the species richness of islands. The observed trend of decreased species richness with increased duration of deer presence suggests that the effect of deer on plant diversity is widespread and may culminate in the extirpation of species from individual islands. However, differences in plant cover and species richness of these islands is striking when examined at a higher resolution. Species accumulation curves showed that the difference in species density is greatest between six and seven plots, indicating that small areas may be highly susceptible to species loss. At the scale of the individual plot, it became apparent that deer have greatly reduced the cover of

vegetation and virtually eliminated many species and plant types from the forest understorey.

6.6 A clear picture

Decreased plant diversity and/or plant abundance have been recorded for many forest systems affected by moderate to high densities of deer (Klein 1965, Alverson et al. 1988, Anderson and Katz 1993, Woodward et al. 1994, deCalesta 1997b, Daufresne and Martin 1997). However, these studies have generally occurred in contexts where other factors (forest industry, agriculture, urban development, predators, other large herbivores) may have played a role in the emerging pattern (but see Hough 1965, and Rooney and Dress 1997b). The absence of other human driven factors affecting the interaction of deer over large areas of Haida Gwaii makes the results of our study especially valuable in determining the precise role of deer in ecosystem modification. The study of areas such as Laskeek Bay indicates that large differences in cover and diversity can result from the release of deer from their natural predators, with little or no external habitat modification.

Although the nature of our study site, small islands, with large edge-to-interior ratios, may serve to make the effect more acute (Vila 2002), similar changes to the understorey of this region have been observed within the large tracts of unbroken old-growth forest occurring on large islands in the archipelago: Moresby and Graham islands (Pojar et al. 1980, Englestoff 2001). The sparse understorey vegetation in Haida Gwaii has been noted by several recent observers (Calder and Taylor 1968, Banner et al. 1989, Pojar et al. 1980, Pojar 1999). This observation contrasts with the dense understorey noted by early foresters and visitors to Haida Gwaii (Gregg 1923, Hopkinson 1931, Hall 1937,

Carr 1951), indicating a recent change in the vegetation contemporary with the spread of deer across the archipelago.

6.7 Why reduced diversity?

Whereas intense deer modification of the forest understory appears to generally result in a reduction in plant diversity, on grasslands plant density and diversity have shown increases in response to intense herbivory (McNaughton 1984, Olff and Ritchie 1998). The increase is thought to arise through reduced competition for resources when dominant plants are removed (Burt 1949, Olff and Ritchie 1998). This effect may not apply to forested systems where, even with greatly reduced biomass in the forest understorey, competition for resources can remain unchanged because large trees with substantial resource requirements escape the immediate effects of browsing by ground-based animals (Rhoads 1997).

The different response of grasslands and forest to intense herbivory is also influenced by compositional differences between the two biomes. The co-evolution of grasses and grazers may be responsible for the ability of many grass species to withstand frequent and extensive defoliation (Caughenor 1985, Olff and Ritchie 1998). Forbs, which dominate forest systems, have high ratios of above to below ground resources, vulnerable apical meristems and usually prove less resilient to defoliation (Crawley 1983, Caughenor 1985).

Levels of migration and foraging frequency may further influence the effects of herbivory on plant diversity (Augustine and McNaughton 1998). With domestic livestock, a short intensive period of herbivory, followed directly by a period without herbivory can result in the increased abundance of palatable species (Milton 1947).

Natural grazing systems dominated by migratory herbivores experience similar conditions, where plants are subject to herbivory for only part of the growing season (Frank and McNaughton 1992, Augustine and McNaughton 1998). Herbivores in forest systems often exhibit more sedentary behaviour with more frequent tissue removal of individual plants (Klein 1965, Danell et al. 1994). When predators are absent from the situation, it follows that herbivores would be even more sedentary (Sharpe 1999). Thus, the mechanisms that are thought to maintain diversity in other herbivore-dominated systems may not be applicable to many forest systems, and a loss of species diversity may be the inevitable result of abundant deer.

6.8 Indirect effects

By directly consuming plants, deer change the structure and diversity of the islands they inhabit. Although a few individuals of each species usually escape this direct consumption, indirect effects may eventually lead to their extirpation. The increased rarity of plants makes species loss due to secondary perturbation more probable (MacArthur and Wilson 1967). Reduced abundance of flowering plants is likely to translate into a reduction of pollinators, as has been found for tropical islands subject to introduced species (Cox and Elmqvist 2000). Reduced pollination can then feed back into the system and further effect the persistence of the flowering plants that remain. Likewise, seed dispersal by birds and small mammals can be affected by the pattern of plant cover (Ferguson and Drake 1999). The elimination of ericaceous shrubs could also eliminate their associated *mycorrhizae* and greatly reduce the availability of minerals in the system (Pojar 1999). Furthermore, a modification of the magnitude recorded on these islands is likely to directly influence ecosystem processes such as nutrient cycling and

disturbance regimes (Hobbs 1996). Pastor et al. (1993) suggested that the effects of herbivores on ecosystems are amplified by positive feedbacks between plant litter and soil nutrient availability. Herbivores may also be instrumental in decreasing slope stability and increasing the likelihood of landslides (Pojar et al. 1980).

Changes to the structure and diversity of plants also alter food and habitat available in the food chain. Significant decreases in the abundance and diversity of bird communities through the modification of vegetation have been recorded in eastern hardwood forests (deCalesta 1994, McShea and Rappole 1999). Likewise, a lower abundance of songbirds on islands inhabited by deer has been shown within Laskeek Bay (Martin and Daufresne 1999). The effect of deer in Laskeek Bay has been to eliminate most of the ecological function of the forest understorey (Martin and Daufresne 1999).

6.9 Crying wolf

A model developed for Southeast Alaska indicates that the addition of wolves into areas of temperate rain forest with overabundant Sitka black-tailed populations would quickly bring deer below ecological carrying capacity (Person et al. 2001). Using this same model, and deer and vegetation data from Haida Gwaii, Kirchoff (in press) predicted that with the addition of wolves, deer population densities would could remain high, but still below ecological carrying capacity. The introduction of wolves to Coronation Island in southeast Alaska demonstrates the potential effectiveness and some of the potential problems of wolf control in this region. The introduction of four wolves to this 70-km^2 island in 1962, resulted in a large reduction in Sitka black-tailed deer density and a substantial recovery of the vegetation within four years (Merriam 1964, Klein 1965). However, within eight years the deer were eliminated from the island and

the wolves had resorted to cannibalism, dying out shortly thereafter, whereupon deer quickly recolonized the island (Klein 1995). Given a slightly larger area, the wolves might have been able to survive and maintain the deer population below ecological carrying capacity (Person et al. 2001). However, in view of the ecological value of Haida Gwaii and the potential for unanticipated consequences in introducing a large predator species, the introduction of the wolf to this region is not a viable alternative.

6.10 Implications for management

Our investigation suggests that, in the absence of predators, or where predator pressure is severely reduced, deer have a strong impact on vegetation structure and diversity, which may greatly modify ecosystem functions. The effect may be broadly applicable to many forest systems. Overabundant deer have become a global concern and the cascading effects of deer browsing to plant-plant and plant-animal species interactions may have far reaching impacts, not only to the vegetation but also to the fauna. In Haida Gwaii, which retains of one of the largest protected tracts of coastal temperate rain forest in North America, the effects may create serious conservation problems for both plant and animal species. Moreover, as many of these species rare (Ogilvie 1984, Taylor 1989) and/or culturally significant (Turner 1995, Turner 1998), modification of the flora and fauna of this region has direct ecological and cultural repercussions. Of special note, in this context, is the extremely high conservation value of the remaining forest areas free of deer or with intact predator complexes. These areas may provide refuge for rare or endemic species sensitive to the effects of deer browse. Preservation of these refuges may be critical in maintaining biodiversity and may provide valuable seed stores for future restoration efforts. Careful maintenance of predator

populations and other deer population control mechanisms, where they exist should be a global conservation priority.

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Table 1: Island characteristics, showing *isolation*, measured as the distance to the main island chain and *area* (both from Martin et al. 1995); *presence*, the duration of deer presence (from Vila 2002), *pellet groups*, pellet group density (means ± SE), based on four 135-m transects for each island; and *deer*, deer density, calculated as pellet group density multiplied by 33.3/0.19 (deer density of E. Limestone; Daufresne and Martin 1997) over the measured pellet group density for E. Limestone.

Island	Isolation (m)	Area (ha)	Presence (years)	Pellet groups (m^{-2})	Deer (km^{-2})
Haswell	150	13.3	>50	0.12 ± 0.02	21.1± 3.6
W. Limestone	350	16.0	>50	0.21 ± 0.03	36.8 ± 5.3
W. Skedans	1350	8.2	<20	0.12 ± 0.02	21.1 ± 3.6
S. Skedans	2400	5.6	<20	0.17 ± 0.04	29.8 ± 7.0
S. Low	2900	4.5	none	0	0
Low	5400	9.6	none	0	0
Lost	7300	5.3	none	0	0

Table 2: Statistics for GLMM analysis of the impact of deer on cover of vegetation in relation to *browsing history*, *island* (nested within *browsing history*), and *habitat* type (edge or interior) for three strata (0-50 cm, 50-150 cm, 1.5-4 m).

Effects	χ^2	df	P	Significance
0-50 cm stratum				
Browsing history	56.62	2	<0.0001	***
Island (browsing history)	38.65	4	<0.0001	***
Habitat	2.80	1	0.0006	***
Browsing history*habitat	31.95	2	<0.0001	***
50-150 cm stratum				
Browsing history	36.43	2	<0.0001	***
Island (browsing history)	16.15	4	<0.0001	***
Habitat	16.65	1	0.7167	n.s.
Browsing history*habitat	7.16	2	0.0132	*
150-400 cm stratum				
Browsing history	6.43	2	0.0402	*
Island (browsing history)	2.28	4	0.6846	n.s.
Habitat	4.72	1	0.0297	*
Browsing history*habitat	5.45	2	0.0656	n.s.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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

Effects	χ^2	df	P	Significance
Herbs				
Browsing history	63.39	2	<0.0001	***
Island (browsing history)	1.24	4	0.87	n.s.
Habitat	7.51	1	0.0061	***
Browsing history*habitat	9.64	2	0.0081	***
Shrubs				
Browsing history	57.18	2	<0.0001	***
Island (browsing history)	25.13	4	<0.0001	***
Habitat	1.10	1	0.2951	n.s.
Browsing history*habitat	19.18	2	<0.0001	***
Salal				
Browsing history	56.77	2	<0.0001	***
Island (browsing history)	7.58	4	0.11	n.s.
Habitat	16.73	1	<0.0001	***
Browsing history*habitat	39.56	2	<0.0001	***
Trees				
Browsing history	14.15	2	0.0008	***
Island (browsing history)	19.43	4	0.0006	***
Habitat	1.23	1	0.27	n.s.
Browsing history*habitat	7.17	2	0.028	*

*** P < 0.05; ** P <0.01; *** P < 0.001**

Table 4: Statistics for GLMM analysis of impact of deer on plot species richness in relation to *browsing history*, *island* (nested within *browsing history*), and *habitat* type (edge or interior).

Effects	χ^2	df	P	Significance
Browsing history	127.73	2	<0.0001	***
Island (browsing history)	4.67	4	0.3233	n.s.
Habitat	9.21	1	0.0024	**
Browsing history*habitat	12.90	2	0.0016	**

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 5: Number of plant species (γ-diversity) recorded in ten, 314-m^2 edge plots, five 314-m^2 interior plots and all 15 plots, on each of seven islands for three durations of deer presence (dark grey, deer present for more than 50 years; light grey, deer present for less than 20 years; white, no deer, past or present).

Island	Edge Species	Interior Species	Total Species
Haswell	36	22	44
W. Limestone	32	19	41
W.Skedans	42	22	49
S.Skedans	37	18	48
S. Low	59	24	64
Low	51	21	57
Lost	53	25	59

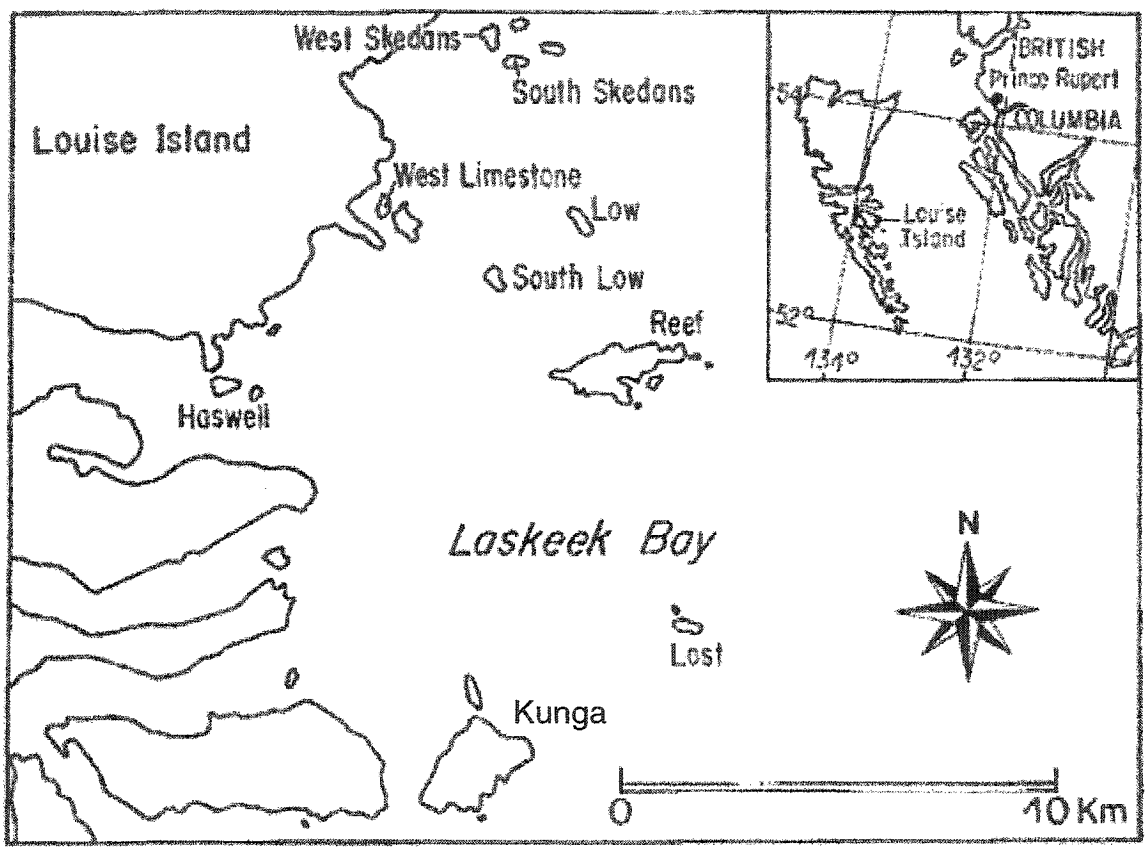

Figure 1: Map of Laskeek Bay showing the relative location of seven study islands, Haswell, W. Limestone, W. Skedans, S. Skedans, S. Low, Low, and Lost. Also shown are Reef and Kunga Islands (see chapter 3).

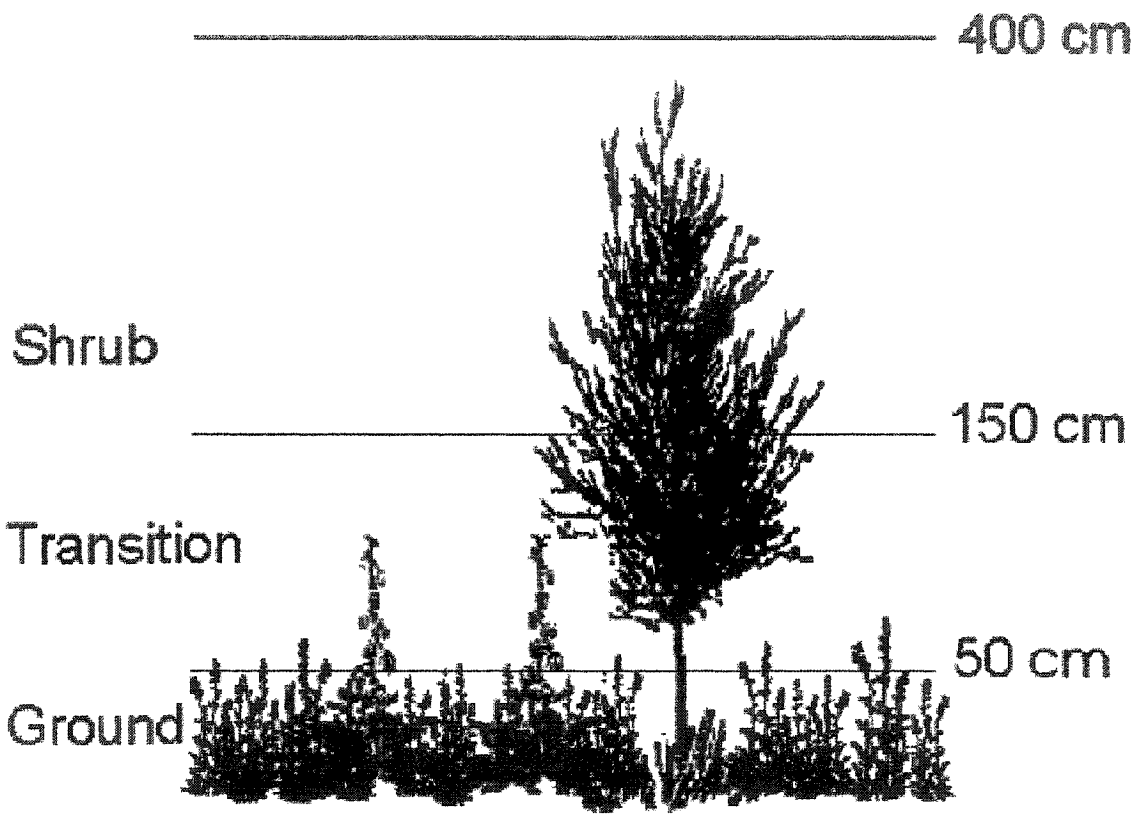

Figure 2: Sampling strata, the percent cover of each species was recorded in strata set between 0 to 50 cm, 50 to 150 cm, and 150 to 400 cm to capture the effects of deer on different vegetation types.

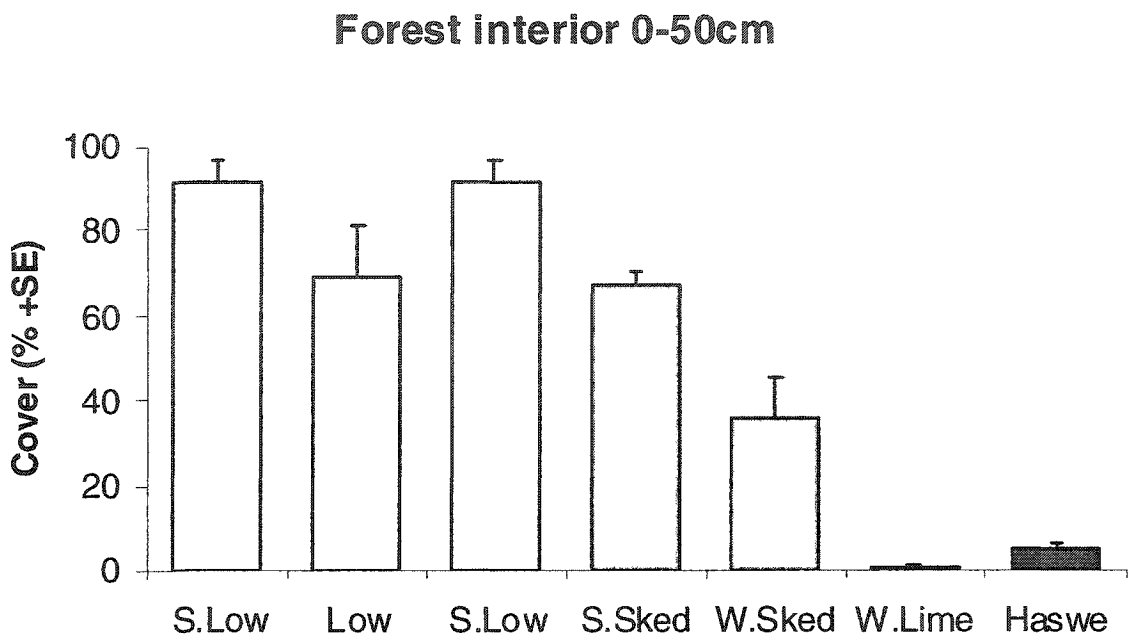

Figure 3: The cover of vegetation in interior habitat from 0 to 50 cm on each of seven islands with three durations of deer presence (n=5 for each island). Shown as means + SE.

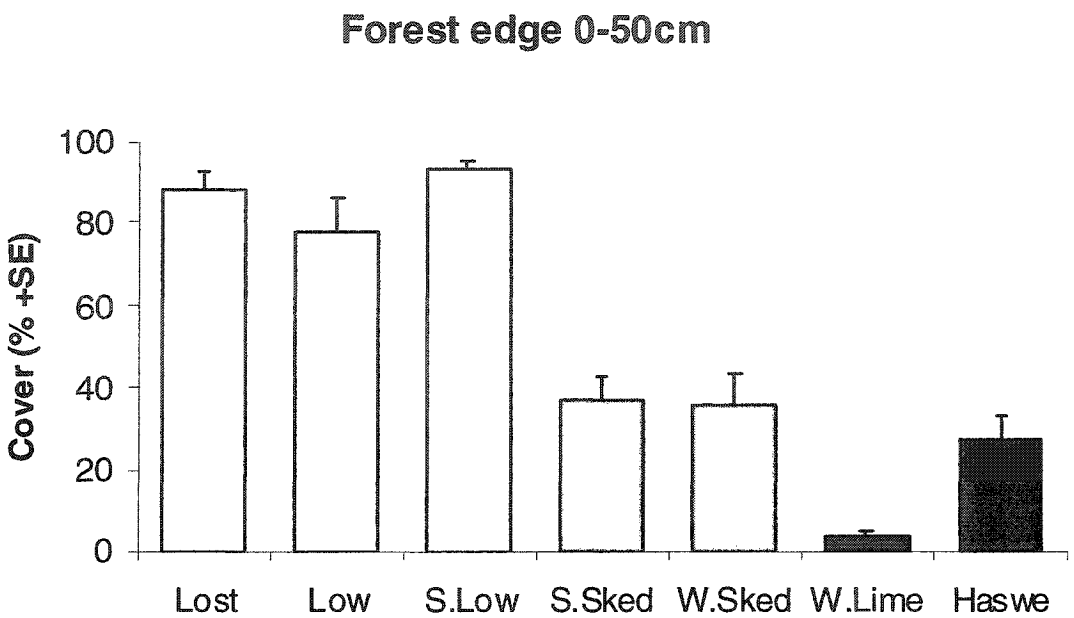

Figure 4: The cover of vegetation in edge habitat from 0 to 50 cm on each of seven islands with three durations of deer presence (n=10 for each island). Shown as means + SE.

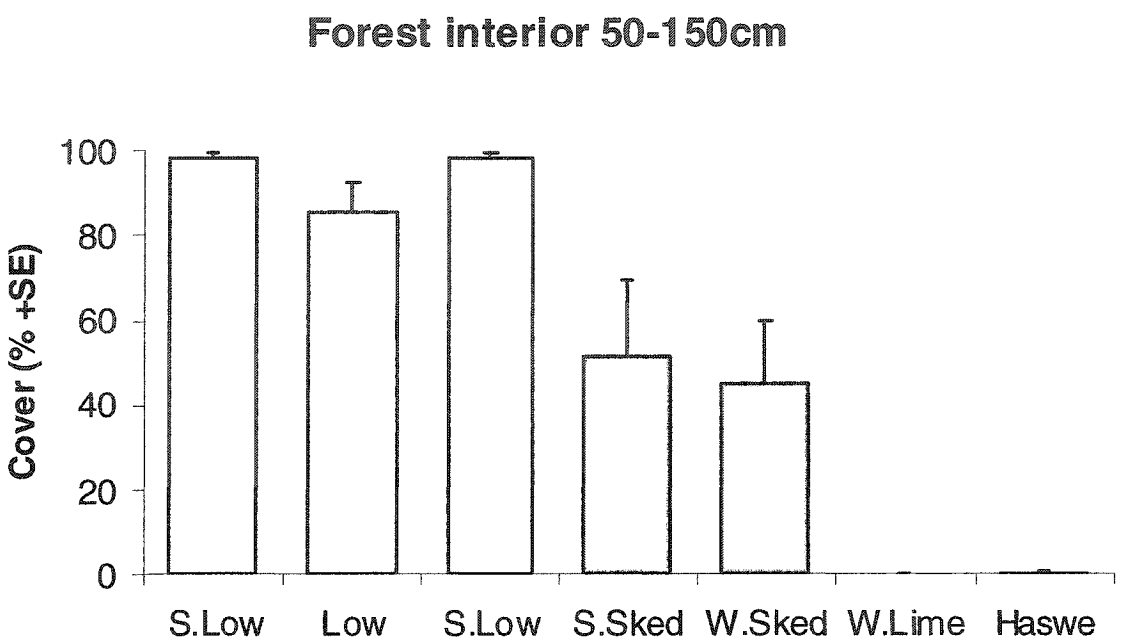

Figure 5: The cover of vegetation in interior habitat from 50 to 150 cm on each of seven islands with three durations of deer presence (n=5 for each island). Shown as means + SE.

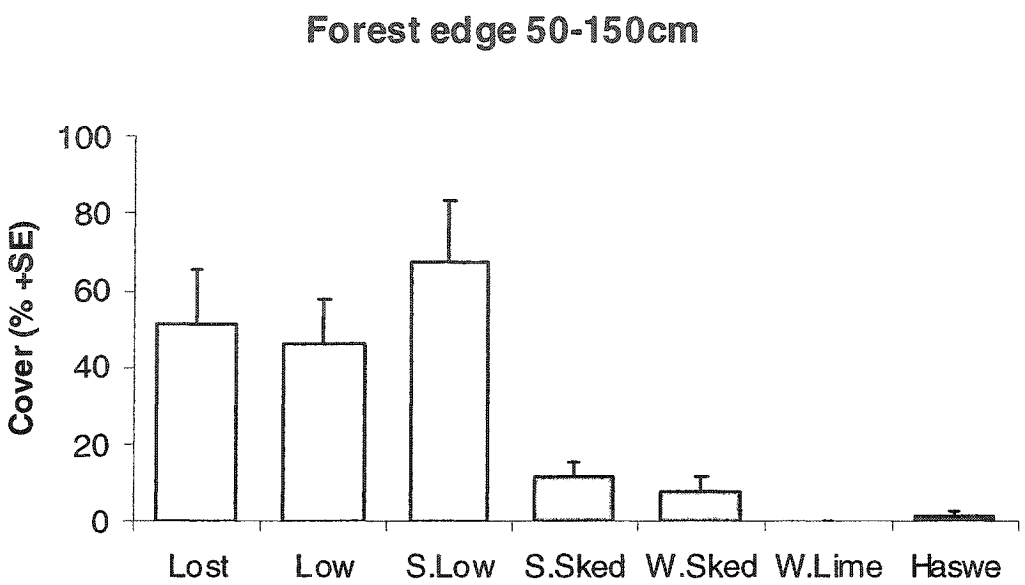

Figure 6: The cover of vegetation in edge habitat from 50 to 150 cm on each of seven islands with three durations of deer presence (n=10 for each island). Shown as means + SE.

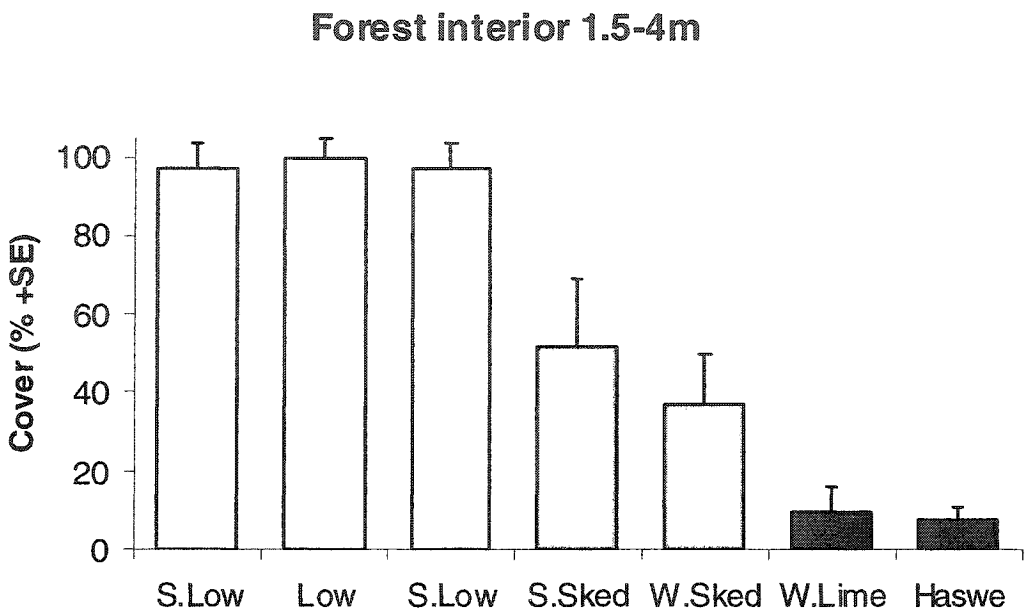

Figure 7: The cover of vegetation in interior habitat from 150 to 400 cm on each of seven islands with three durations of deer presence (n=5 for each island). Shown as means + SE.

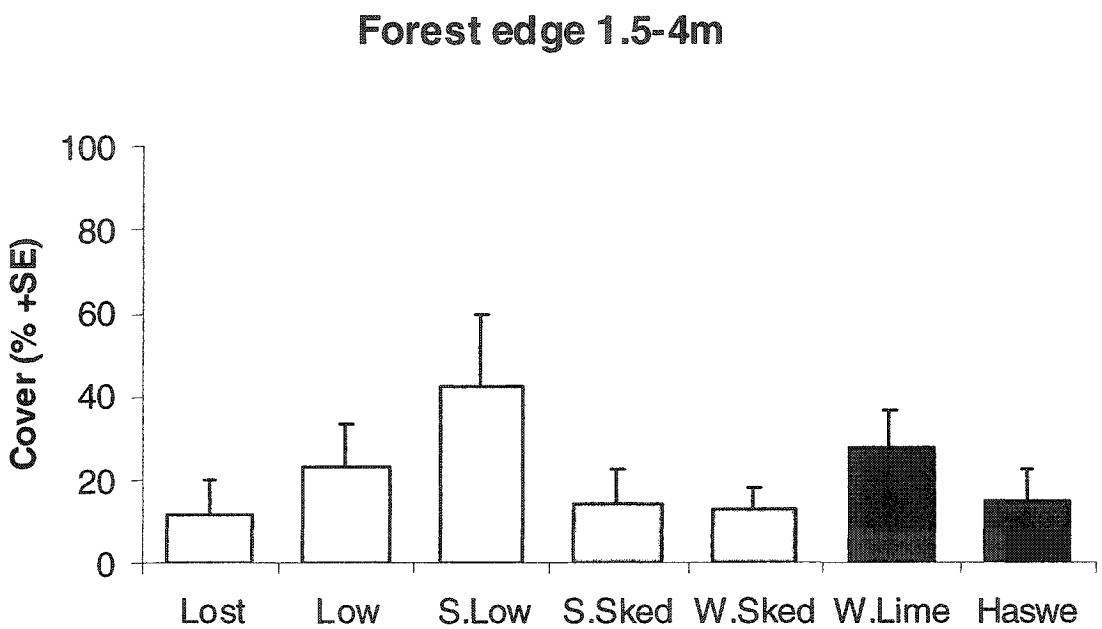

Figure 8: The cover of vegetation in edge habitat from 150 to 400 cm on each of seven islands with three durations of deer presence (n=10 for each island). Shown as means + SE.

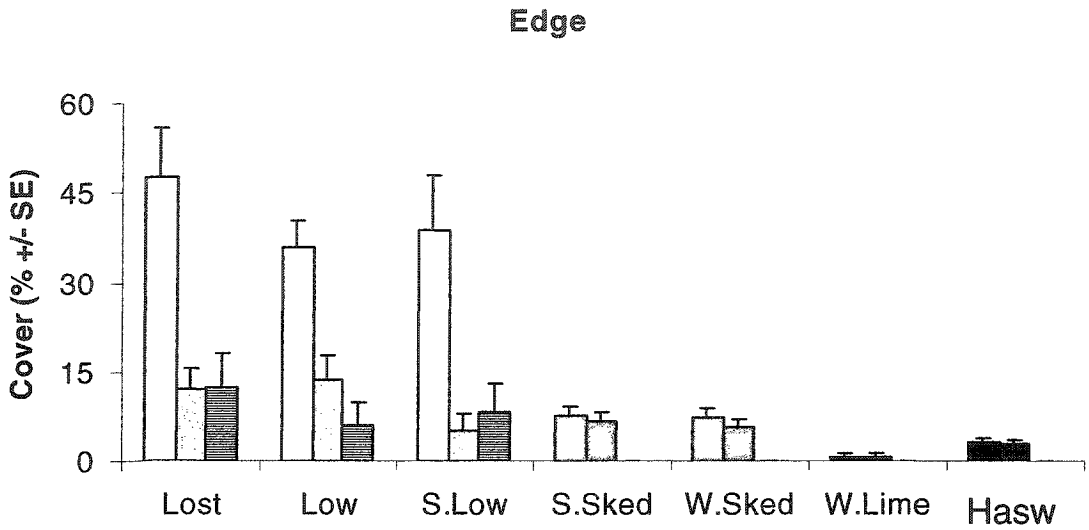

Figure 9: The cover of herbaceous vegetation in edge habitat from 0 to 150 cm on each of seven islands with three durations of deer presence (n=10 for each island). Also shown are the contributions to herb cover of the grass *Elymus mollis* (horizontal stripes), and all other graminoids (dots). All measures shown as means + SE.

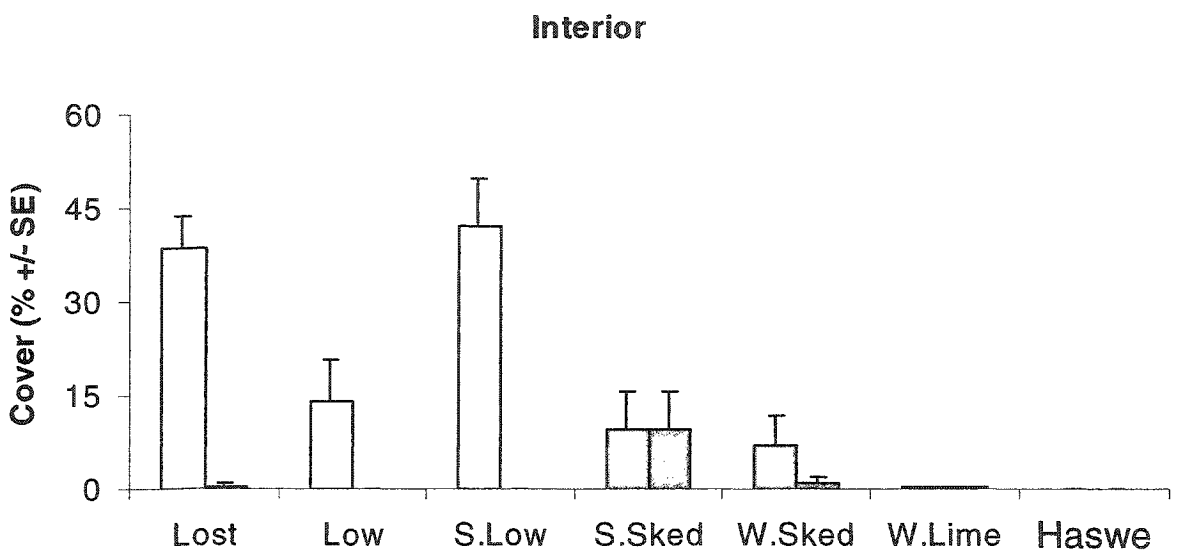

Figure 10: The cover of herbs in interior habitat from 0 to 150 cm on each of seven islands with three durations of deer presence (n=5 for each island). Also shown are the contributions to herb cover of graminoid species (dots). All measures shown as means + SE.

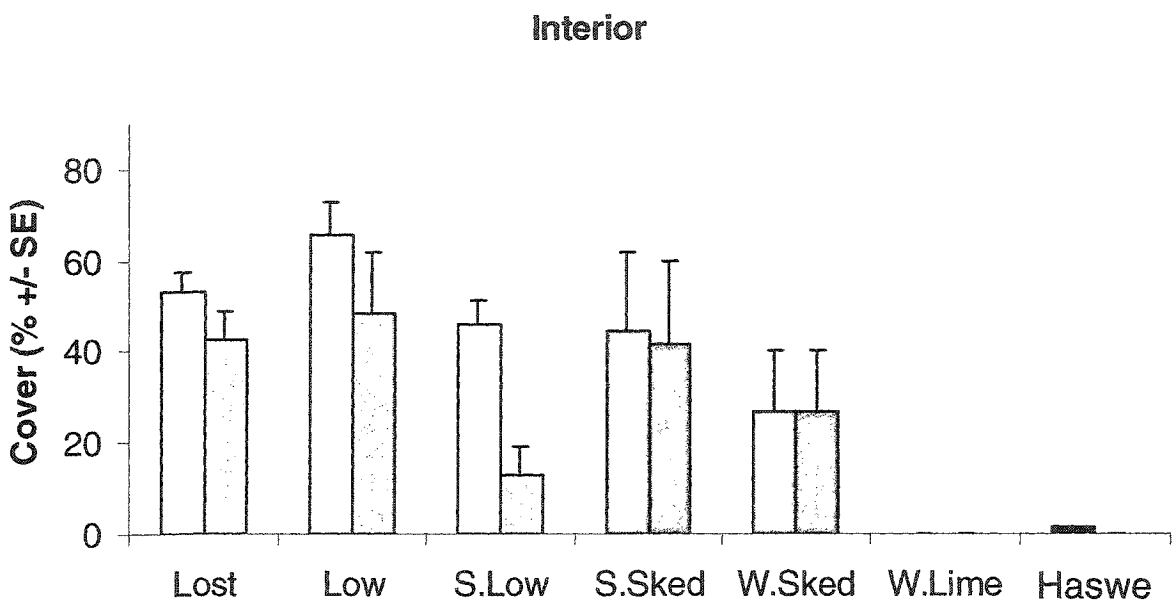

Figure 11: The cover of shrubs in interior habitat from 0 to 150 cm on each of seven islands with three durations of deer presence (n=5 for each island). Also shown is the contribution to shrub cover of *Gaultheria shallon* (dots) below 150 cm. Both are shown as means + SE.

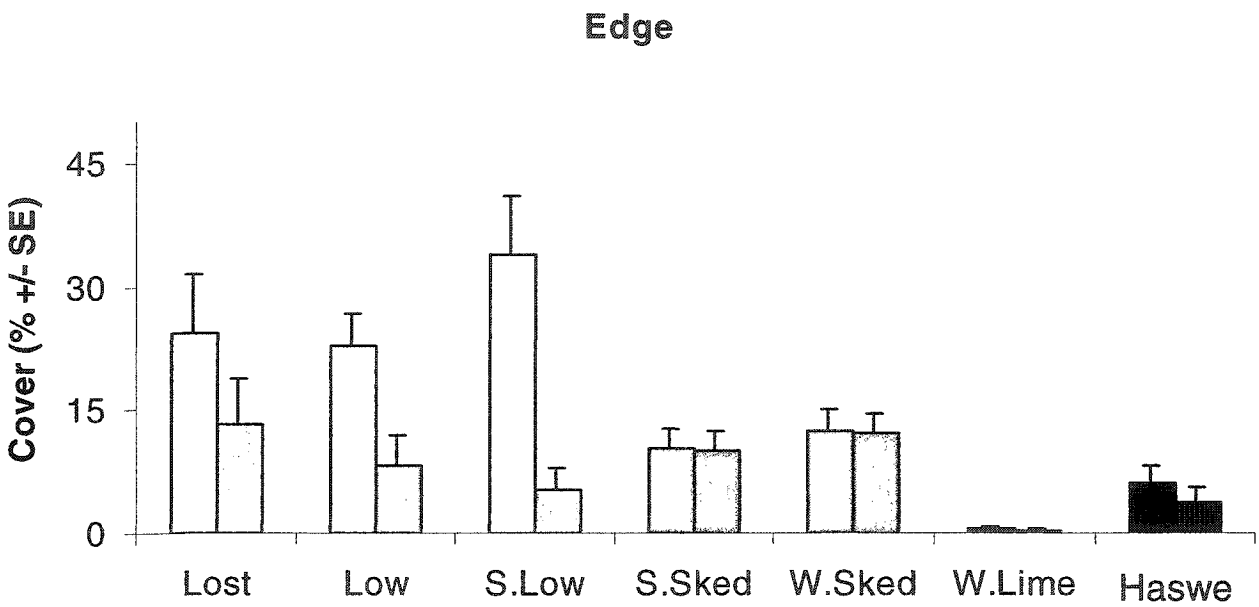

Figure 12: The cover of shrubs in edge habitat from 0 to 150 cm on each of seven islands with three durations of deer presence (n=10 for each island). Also shown is the contribution to shrub cover of the shrub *Gaultheria shallon* (dots) below 150cm. Both are shown as means + SE.

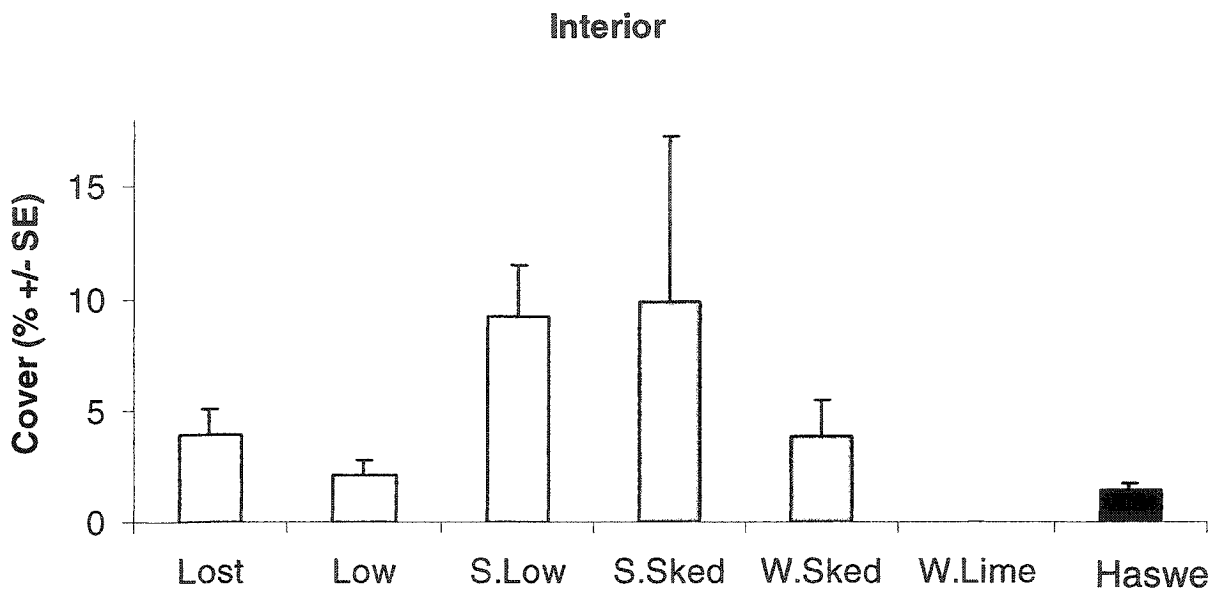

Figure 13: The cover of trees in interior habitat from 0 to150 cm on each of seven islands with three durations of deer presence (n=5 for each island). Shown as means + SE.

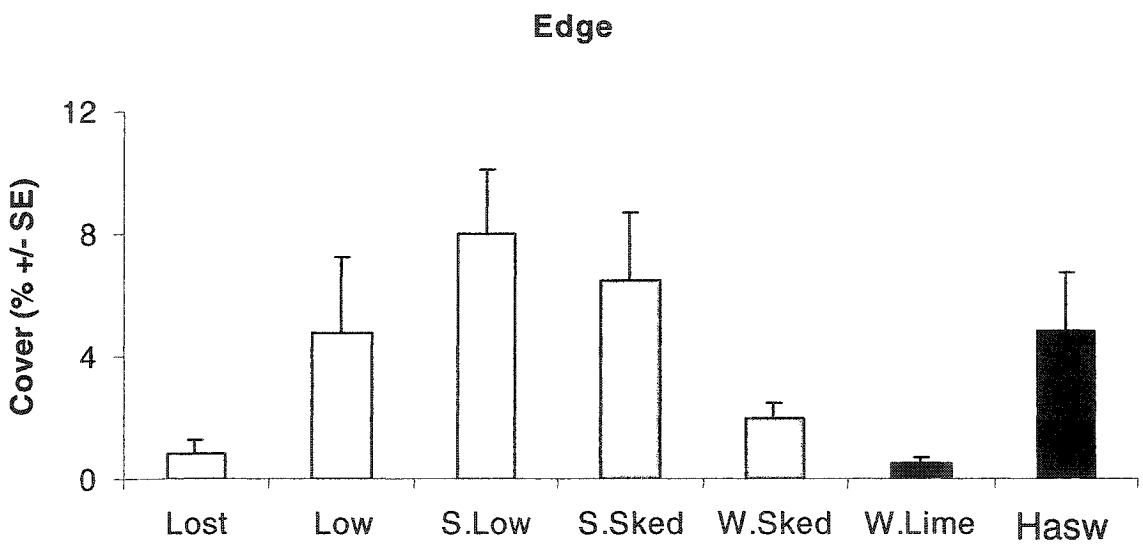

Figure 14: The cover of trees in edge habitat from 0 to150 cm on each of seven islands with three durations of deer presence (n=10 for each island). Shown as means + SE.

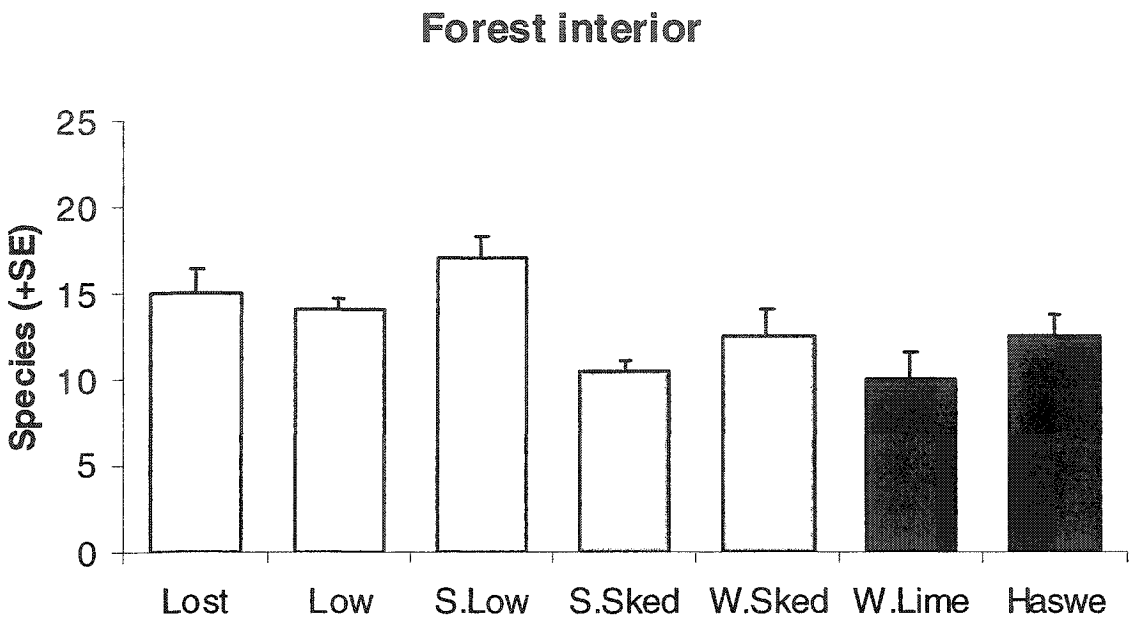

Figure 15: The species richness in interior habitat on each of seven islands with three durations of deer presence (n=5 for each island). Shown as means + SE.

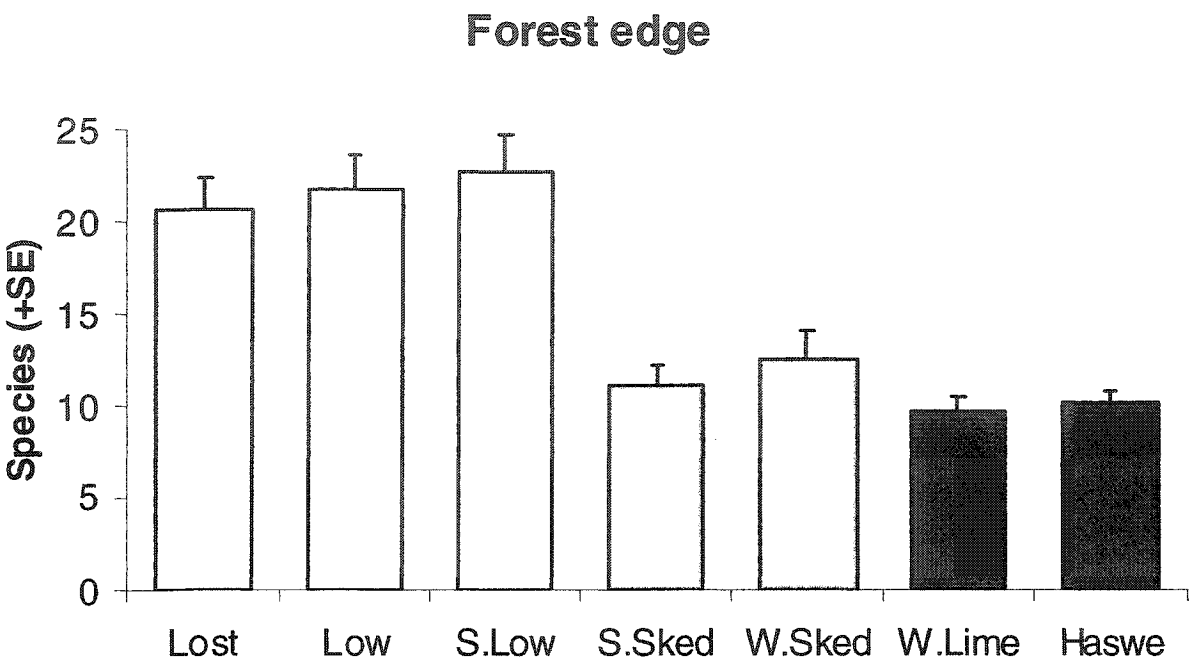

Figure 16: The species richness in edge habitat on each of seven islands with three durations of deer presence (n=10 for each island). Shown as means + SE.

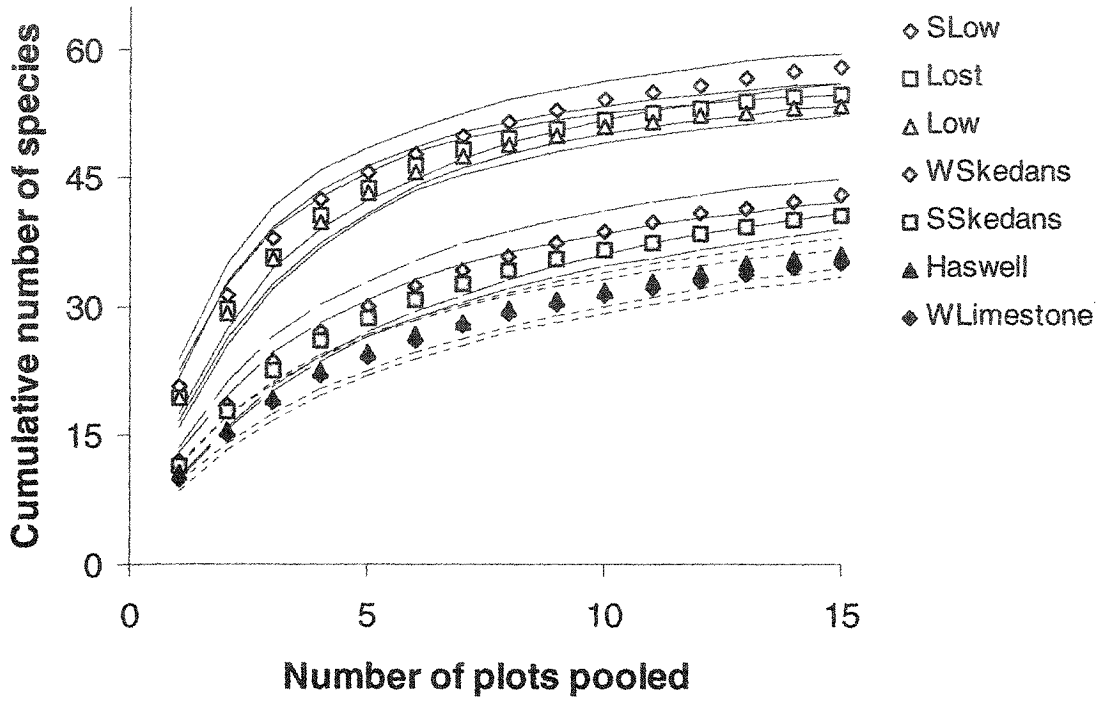

Figure 17: Species accumulation curves for vascular species occurring on seven islands (n=15 for each island). Symbols represent estimates of mean species richness and lines represent 95% confidence intervals for 500 random combinations of n samples (n=1,2,…,15).

Chapter 2:

process of deer modification

in the forest understorey

1 Abstract

In a natural experiment utilising the introduction of Sitka black-tailed deer, *Odocoileus hemionus sitkensis* Merriam, to Haida Gwaii (Queen Charlotte Islands) in the late 19th century, we examined the response of understorey plant communities and individual species throughout the process of forest modification due to herbivory. Within a natural laboratory, consisting of a series of seven islands: two affected by deer for more than 50 years, two for less than 20 years, and three with no history of deer presence, modification of the forest understorey vegetation followed a series of punctuated steps towards a greatly simplified community, consisting largely of tree seedlings and grass species. We identified four functional response patterns describing the ways in which different plant species were affected by deer over time. Plant species that maintained substantial cover after 50 years of deer presence tended to possess mechanisms to keep developing plant tissue inaccessible to deer. The revealed process may be useful in identifying, isolating, and quantifying the effects of deer as well as providing insight into the conservation and potential for recovery of deer modified forest systems.

2 Hypothesis

Over time, deer simplify the community composition of the forest ecosystem through the systematic modification of the plant species found in the forest understorey.

3 Introduction

The conservation of biodiversity demands a clear understanding of the processes that control it. Herbivory is a key process determining the biodiversity of plant species in many systems (Chew 1974, McNaughton 1985, Crawley 1997a, Milchunas and Lauenroth 1993, Olff and Ritchie 1998). The effect of herbivory may be especially important for the conservation of forested systems as exploding deer populations are presently contributing to the large-scale modification of North American forests (McShea and Rappole 1997, Waller in press). As forests become further modified by deer, the need to identify the key factors at work becomes increasingly important.

The island archipelago of Haida Gwaii (Queen Charlotte Islands), British Columbia, Canada provides a natural laboratory (*sensu* Diamond 1983) to examine the biological processes that govern deer-modified forest systems. This natural laboratory of islands provides a simplified system of discrete, identifiable units for comparison (*sensu* A. R. Wallace in Whitaker 1998) with varying degrees of herbivore modification. Because many islands in this region remain largely unaffected by human activities (Martin and Daufresne 1999), and none possesses large predators or climatic constraints (Pojar 1999), the natural laboratory neatly isolates the relationship between a large terrestrial herbivore and its food source. Furthermore, despite a number of endemics found in this region (Taylor 1989) the flora of Haida Gwaii is largely similar to that of the mainland (Alaback 1990).

In chapter one, we utilized this natural laboratory of islands to examine the effects of deer on the cover of vegetation, species composition and species richness of the forest understorey. However, this natural laboratory consists of islands without deer, islands

with deer for less than 20 years and islands with deer for more than 50 years, allowing an unusual opportunity for the examination of not just the end-point of this modification but also the steps along the way. As such, we now utilize the same data set we used in the previous chapter to examine the response of communities and individual species throughout the process of modification. We develop this picture by first examining trends in the deer modification of plant-types and dominant species and then shifting to a finer scale and examining the response of individual species to deer browsing at three stages of deer modification.

4 Methods

4.1 Sampling

Vegetation data was collected on a series of seven islands with three durations of deer modification: greater than 50 years, less than 20 years and no modification. The same data used in chapter 1 was used here (see chapter 1 section 3.5 for details).

4.2 Statistical analysis

Scheffe tests (Sokal and Rolf 1995) were used to determine the significance of differences in the cover of salal between 50 and 150 cm between interior plots on individual islands.

4.3 Principal components analysis

To examine patterns in deer modification among different plant-types over time, we examined vegetation data using principal components analysis. PCA is a linear dimensionality reduction technique, which identifies orthogonal directions of maximum

variance in a set of data, and projects it into a lower-dimensionality space formed by a sub-set of the highest-variance components (Bishop 1995). PCA was first described by Hotelling (1933) and first used in ecology by Goodall (1954). Due to a well-known problem with this technique in properly ordering non-linear relationships among samples, the *horseshoe effect* (Orloci 1974), PCA is often deemed inappropriate for the analysis of species data along long gradients.

With longer gradients, many species are usually replaced by other species, producing zeroes abundance scores in the data. To minimize the number of zero abundance scores, cover estimates for each species in each plot for 0- to 50-cm and 50- to 150-cm strata were grouped according to plant-type (tree, shrub, forb, fern, and graminoid), unless cover of individual species averaged more than 2% cover in either stratum. As such, zero abundance data was relatively rare for our data, less than 30% of cells in the interior PCA and less than 40% in the edge PCA. Zero abundance scores for most species tended to occur in plots with more than 50 years of deer browsing, demonstrating a unimodal response to deer modification over time.

PCA is quite appropriate for the analysis of samples along relatively short gradients and is extremely useful when species are linearly (or even monotonically) related to each other (Jongman et al. 1995). A simple method to determine if PCA will accurately portray data is to measure the maximum gradient length of the data set using detrended correspondence analysis, DCA. If the maximum gradient length as measured with DCA is greater than 4.0, use of a linear method is thought to be inappropriate, but if the gradient length measures less than 3.0, a linear method such as PCA is probably the best choice (ter Braak and Smilauer 1998, Leps and Smilauer 1999). For our data, DCA

revealed relatively short gradient lengths for both interior and edge data sets (1.96 and 1.06 respectively) verifying PCA as an appropriate technique for ordination of our data.

PCA allows the use of variables that are not measured in the same units, which allowed us to include measures of species richness in order to examine the interaction of diversity, plant-type and deer modification. Including variables of different units in PCA necessitates that variables be standardized (means of zero and variances of one) and so PCA was carried out on the correlation matrix as opposed to the correspondence matrix. This has the added benefit of preventing the swamping of uncommon measures by common ones (Stevens 1986).

The *Kaiser criterion*, which accepts only components with eigenvalues greater than one, is a useful criterion in determining the cutoff of meaningful components (Catell 1966, Cooley and Lohnes 1971, Hakstian et al. 1972). Although the *Kaiser criterion* usually retains many factors (Statsoft 2002), we chose to use it in order to guarantee that all meaningful data was retained.

4.4 Guild determination

Based on their cover below 150 cm, we classified each species identified on the seven islands into one of four response guilds (Boutin and Keddy 1993, Wilson 1999). The four guilds describe four possible responses of the cover of a species to deer modification (Fig. 1). In the first pattern (guild I), cover is greatly reduced after less than 20 years of deer presence. In the second (guild II), cover is unchanged after less than 20 years but is greatly reduced by 50 years. In the third (guild III), cover gradually declines with longer deer presence. In the final pattern (guild IV), cover is unchanged or increased with deer presence.

If species were present on only a single island, we excluded their membership from any guild (NA). Membership in guild IV was determined if the average cover of a species on islands with deer for 20 or 50 years was equal to or greater than the average cover of that species on islands with no deer. To determine guild membership of the remaining species we compared the actual cover of each species below 150 cm in each plot to the expected cover (as determined below).

Guild membership was determined based on a first-order least squares fit: residuals were calculated based on the square of the difference between actual and expected covers for each plot and totals were summed for each species for each guild (see Appendix 3). Expected cover (E) for guilds I, II and III was calculated as follows:

Guild I: $E_{NO} = \Sigma X_{NO} / 15$

$E_{20} = (\Sigma X_{20} + \Sigma X_{50}) / 30$

$E_{50} = (\Sigma X_{20} + \Sigma X_{50}) / 30$

Guild II: $E_{NO} = (\Sigma X_{NO} + \Sigma X_{20}) / 30$

$E_{20} = (\Sigma X_{NO} + \Sigma X_{20}) /30$

$E_{50} = \Sigma X_{50} / 15$

Guild III: $E_{NO} = \Sigma X_{NO} / 15$

$E_{20} = (\Sigma X_{NO} + \Sigma X_{50}) / 30$

$E_{50} = \Sigma X_{50} / 15$

X_{NO} = plot cover on islands with no deer

X_{20} = plot cover on islands with deer for less than 20 years

X_{50} = plot cover on islands with deer for more than 50 years

5 Results

5.1 Principal components analysis

Species loadings for PCA of edge plots (Table 1) revealed coherent meanings for the first five principal components, all five possessing eigenvalues over 1.0. The first principal component for edge data was interpreted as a measure of shrub cover between 50 and 150 cm, as well as forb cover, dunegrass, *Elymus mollis*, cover and species richness from 0 to 150 cm. High values for these measures tended to occur together or not at all. The second principal component for edge data was interpreted as a measure of shrub cover below 50 cm. The third principal component for edge data was interpreted as a measure of salal, *Gaultheria shallon*, cover from 0 to 150 cm. The fourth principal component for edge data was interpreted as a measure of red fescue, *Festuca rubra*, and other graminoid cover below 50 cm and the fifth principal component for edge data was interpreted as a measure of Sitka spruce, *Picea sitchensis*, from 0 to 150 cm.

Species loadings for PCA of interior plots (Table 2) revealed coherent meaning for the first three principal components, all of which possessed eigenvalues over 1.0. The first principal component for interior data was interpreted as a measure of shrub, forb and fern cover from 0 to 150 cm, as well as species richness from 50 to 150 cm. The second principal component for interior data was interpreted as a measure of salal cover from 0 to 150 cm. The third principal component for interior data was interpreted as a measure of tree cover from 0 to 150 cm.

Vegetation in plots on islands without deer consisted of a large number and a broad range of plant-types and plant species (Figs. 2 to 9). The composition of these plots varied greatly, ranging from those possessing highly diverse assemblages of shrubs

and forbs to those dominated by salal. Along the forest edge, plots dominated by dunegrass also occurred (Figs. 2, 3, and 4), while in the interior, ferns (sword fern, *Polystichum munitum,* bracken fern, *Pteridium aquilinum,* shield fern, *Dryopteris expansa,* and lady fern, *Athyrium filix-femina*) contributed abundant cover (Figs. 7 and 8).

Vegetation in plots on islands with more than 50 years of deer browsing was greatly simplified (PCA showed little spread between plots) relative to plots on islands without deer (Figs. 2 to 9). This was true both in the interior and at the edge of the forest. Fewer species and less cover, with greatly reduced cover of forbs, shrubs and ferns, occurred in plots on islands with greater than 50 years of browsing compared to plots on islands without deer. The limited cover of vegetation that occurred in plots on islands with greater than 50 years of browsing consisted mainly of coniferous tree seedlings, mostly Sitka spruce (Figs. 6, 8, and 9), red fescue (Fig. 5). Simplification of these plots was especially pronounced from 50-150 cm, where vegetation was nearly eliminated.

Vegetation in plots on islands with less than 20 years of browsing was more simplified than the vegetation in plots on islands without deer, but less simplified than the vegetation in plots on islands with more than 50 years of browsing. Along the forest edge, the cover and number of species in plots on islands with less than 20 years of browsing were intermediate to plots at the other two stages, consisting largely of Sitka spruce, red fescue, other grass species and a small amount of salal. In the interior, plots on islands with less than 20 years of browsing formed two groups with a single outlier plot (Figs. 7, 8, and 9). In the first group, plots were very similar to plots on islands with more than 50 years of browsing. In the second group, plots were more similar to plots on islands without deer, possessing dense cover of salal from 50-150 cm. Cover of salal

from 50 to 150 cm in interior plots was usually abundant on islands without deer and islands with deer for less than 20 years, but on islands with deer for greater than 50 years, salal was entirely missing in this stratum (Fig. 10). The outlier plot on islands with less than 20 years of deer browsing possessed abundant cover of trees (Figs. 8 and 9).

5.2 Response patterns of plant species to herbivory

We identified four basic response patterns describing the ways in which different plant species were affected by deer over time (Fig. 1). Although variation between islands was often large, the average of measures within categories resulted in clear patterns. In the first pattern (guild I), cover is greatly reduced after less than 20 years of deer presence. In the second (guild II), cover is unchanged after less than 20 years but is greatly reduced by 50 years. In the third (guild III), cover gradually declines with longer deer presence. In the final pattern (guild IV), cover is unchanged or increased with deer presence.

Most forb, fern and shrub species exhibited a guild I pattern (Table 3). The lone grass species to exhibit this pattern, dunegrass, occurred exclusively on loose cobble substrate at the forest edge, alongside fireweed, *Epilobium angustifolium*, another abundant species that exhibited a guild I response. False lily-of-the-valley, *Maianthemum dilatatum*, thimbleberry, *Rubus parviflorus*, and salmonberry, *Rubus spectabilis*, guild I species which occurred in abundance in the interior of islands without deer, contributed little cover on islands with deer. Guild I species dominated the edge habitat of islands without deer but were slightly less prevalent in the interior of these islands (Figs. 11 and 12).

The guild II response pattern was exhibited exclusively by the shrub, salal (Figs. 10 to 12). Salal was abundant in both interior and edge habitat types on most islands (Figs. 11 and 12). Salal was the most abundant species in both habitats on Low and Lost islands (islands without deer), forming impenetrable thickets. On islands with less than 20 years of browsing, these thickets persisted and salal was again the most abundant species in both habitats. In either habitat on islands with more than 50 years of browsing, salal persisted only in inaccessible areas such as cliff faces and the tops of stumps.

Red fescue was the most abundant species in the forest edge to show the gradual reduction with increased deer presence of the guild III pattern (Fig. 11). Reduced cover in red fescue resulted primarily from reduced size rather than reduced numbers and although the absolute abundance of red fescue was decreased with deer over time, the remaining cover counted for a large amount of the total cover remaining in the understorey. The most abundant species in the forest interior to show a guild III pattern was sword fern (Fig. 12), which occurred as many densely packed large individuals (over 1.5 m tall) in limited areas on both cliffs and flats of islands without deer. On islands with less than 20 years of browsing, sword fern was browsed heavily where it was accessible, at times retaining only a few fronds, none of them new growth, but nonetheless maintained substantial cover. On islands with more than 50 years of browsing, sword fern occurred only in inaccessible areas. Red huckleberry, *Vaccinium parvifolium*, also exhibited a guild III pattern. Remnant populations of this shrub occurred in both habitats on islands with deer, but in a highly modified state. Mature individuals were heavily browsed and largely defoliated below 1.5 m, however numerous seedlings persisted. These also showed signs of repeated browsing but often grew within

a thick layer of lanky moss, *Rhytiadelphus loreus,* which appeared to offer limited protection. Another species to exhibit a guild III pattern, licorice fern, *Polypodium glycyrrhiza,* commonly grew on cliff faces or was often epiphytic.

Graminoids that exhibited guild IV pattern include Nootka reedgrass, *Calamagrostis nutkaensis,* and many-flowered wood-rush, *Luzula multiflora.* Tree species that exhibited a guild IV pattern were Sitka spruce and western hemlock, *Tsuga heterophylla.* Browsed Sitka spruce individuals, below 1.5 m, often occurred in *bonsai* form, possessing densely packed foliage within a layer of protruding dead branches. Western hemlock individuals occasionally occurred within this protective layer of dead Sitka spruce branches. Three exotic forb species exhibited a guild IV pattern.

6 Discussion

6.1 The process of deer modification

The impact of deer upon the forests of Haida Gwaii has been a progressive and systematic simplification of the forest understorey. The forest understorey on islands without deer consisted of a dense array of forb, shrub, fern, grass and tree cover. On islands with less than 20 years of deer browsing, forb, shrub and fern cover was greatly reduced. On islands with more than 50 years of deer browsing, the understorey was virtually empty; only tree and grass cover occurred in any abundance. Examination of the response of individual species revealed patterns largely consistent with the plant-type cover pattern. Most forb, shrub and fern species exhibited a response with a large reduction in cover on islands with deer. Most grass and tree species exhibited a response

pattern of either gradually reduced cover or increased cover with longer durations of deer modification.

Forb species usually provide most of the summer forage for deer (McCaffery et al. 1974). Highly preferred forb species such as fireweed provide easily digestible, high-energy food for deer (Bunnell 1990). However many forb species are highly susceptible to repeated browsing and experience greatly reduced abundance at high deer densities (Miller et al. 1992, Rooney 1997, Rooney and Dress 1997, Augustine et al. 1998, Rooney 2001, Waller in press). In our study, the cover of forbs was greatly reduced on islands with deer and most forb species exhibited a guild I response. The two forb species to exhibit a guild III response, blue-eyed grass, *Sisyrinchium littorale*, and purple willow herb, *Epilobium ciliatum*, usually occurred in the cracks of rocks at the shoreline. Of the five forb species to exhibit a guild IV response, three (bull thistle, *Cirsium vulgare*, marsh cudweed, *Gnaphalium uliginosum*, and wood groundsel, *Senecio sylvaticus*) were introduced species. The fourth (coastal pearlwort, *Sagina maxima*) occurred as a low lying plant in the cracks of rocks on the shoreline, while the fifth, sweet-scented bedstraw, *Galium triflorum*, was strongly associated with Nootka reedgrass. None of the seven was common or abundant.

Ferns are also a heavily used food source for black-tailed deer in western forests (Cowan 1945, Pojar et al. 1980, Bunnell 1990) as well as for black bear, *Ursus americanus* (Pojar et al. 1980). The fronds of deer fern, *Blechnum spicant,* and the rhizomes of shield fern provide an important winter food source, while the fiddle-heads of bracken fern provide an important spring food source for black-tailed deer (Cowan 1945, Bunnell 1990, Gillingham et al. 2000). However, on Haida Gwaii, lady fern, shield

fern and sword fern appear to be higher preference food items than either deer fern or bracken fern (Pojar et al. 1980). Most ferns are relatively rare in Haida Gwaii except deer fern, which is still common as small browsed rosettes, and sword fern, which is locally abundant in the second-growth forests on Graham Island but rare elsewhere (Pojar et al. 1980). The effect of white-tailed deer, *Odocoileus virginianus,* on ferns in eastern forests is profoundly different. There, ferns are usually low preference food items and selective browsing by deer contributes to the formation of fern glades (mostly hay-scented fern, *Dennstaedtia punctilobula*, and New York fern, *Thelypteris noveboracensis*) that can interfere with tree seedling recruitment (Horsley and Marquis 1983, Waller in press). Intermediate shield fern, *Dryopteris intermedia*, sword fern and lady fern are considered deer-resistant plants by nurseries in eastern North America (Deer-resistant landscape nursery 2000). In our study, the cover of ferns was greatly reduced on islands with deer. All fern species adhered to this pattern (guild I), except sword fern and licorice fern, which showed only gradual reduction with increased deer presence (guild III).

Deer are generally thought to avoid grasses, sedges, and rushes in favour of forbs and shrubs. However, many grasses are heavily utilized by black-tailed deer in spring and summer forage (Bunnell 1990). Cowan (1945) found that several sedge species were heavily utilized by Columbia black-tailed deer in some habitats on Vancouver Island but were hardly utilized in others. Woodward et al. (1994) recorded that black-tailed deer and elk, *Cervus elaphus*, browsing in Washington maintained grassy patches by limiting salmonberry and huckleberry. Similarly, selective browsing by white-tailed deer in eastern forests contributes to the formation of grassy areas that interfere with tree

seedling recruitment (Horsley and Marquis 1983, Waller in press). In our study, the cover of graminoids (excluding that of dunegrass), was only minimally affected by deer. While the cover of most graminoid species declined gradually with longer deer presence (guild III), the cover of Nootka reedgrass (guild IV) was substantially higher on islands with deer for less than 20 years than on other islands. This pattern may be strongly influenced by habitat availability as Nootka reedgrass is associated with lightly-wooded draws (Gaston et al. in press), a habitat type which is present on islands without deer and islands with deer for less than 20 years but absent on both islands with deer for more than 50 years. Dunegrass (guild I) occurred exclusively on loose cobble substrate at the forest edge.

In the coastal western forest, shrubs provide a large and important component of deer forage throughout the year (Bunnell 1990). Because the nutrient availability of woody plants changes greatly with the seasons, deer usually switch from species to species as the year progresses (Wallmo and Schoen 1981). Rubus and willow species provide important spring forage, while huckleberry provides important winter forage (Cowan 1945, Bunnell 1990). Salal does not digest well on its own, but makes up an important component of both summer and winter diets when eaten with arboreal lichens (Bunnell 1990). As such, deer tend to focus on a small number of shrub species for a limited period of time, intensifying their impact as a large percentage of the edible plant tissue on a single plant may be taken all at once. Furthermore, as new growth of woody species is easier to digest than established branches and leaves (new growth contains less lignin and more starch), deer usually select for new leaves and twigs (Bunnell 1990). This behaviour, coupled with the sedentary lifestyle of deer with few predators (see

chapter 1), appears to lead to the demise of many shrub species on Haida Gwaii. As new sprouts, suckers and buds are repeatedly browsed, the plant is unable to regenerate. The abundance of salmonberry, devil's club, *Oplopanax horridus*, false azalea, *Menziesii ferruginea*, red huckleberry, and salal have all been greatly reduced in forests of Haida Gwaii since the introduction of deer (Pojar et al. 1980). In our study, shrub cover was reduced in a multiple-step process. Most shrubs (guild I) were far less abundant on islands with deer than on islands without deer. However, limited cover of red huckleberry (guild III) occurred on islands with deer, mainly as scattered seedlings. Salal (guild II) occurred in abundance on islands with less than 20 years of browsing, but was greatly reduced on islands with more than 50 years of browsing.

The impact of deer on the growth and survival of tree seedlings has been recognized for many years (Leopold et al. 1947). In eastern forests, eastern hemlock, *Tsuga canadensis*, and eastern white cedar, *Thuja occidentalis*, seedlings are highly susceptible to deer browsing (Anderson and Loucks 1979, Frelich and Lorimer 1985, Alverson et al. 1988, Epstein et al. 1999). On Haida Gwaii, western red cedar, *Thuja plicata*, is known to be a highly preferred browse-item and deer browsing severely limits its regeneration over the archipelago (Pojar et al. 1980, Coates et al. 1985, Daufresne and Martin 1997, Baltzinger and Martin 1998, Pojar 1999). Sitka spruce and western hemlock can also be heavily browsed (Vila 2002) especially in the winter and early spring when herbaceous vegetation is scarce (Bunnell 1990). However, Daufresne and Martin (1997) suggest that through reduced competition with depleted shrub species, browsing can favour regeneration of Sitka spruce. In our study, tree cover was highest on islands with deer for 20 years. The covers of Sitka spruce and western hemlock were

largely responsible for this trend (guild IV). Cover of western red cedar (guild I) was greatly reduced on islands with deer as was the cover of deciduous trees (Pacific crabapple, *Malus fusca*, Scouler's willow, *Salix scouleriana*, and Sitka alder, *Alnus crispa ssp. Sinuate*; all guild I species).

6.2 Community simplification

Deer browsing appears to have greatly simplified the plant communities of the forest understorey in Laskeek Bay. Systematic declines in the abundance of guild I and II species have led to highly uniform community composition on deer-affected islands. Based on the plant existing communities at three points in the deer modification process we were able to trace the probable progress of simplification as follows. As sensitive forb and shrub species (guild I) were stripped away, the communities that remained were either salal-(guild II) dominated or consisted of sword fern, conifer and grass species (guilds III and IV). As deer modification progressed, salal and sword fern were greatly reduced and guild IV species became proportionally dominant in almost all plots. The large variation in community composition that occurred on islands without deer was replaced by a highly uniform grass and tree dominated community after 50 years of deer modification. With intense deer browsing pressure, community composition has evidently become predicated on the ability of a plant to withstand herbivory rather than its competitive ability or ability to withstand environmental conditions. Other studies have revealed similar outcomes of the process of deer modification (Anderson and Loucks 1979, Frelich and Lorimer 1985, Alverson and Waller 1997, Waller and Alverson 1997). The process is one of biotic *homogenization* (McKinney and Lockwood 1999) where sites become increasingly similar to one another. Simplified communities such as

this possess little redundancy and may be less likely to be able to adapt to secondary perturbation (Ehrlich and Walker 1998, Naeem 1998).

Biotic homogenization often progresses undetected by simple species counts as native species decline and introduced species become more abundant (McKinney and Lockwood 1999, McKinney 2002). In many systems across North America, introduced plant species with greater resistance to herbivory have invaded herbivore-modified communities (Laycock 1991). Deer may facilitate the invasion of introduced plant species in a number of ways. Firstly, by reducing the abundance of native plants, competition is reduced and successful colonisation of introduced species becomes easier (Cabin et al. 2000). Secondly, disturbance created by trampling and tearing is known to greatly increase the likelihood of introduced plant species becoming established (Crawley 1987, Burke and Grime 1996, Crawley et al. 1999). Thirdly, deer may act directly as seed vectors, transporting seed from one island to another (Vitousek 1988). Woodward et al. (1994) reported an increased abundance of introduced plant species in areas subject to browsing by black-tailed deer and elk. Waller (in press) found an increased percentage of non-native species over time in forests in Wisconsin modified by white-tailed deer. George and East Copper Islands, islands to the south of Laskeek Bay (inhabited by deer), both possessed large populations of the exotic wildflower, common foxglove, *Digitalis purpurea* (pers. obs.). In Laskeek Bay, introduced species generally followed a guild IV pattern and became more prevalent on islands with deer. However, the proximity of these islands to the main island chain and to human habitation makes it impossible to separate the effect of deer on the influx of exotic plant species from the effects of natural

and human aided seed dispersal. Determining the role of deer in facilitating the invasion of introduced plant species to the islands of Haida Gwaii will require further study.

6.3 The traits of a survivor

The effect of a herbivore on any given plant species is usually derived from a combination of the ability of a plant to sustain tissue loss and its palatability to the herbivore (Huston 1979, Augustine and McNaughton 1998). However, the relative importance of these factors is likely to vary depending on the intensity of the herbivore pressure. As the intensity of browse increases, a third factor, the accessibility of plant tissue to the herbivore, becomes increasingly important to the survival of a plant. With low densities of deer, the most preferred plant species experience the highest level of tissue loss (Rhoads 1997). With moderate densities, plant species composition is often greatly affected by selective foraging and differential recovery (Marquis 1981, Tilghman 1989, McInnes et al. 1992). High-density deer populations have the potential to bring about a complete switch in community types if all species are edible (Healy 1971, Marquis 1974). However, as deer density increases, selectivity decreases, because availability of preferred forage is greatly reduced (Augustine and McNaughton 1998). As the availability of forage decreases, the proportion of the plant removed increases, and the ability of the plant to sustain tissue loss can be quickly exhausted (Burt 1949). Systems without an evolutionary history of intense herbivore modification, are unlikely to possess many highly defended or toxic species (Vourc'h et al. 2001) so any accessible plant is likely to eventually fall prey to herbivory. Plant tissue is also vulnerable to the effects of trampling and breaking associated with large animals (Crawley 1997b). As such, the ability of a plant to minimize tissue loss can become the key factor in its

survival. If seed production can also continue throughout periods of intense herbivory, a plant species may be well positioned to recover after a cessation in browsing pressure. In situations of high-density deer populations over long periods of time, the presence of herbivore-inaccessible foliage and reproductive mechanisms becomes the key factor in a plant's survival.

We identified four common features among plant species that demonstrated low sensitivity to browsing, each of which appeared to reduce the accessibility of plant tissue to browsing. The first feature was an induced physical barrier creating refuge for new tissue. Constitutive physical defenses such as the thorns, spines, and prickles of black gooseberry, *Ribes lacustre*, and Nootka rose, *Rosa nutkana*, provided little protection from the long-term effects of deer. Similarly, the heavily armed devil's club, *Oplopanax horridus*, has been greatly reduced over much of Haida Gwaii (Pojar et al. 1980, Pojar 1999). Dense thickets of salal, a low preference diet item (Cowan 1945), offered adequate protection to new growth for less than 20 years but gave out after more than 50 years of sustained deer modification. In contrast, the induced physical response of Sitka spruce appeared to remain quite effective over time. Browsed Sitka spruce individuals often produced a dense, highly branched outer barrier of dead branches with foliage occurring inside, making it less accessible to browsers. Woody plants in herbivore-dominated systems commonly develop protective surfaces of branches in response to herbivory (Vesey-Fitzgerald 1972). Graminoid species, which were also little affected by deer, are known to respond similarly, with the basal meristem protected by the dense branching of old foliage (Caughenor 1985). Physical protection arising in response to

deer herbivory appeared to provide better protection over the long run than constitutive thorns and prickles.

The second feature we identified was plant morphology that allowed for the production of foliage beyond the reach of deer, atop a rigid stem. Growth atop a rigid stem necessitates that the stem is both tall and rigid enough to keep foliage and developing seeds out of the immediate reach of deer. Salal and red huckleberry both possess rigid upright stems and were less affected than other shrubs after less than 20 years of deer modification, (guilds II and III respectively). Both species maintain foliage and develop seeds above the browse-line even when foliage is severely reduced beneath it (Martin and Daufresne 1999). However, recruitment through the browse-zone leaves these species susceptible to eradication as old plants die. Furthermore, deer occasionally push over these shrubs to get at upper foliage (Stockton et al. 2001). As such, mature individuals were relatively rare after more than 50 years. The thicker stems and longer lifespan of Sitka spruce, coupled with the induced protection of dead branches through the period of recruitment through the browse-zone, proved effective even after more than 50 years of deer modification.

Habitat tolerance for vertical surfaces proved to be another important indicator of deer resistance. In our natural laboratory, cliff faces on islands with deer invariably showed dense vegetation similar to that found on islands free of deer (Stockton et al. 2001). Sword fern and salal were common species on these cliff faces on all islands regardless of the presence of deer. Epiphytes such as licorice fern, *Polypodium glycyrrhiza*, also managed to escape deer browsing.

Defensive associations can also offer limited protection from herbivory (Hjalten and Price 1997). On islands with deer, areas of thick lanky moss contained seedlings of highly palatable species such as red huckleberry. Although western hemlock is not known as a highly palatable species (Cowan 1956, Pojar and Banner 1984), in heavily modified areas, small individuals often occurred within a protective layer of dead Sitka spruce branches.

6.4 Implications for management

Based on the processes revealed in our natural laboratory we were able to determine that the deer modification of forest systems is likely to progress in a series of punctuated steps based on the relative sensitivity of plants to deer browsing. Without an evolutionary history of herbivore modification, plant sensitivity to high-density deer over an extended period of time appears to be a function of accessible plant tissue. The consideration of this process by wildlife managers can clarify habitat management for many forest species.

The persistence of less sensitive species may provide limited habitat for many years to species dependent on the structure provided by a forest understorey. This stage could be potentially perpetuated with only short-term manipulation of herbivore populations. Although hunting in coastal areas has shown little long-term effect on black-tailed deer population numbers (Connolly 1981), hunting pressure can reduce the sedentary behaviour of deer and has been shown to increase the abundance of highly browse-sensitive plant species (Batzinger and Martin 1998). An interruption in browsing pressure, long enough to allow recruitment of stems above the browse-line could greatly extend the persistence of many shrub species. Other measures such as herbivore

exclosures placed to conserve browse-sensitive plant species could help to perpetuate seed production and forestall some of the potential cascading effects of forest simplification such as pollinator failure (Cox and Elmqvist 2000). By manipulating the natural processes at work in a herbivore-modified forest system, wildlife managers can maximize their efforts and may be able to maintain suitable habitat in these regions for a great many species.

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Table 1: Principal Components factor loadings of 14 synthetic vegetation measures at the forest edge. Synthetic measures were developed from cover estimates for each species in each plot for 0- to 50-cm and 50- to 150-cm strata, which were grouped according to plant-type (tree, shrub, forb, fern, and graminoid) except in the cases where the cover of individual species averaged more than 2% cover in either stratum and was considered as a separate measure. Factor loadings over 0.60 are shown in bold.

Measure	PC 1	PC 2	PC 3	PC 4	PC 5
Species richness 0–50 cm	**0.72**	0.37	-0.066	0.18	-0.0059
Species richness 50-150 cm	**0.89**	0.28	-0.029	-0.079	-0.0027
Sitka spruce cover 0-50 cm	-0.23	0.24	-0.040	0.036	**-0.77**
Sitka spruce cover 50-150 cm	-0.055	0.48	0.14	-0.016	**-0.68**
Shrub cover 0-50cm	0.50	**0.60**	-0.21	-0.29	0.20
Shrub cover 50-150cm	**0.71**	0.39	-0.26	-0.32	0.11
Gaultheria shallon cover 0-50 cm	-0.12	0.41	**0.80**	0.12	0.083
Gaultheria shallon cover 50-150 cm	0.16	0.52	**0.67**	0.20	0.22
Forb cover 0-50 cm	**0.78**	-0.10	-0.16	-0.021	-0.14
Forb cover 50-150 cm	**0.80**	-0.33	-0.050	0.065	-0.24
Graminoid cover 0-50 cm	-0.026	0.22	-0.42	**0.73**	0.12
Elymus mollis cover 0-50 cm	0.69	-0.46	0.34	0.30	-0.066
Elymus mollis cover 50-150cm	0.70	-0.49	0.30	0.29	-0.087
Festuca rubra cover 0-50 cm	-0.16	0.33	-0.34	**0.72**	0.036
Explained Variation (s.d.)	4.40	2.18	1.76	1.50	1.26
Proportion of Total Variation	0.31	0.16	0.13	0.11	0.09

Table 2: Principal Components factor loadings of 12 synthetic vegetation measures in the forest interior. Synthetic measures were developed from cover estimates for each species in each plot for 0- to 50-cm and 50- to 150-cm strata, which were grouped according to plant-type (tree, shrub, forb, fern, and graminoid) except in the cases where the cover of individual species averaged more than 2% cover in either stratum and was considered as a separate measure. Factor loadings over 0.60 are shown in bold.

Measure	PC 1	PC 2	PC 3
Species richness 0-50 cm	0.49	0.34	0.22
Species richness 50-150 cm	**0.89**	-0.33	-0.07
Shrub cover 0-50cm	**0.84**	0.18	-0.06
Shrub cover 50-150cm	**0.89**	0.05	0.03
Forb cover 0-50 cm	**0.80**	-0.24	0.22
Fern cover 0-50 cm	**0.85**	0.03	0.22
Fern cover 50-150 cm	**0.86**	-0.11	0.23
Gaultheria shallon cover 0-50 cm	0.02	**-0.91**	-0.31
Gaultheria shallon cover 50-150 cm	-0.01	**-0.93**	-0.30
Tree cover 0-50 cm	0.22	0.46	**-0.80**
Tree cover 50-150 cm	0.50	0.26	**-0.78**
Graminoid cover 0-50 cm	-0.26	0.14	-0.02
Explained variation	5.00	2.32	1.66
Proportion of total variation	0.42	0.19	0.14

Table 3: The response guilds of different plant-types showing the number of species of each plant-type (Tree, Shrub, Wildflower, Fern, Graminoid) fitting each response pattern (I, II, III, IV). Twenty-three species were not included in any response guild because individuals were only encountered within sample plots on a single island.

Plant-type	I	II	III	IV
Tree (7)	4	0	1	2
Shrub (11)	9	1	1	0
Forb (38)	31	0	2	5*
Fern (5)	4	0	1	0
Graminoid (10)	1	0	7	2
Total (94)	49	1	12	9

* including three exotic species

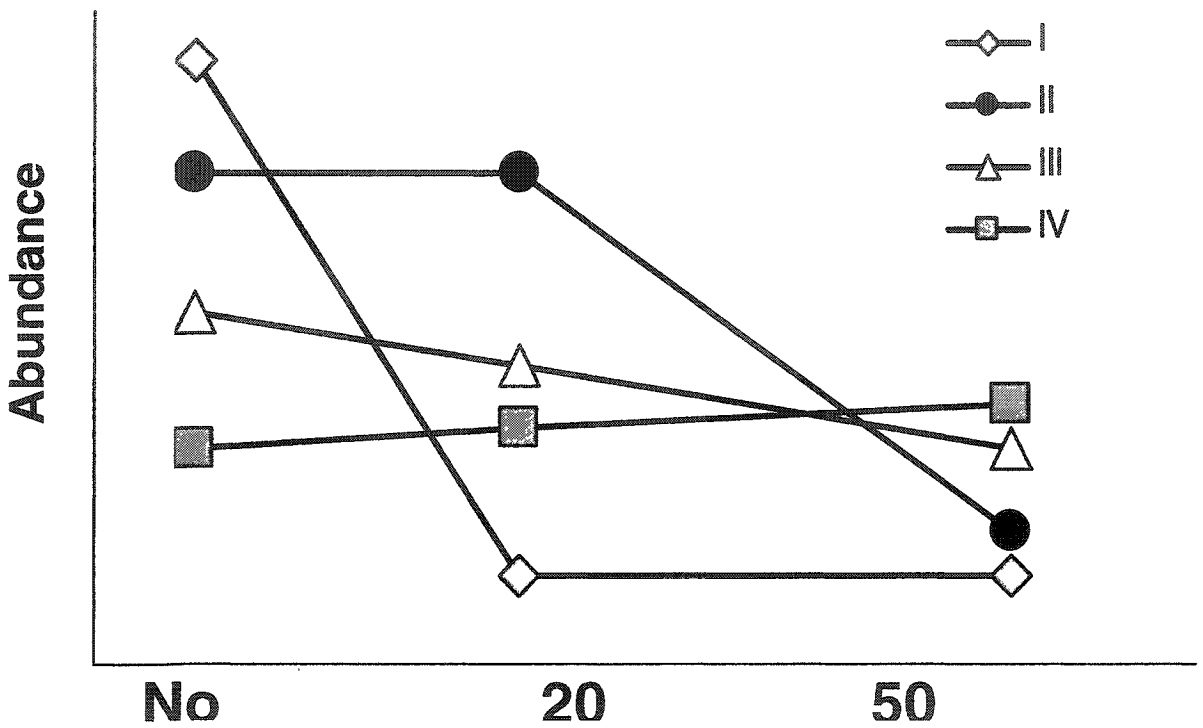


Figure 1: Four theoretical response patterns of vegetation to modification by deer. Species were classified to guilds according to which pattern best described their average cover on islands at three levels of browsing.

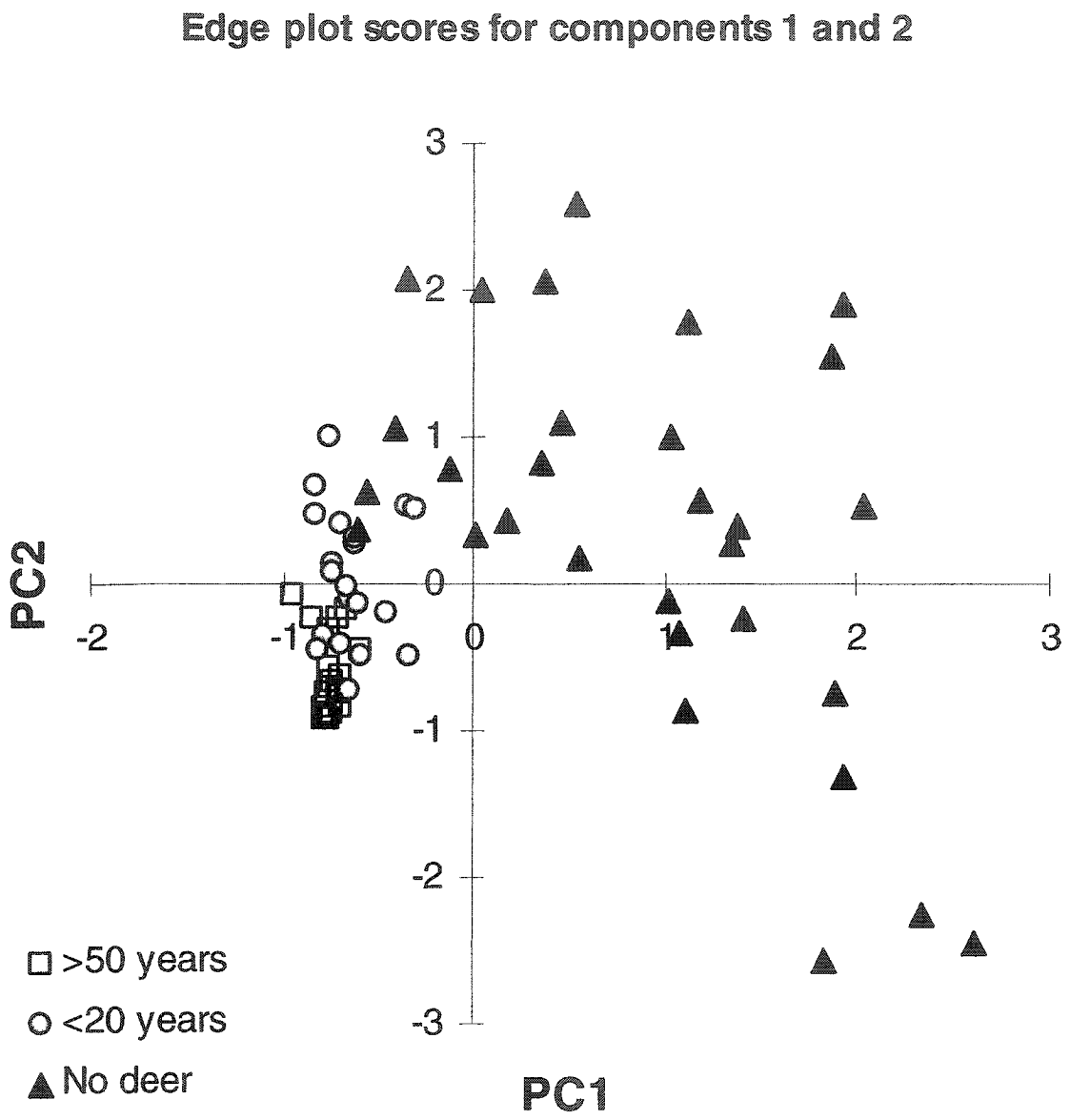


Figure 2: Principal Components Analysis, PCA, of edge vegetation, showing principal components 1 and 2 of 14 synthetic measures of vegetation from 0-150 cm (see Table 1) in 70 edge plots with three different browsing histories. PC 1 explains 31% of the variation in the data set and has factor loading above 0.60 for shrub cover between 50 and 150 cm, as well as forb cover, *Elymus mollis* cover and species richness from 0 to 150 cm. PC 2 explains 16% of the variation in the data set and represents shrub cover below 50 cm. Axes are unrotated and represent principal eigenvalues in the data set.

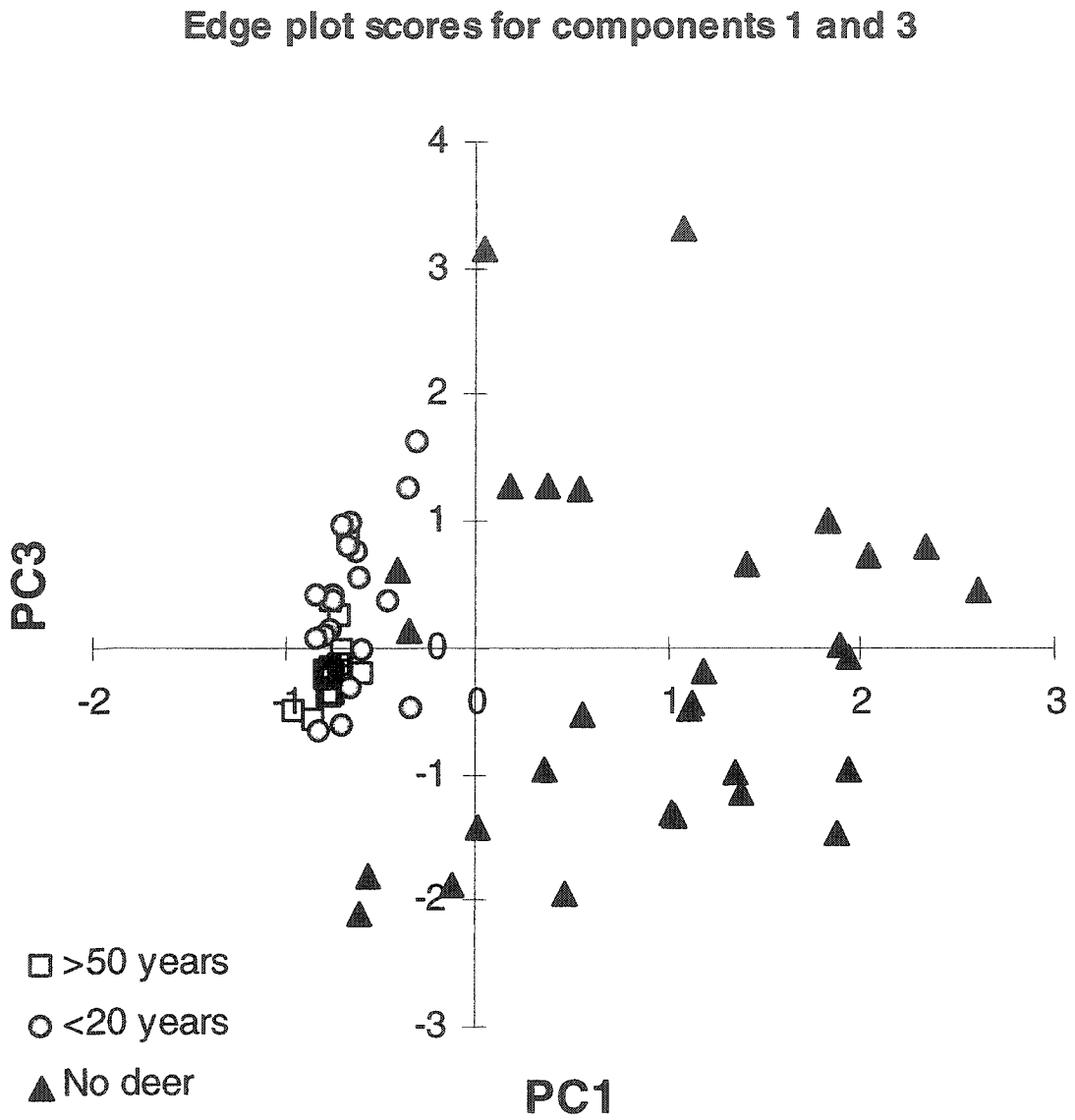


Figure 3: Principal Components Analysis, PCA, of edge vegetation, showing principal components 1 and 3, for 14 synthetic measures of vegetation from 0-150 cm (see Table 1) in 70 edge plots with three different browsing histories. PC 1 explains 31% of the variation in the data set and has factor loading above 0.60 for shrub cover between 50 and 150 cm, as well as forb cover, *Elymus mollis* cover and species richness from 0 to 150 cm. PC 3 explains 13% of the variation in the data set and has a factor loading of over 0.60 for *Gaultheria shallon* cover below 150 cm. Axes are unrotated and represent principal eigenvalues in the data set.

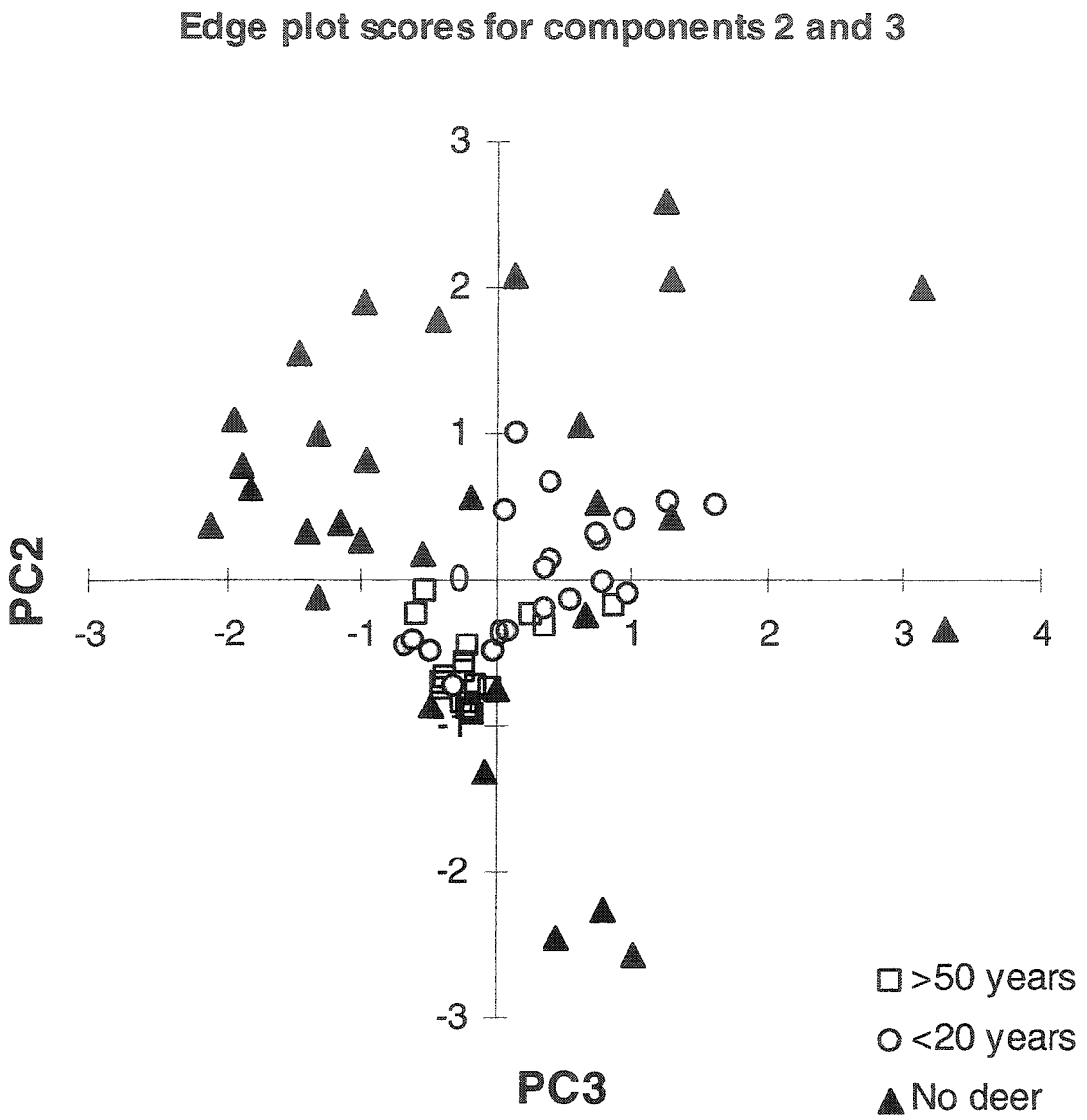
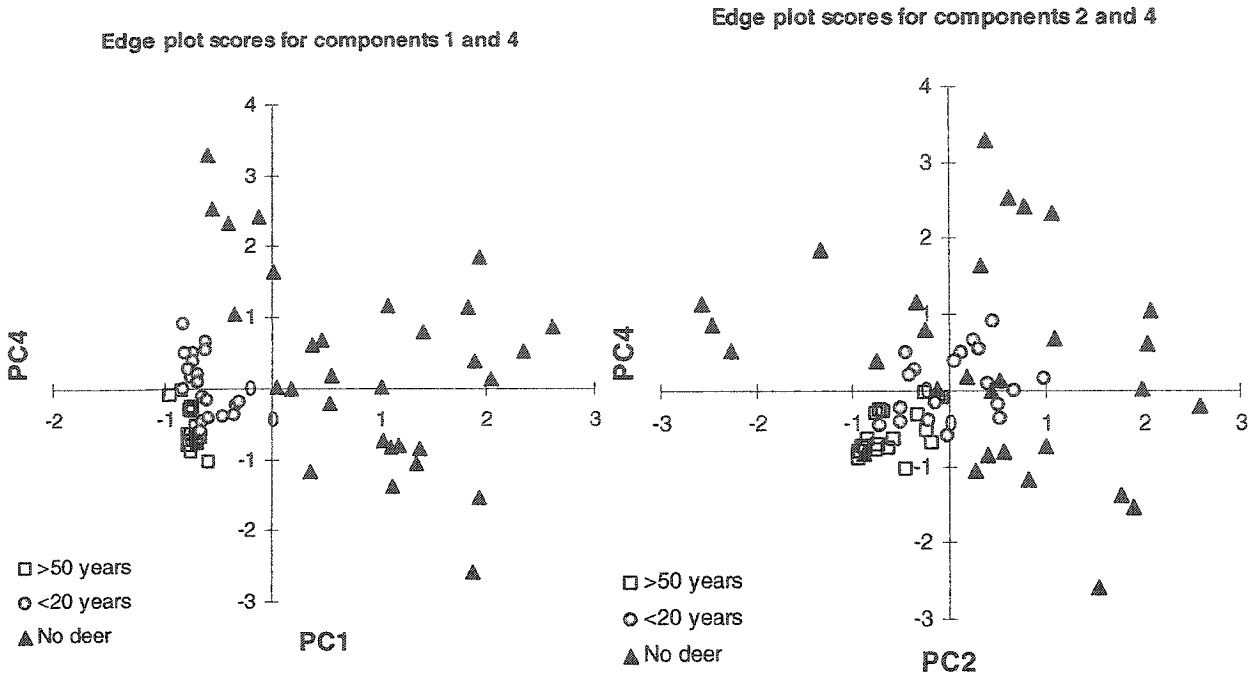


Figure 4: Principal Components Analysis, PCA, of edge vegetation, showing principal components 2 and 3 of 14 synthetic measures of vegetation from 0-150 cm (see Table 1) in 70 edge plots with three different browsing histories. PC 2 explains 16% of the variation in the data set and represents shrub cover below 50 cm. PC 3 explains 13% of the variation in the data set and has a factor loading of over 0.60 for *Gaultheria shallon* cover below 150 cm. Axes are unrotated and represent principal eigenvalues in the data set.



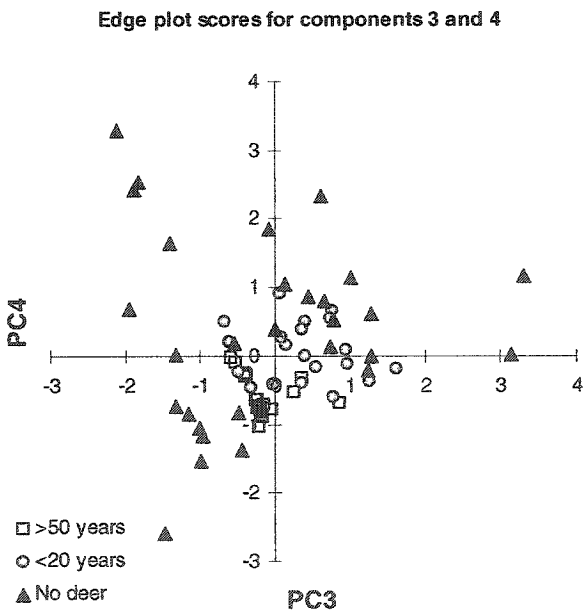


Figure 5: Principal Components Analysis, PCA, of edge vegetation, showing principal component 4 against principal components 1, 2 and 3, for 14 synthetic measures of vegetation from 0-150 cm (see Table 1) in 70 edge plots with three different browsing histories. PC 4 explains 11% of the variation in the data and has factor loadings over 0.60 for *Festuca rubra* and other graminoid cover below 50 cm. Axes are unrotated and represent principal eigenvalues in the data set.

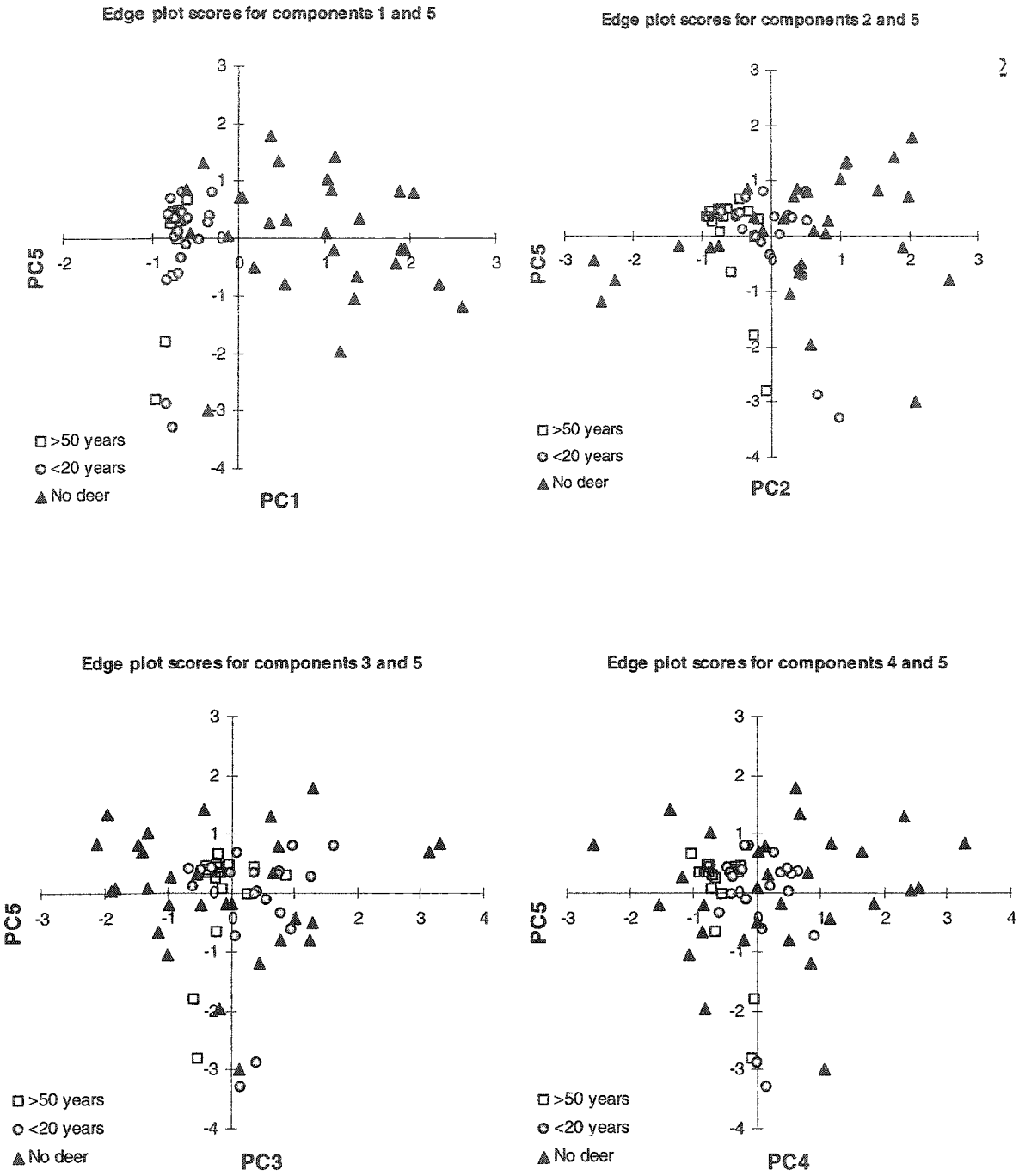


Figure 6: PCA, of edge vegetation, showing PC 5 against PCs 1, 2, 3 and 4, for 14 synthetic measures of vegetation from 0-150 cm (see Table 1) in 70 edge plots with three different browsing histories. PC 5 explains 9% of the variation in the data and has factor loadings of over 0.60 for *Picea sitchensis* below 150 cm. Axes are unrotated and represent principal eigenvalues in the data set.

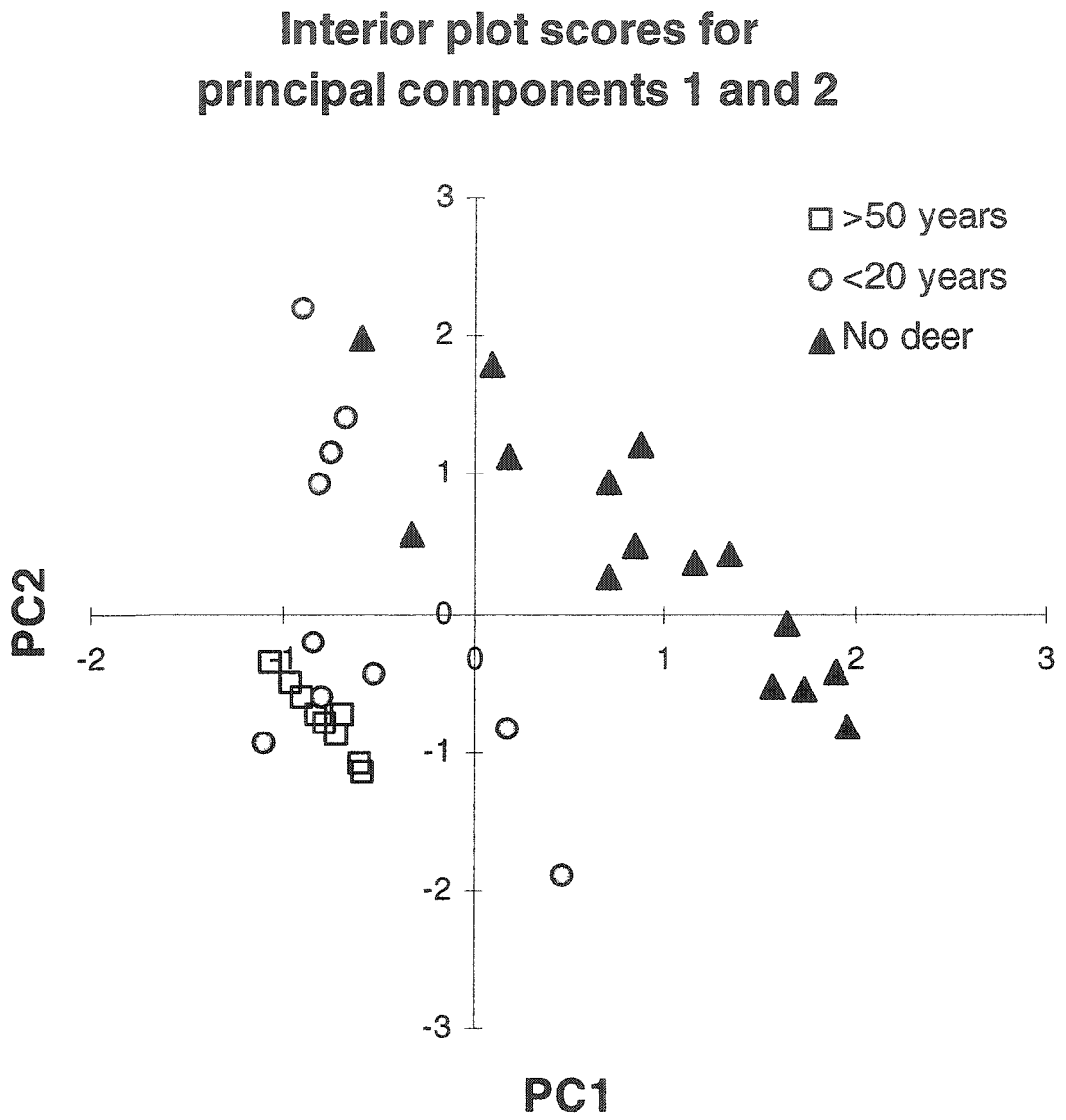


Figure 7: Principal Components Analysis, PCA, of interior vegetation, showing principal components 1 and 2 of 12 synthetic measures of vegetation from 0-150 cm (see Table 2) in 35 interior plots with three different browsing histories. PC 1 explains 42% of the variation in the data set and has factor loading above 0.60 for species richness from 50 to 150 cm, forb cover below 50 cm, as well as shrub and fern cover cover below 150cm. PC 2 explains 19% of the variation in the data set and has factor loadings over 0.60 for the cover of *Gaultheria shallon* below 150 cm. Axes are unrotated and represent principal eigenvalues in the data set.

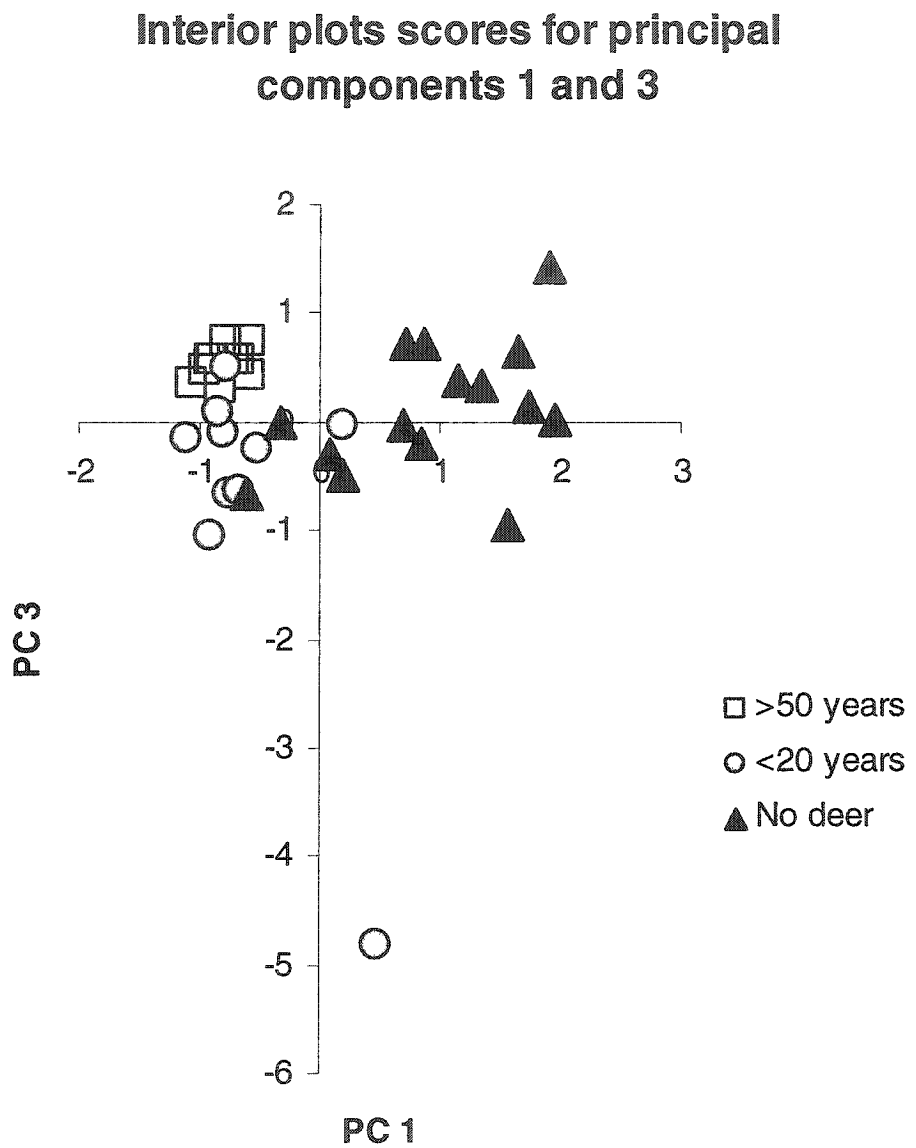


Figure 8: Principal Components Analysis, PCA, of interior vegetation, showing principal components 1 and 3 of 12 synthetic measures of vegetation from 0-150 cm (see Table 2) in 35 interior plots with three different browsing histories. PC 1 explains 42% of the variation in the data set and has factor loading above 0.60 for species richness from 50 to 150 cm, forb cover below 50 cm, as well as shrub and fern cover cover below 150cm. PC 3 explains 14% of the variation in the data set has factor loading over 0.60 for tree cover below 150 cm. Axes are unrotated and represent principal eigenvalues in the data set.

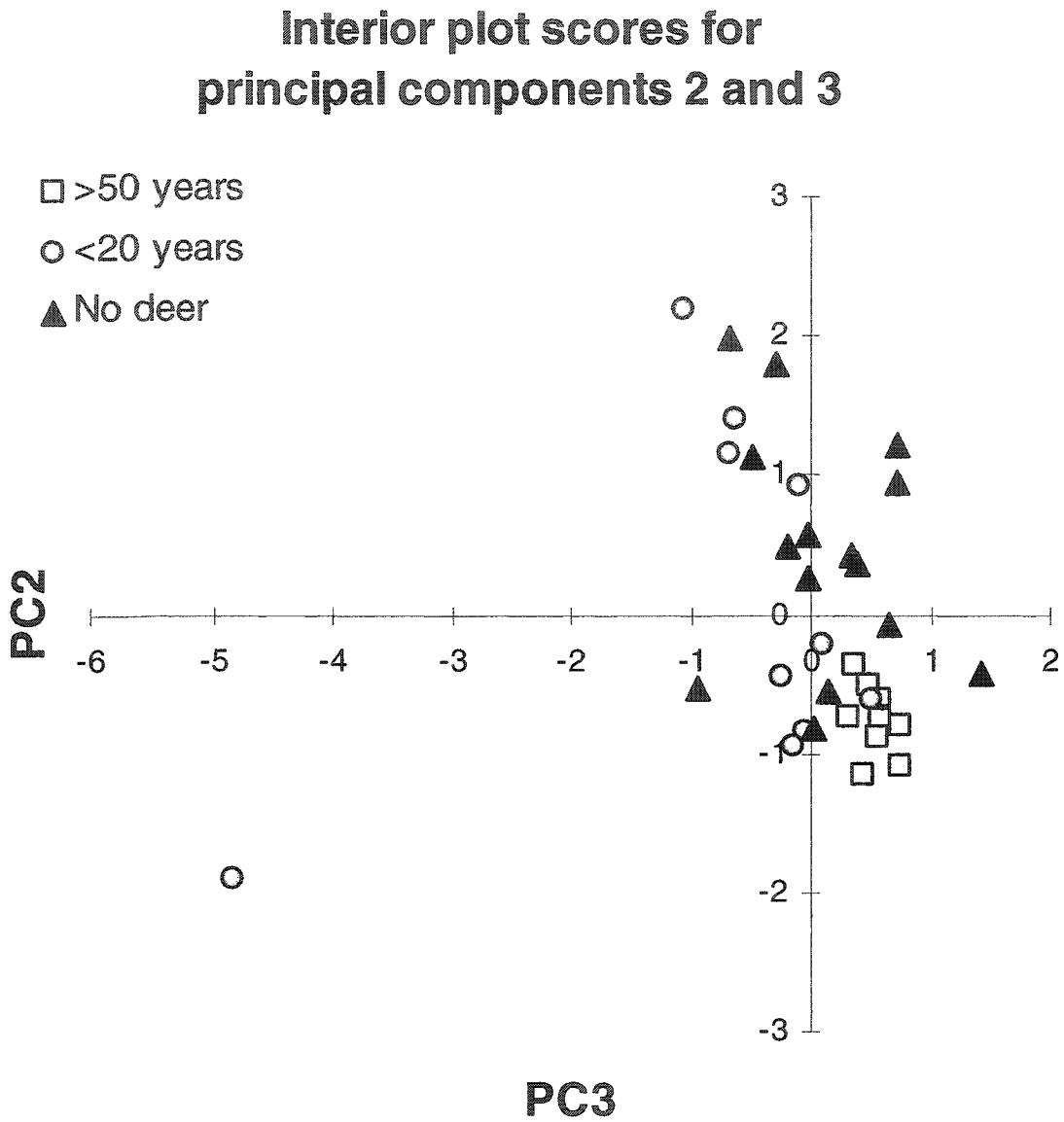


Figure 9: Principal Components Analysis, PCA, of interior vegetation, showing principal components 2 and 3 of 12 synthetic measures of vegetation from 0-150 cm (see Table 2) in 35 interior plots with three different browsing histories. PC 2 explains 19% of the variation in the data set and has factor loadings over 0.60 for the cover of *Gaultheria shallon* below 150 cm. PC 3 explains 14% of the variation in the data set has factor loading over 0.60 for tree cover below 150 cm. Axes are unrotated and represent principal eigenvalues in the data set.

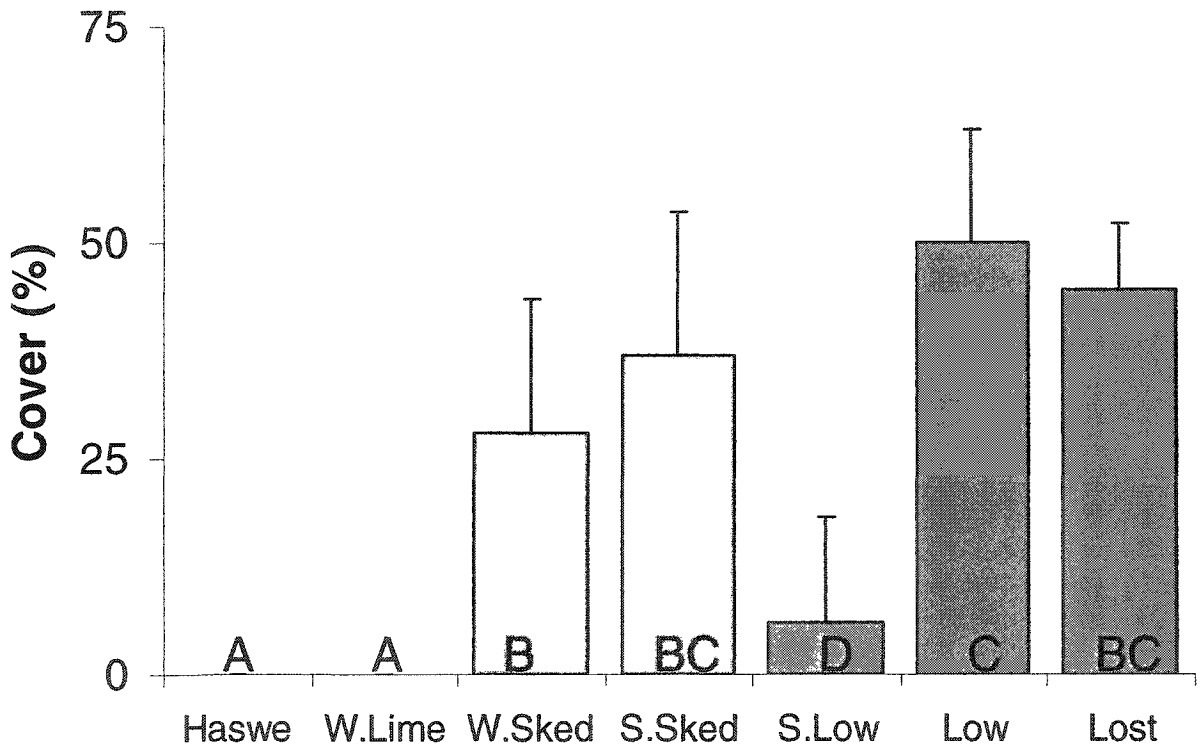


Figure 10: Average cover of *Gaultheria shallon* (+ SE) from 50 to 150 cm in forest interior plots on seven islands at three different browsing histories (n=5 for each island). Levels significantly different from one another (as determined through post-hoc Scheffe tests p=0.05) are denoted with different letters.

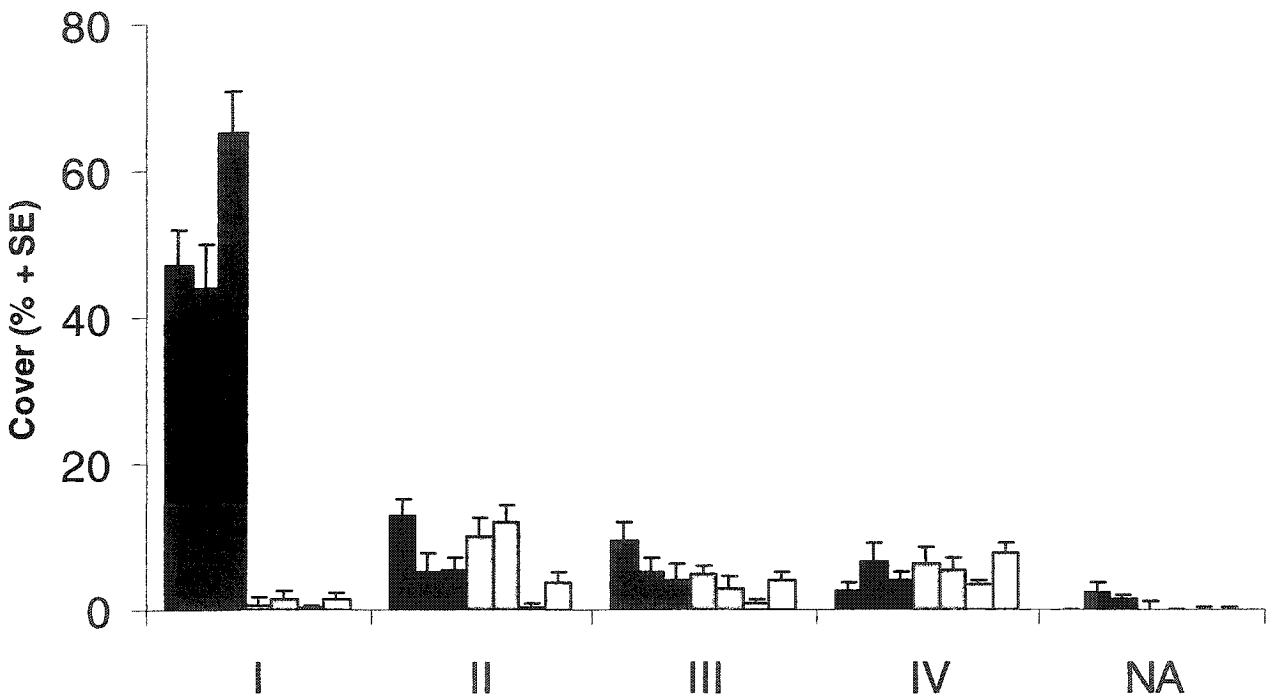


Figure 11: Average cover (+ SE) below 150 cm of guilds at the forest edge for seven islands at three levels of deer modification (black = no deer, grey = <20 years browsing, white = >50 years browsing). Guild membership was based on the response of individual plant species to deer browse.

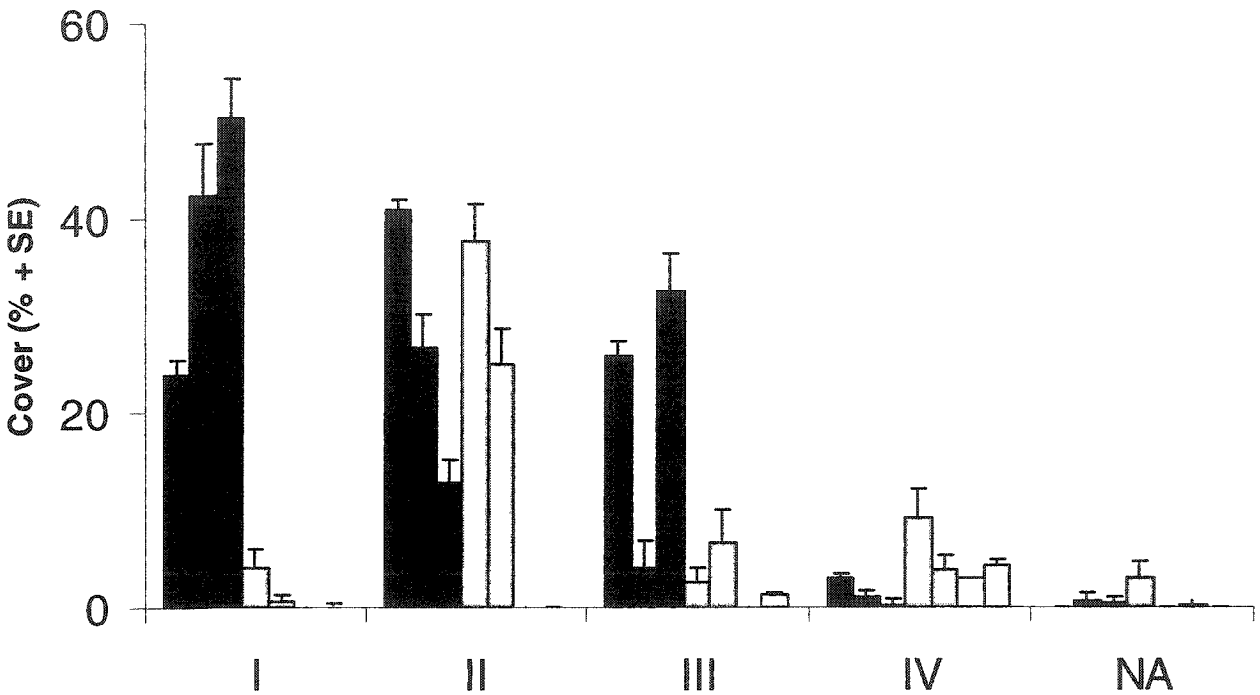


Figure 12: Average cover (+ SE) below 150 cm of guilds in the forest interior for seven islands at three levels of deer modification (black = no deer, grey = <20 years browsing, white = >50 years browsing). Guild membership was based on the response of individual plant species to deer browse.

Chapter 3:

Recovery of the forest understorey

following release from deer browsing

1 Abstract

Understanding the factors that affect the reversibility of herbivore-modified systems may be necessary for the conservation and rehabilitation of forest vegetation. Evidence to date suggests that the modification of plant communities through herbivory is not always reversible. In many ecological systems, habitat conversion exhibits a high degree of *hysteresis* or *multiple stable states*. In this study we utilized the cull of Sitka black-tailed deer from two large islands (295 ha and 170 ha) in Haida Gwaii as an experimental manipulation to investigate ecological release of forest plant communities from a large herbivore. Using a paired-island approach, deer were culled on two experimental islands but remained at unmodified densities on three adjacent control islands. Superficially, the recovery of vegetation after the release from deer browsing shows evidence of a high degree of resilience. Clear increases in species richness and cover as well as changes in the community composition of the forest understorey of experimental islands suggest a quick return to the forest understorey communities thought to exist before deer modification. However, failure of key shrub species to establish coupled with the development of closed canopy stands of Sitka spruce suggest a possible alternate stable-state for some communities. Management alternatives to avoid this alternate stable-state are discussed.

2. Hypothesis

After the pressure of deer browsing is reduced or eliminated, the cover of vegetation, and species richness in the forest understorey will increase relative to control sites with unchanged deer browsing pressure.

3. Introduction

Large herbivores are agents of major habitat change in many ecosystems (Anderson and Loucks 1979, Alverson et al. 1988, McInnes et al. 1992, Pastor et al. 1993, Augustine and McNaughton 1998, Cabin et al. 2000). Among these, deer are particularly important in shaping forest ecosystems (Leopold 1943, Tilghman 1989, Waller and Alverson 1997).

Over the past century, deer populations have greatly increased in North America, Europe and around the world (Alverson et al. 1988, Wardle and James 1973, Stewart and Burrows 1989, Warren 1991, Shimoda et al. 1994, Takatsuki and Gorai 1994, McCabe and McCabe 1997, Nomiya et al. 2003). As populations have grown, deer-modification of forests has become increasingly prevalent (Sullivan et al. 1990, Diamond 1992, Hester et al. 1991, Baines et al. 1994, Chapters 2 and 3). Deer have been implicated in the extensive modification of forest vegetation (Alverson et al. 1988, Warren 1991, Balgooyen and Waller 1995) and in some cases have been identified as a *keystone species* in forest ecosystems (Waller and Alverson 1997, Rooney 2001).

There are few clearer cases of the potential of deer to modify a forest system than the introduction of Sitka black-tailed deer to Haida Gwaii (Pojar et al. 1980, Pojar and Banner 1984, Pojar 1999). The addition of deer, the only large herbivore over large parts of the archipelago, to this predator-free system has resulted in a large reduction in the cover and diversity of forest understorey vegetation (see Chapter 1) and a radical simplification and shift in understorey plant composition (see Chapter 2).

As the potential for deer to modify forest ecosystems has revealed itself, a shift in deer management from establishing and augmenting deer herd expansion to controlling

deer population growth has taken place (McCabe and McCabe 1997, Rooney 2001). Because deer population expansion can be attributed, at least in part, to the virtual elimination of predators (mainly wolves, *Canis lupus* L., and cougars, *Puma concolor* L.) over most of North America (Marquis 1975, McCabe and McCabe 1997, Waller and Alverson 1997, Rooney 2001), forest and wildlife management have attempted to substitute human hunting for natural predation (Sullivan et al. 1990). However, modified forests over broad regions of North America bear little resemblance to those of even 200 years ago (Braun 1974) and the ability of plants to recover following the removal of deer browsing pressure is mostly unknown (Schmitz and Sinclair 1997).

Evidence to date suggests that the modification of plant communities through herbivory is not always reversible (Friedal 1991, Laycock 1991, Cabin et al. 2000). In many ecological systems, habitat conversion exhibits a high degree of *hysteresis* or *multiple stable states* (Holling 1973, Noy-Meir 1975, May 1977). A growing body of evidence suggests that it may be the norm for natural systems to shift to alternate stable-states after a large perturbation (Kneidal 1983, Robinson and Dickerson 1987, Barkai and McQuaid 1988, Dublin et al. 1990, Law and Morton 1993, Luh and Pimm 1993, Augustine and Frelich 1997, Schmitz and Sinclair 1997, Stromayer and Warren 1997, Cabin et al. 2000). Understanding the factors that affect the reversibility of herbivore-modified systems may be necessary for the conservation and rehabilitation of forest vegetation.

The use of exclosures, in which areas (usually less than 1 ha) are fenced off from herbivores, is a commonly used method to measure the recovery of vegetation after herbivore modification (Tansley and Adamson 1925, Frelich and Lorimer 1985, Alverson

et al. 1988, Tilghman 1989, Bowers 1993, Woodward et al. 1994, Nominya et al. 2003). However, the results of these studies can be affected by the limited size and numbers of exclosures used (e.g. Mueggler and Bartos 1977). Subjective placement of fences, and modification of soil moisture and soil temperature regimes by fences themselves, can also affect the recovery of vegetation within exclosures (Daubenmire 1940, Heady 1968, Houston 1982, Allen et al. 1984, Mladenoff and Stearns 1993). Furthermore, ungulates may be attracted to fences, and thus confound apparent differences between inside and outside (Heady 1968). Nevertheless, exclosures can provide insight into recovery processes if results are interpreted carefully (Woodward et al. 1994).

Large-scale experiments in which herbivores are removed from large areas (usually islands 1-100 ha) can also be used to examine vegetation recovery after herbivore modification, but because of the expense and expertise required, these tend to be rare (Donlan et al. 2002). Lack of valid controls and replication hampers the analysis of plant recovery in most of the herbivore removal studies that exist (Klein 1965, Terborgh et al. 2001). However, the large-scale removal of herbivore populations is free from the size, placement and fence artifact limitations of small-scale exclosure experiments. Furthermore, the manipulation of large areas allows for the incorporation of broad-scale effects, such as changes to animal habitat that can cause a positive feedback to seed dispersal (Ferguson and Drake 1999).

In this study, we utilized the cull of Sitka black-tailed deer from two large islands (295 ha and 170 ha) in Haida Gwaii as an experimental manipulation to investigate ecological release of forest plant communities from herbivory. Using a paired-island approach, deer were culled on two experimental islands but remained at unmodified

densities on three adjacent control islands. Exclosures were erected on the three control islands as control checks to test the potential of these islands for change. On each island we intensively sampled the vegetation before and for five-years following the initiation of culls to determine changes to vascular plant diversity, cover and composition. On the two experimental islands, sampling was conducted every year throughout this period to examine the emerging patterns.

4 Methods

4.1 A Experimental Island A: Reef Island

Reef Island is situated 6 km from Louise Island, the most likely point of origin for immigrating deer (see Chapter 1, Fig.1). The island is 295 ha in area and rises to a maximum of 150 m asl. It falls within the coastal western hemlock biogeoclimatic zone (Pojar et al. 1987) in the submontane wet hypermaritime variant region (Green and Klinka 1994). The vegetation on Reef Island in 1997 consisted primarily of two associations: (1) old-growth, multiple aged stands of western hemlock, *Tsuga heterophylla* / Sitka spruce, *Picea sitchensis*, with scattered mature western redcedar, *Thuja plicata*, and a mostly vacant understory except for patches of Sitka spruce or western hemlock regeneration; (2) open forest, mainly scattered mature Sitka spruce and red alder, *Alnus rubra*, with a dense ground cover of Nootka reedgrass, *Calamagrostis nutkaensis*. In a few small and isolated areas of multiple aged stands of western hemlock and Sitka spruce, a dense understorey of salal, *Gaultheria shallon*, persisted.

The arrival of deer on Reef Island appears to have occurred in approximately 1950, based the oldest fraying scar (see Chapter 1) found on this island (Vila et al. unpublished).

4.1 B Experimental Island B: S'Gaang Gwaii

S'Gaang Gwaii is situated 1.5 km from the nearest point of Moresby Island, the most likely the point of origin for immigrating deer. The main island of S'Gaang Gwaii is 135 ha in area with 17 smaller islands and several rocky islets and reefs making up a total area of over 170 ha. Elevation on S'Gaang Gwaii does not exeed 30 m asl. S'Gaang Gwaii falls within the coastal western hemlock biogeoclimatic zone (Pojar et al. 1987), but in the central very wet hypermaritime variant region (Green and Klinka 1994). The vegetation on S'Gaang Gwaii in 1997 consisted primarily of a dense uninterrupted canopy of western hemlock / western redcedar with scattered large spruce and a vacant understorey except for patches of spruce or hemlock regeneration.

4.2 The deer culls

Culls were conducted by local hunters from Haida Gwaii under the authority of the British Columbia Ministry of Environment (now Ministry of Water, Land and Air Protection) and Parks Canada. The first cull of deer took place in September 1997, when 50 deer were killed on Reef Island. In 1998, 37 deer were killed on S'Gaang Gwaii. However, culling was incomplete on both islands after the first cull and substantial browsing continued. Subsequent culls have taken place once or twice annually, so that by the summer of 2000, browsing had been greatly reduced and by the summer of 2001, browsing had effectively been eliminated over both islands. In the summer of 2002, only

one set of deer tracks was seen on Reef Island while two or three sets of tracks were seen on S'Gaang Gwaii. A total of 82 and 48 deer have been killed to date on the Reef Island and S'Gaang Gwaii respectively since 1997. The number of deer killed on Reef Island corresponds closely with a population estimate of 81 deer made by Daufesne and Martin (1997) and suggests an overall deer density of 33.1 deer km $^{-2}$ prior to the cull. On S'Gaang Gwaii, numbers killed suggest 32.4 deer km $^{-2}$ prior to the cull.

4.3 Vegetation monitoring

Vegetation on Reef Island was monitored in 38 permanent vegetation study plots. The first series of 23 plots (interior plots) was distributed at 200-m intervals approximately 100 to 200 m inland along a trail making a loop around the island periphery. Each interior plot was circular in shape (25-m radius) with a central permanent post. Within each interior plot, two 3.6-m radius subplots were placed 10 m to the north and south of the centre post, and likewise marked with permanent posts. A second series of 15 plots (edge plots) was established 15 m inland from the seaward edge of the vegetation. Edge plots were established to incorporate different types of edge habitat; differing in substrate (gravel, boulder, rock), aspect and exposure. Each edge plot was circular in shape (10-m radius) with a central permanent post. Within each edge plot a single 3.6-m subplot was centered on the same post as the 10-m plot. One edge plot (15, *hidden valley*) was placed in a small cove cut off from the rest of the island by steep cliffs. No evidence of deer browse was found in this cove and the vegetation is believed to represent that characteristic of sheltered coves on Reef Island prior to the arrival of deer.

Vegetation on S'Gaang Gwaii was monitored in 17 permanent plots. Twelve interior plots, identical to interior plots on Reef Island, were distributed at 200-m intervals approximately 100 to 200 m inland along a trail making a loop around the island periphery. Five edge plots, identical to edge plots on Reef Island, were established to represent different types of edge habitat; substrate (gravel, boulder, rock), aspect and exposure.

Vascular plant species were identified according to Pojar and MacKinnon (1994), and Hitchcock and Cronquist (1973). Each year, a list of the vascular plant species growing in each plot was compiled by two observers searching the entire area for 20 min (more, if the area was densely vegetated). Voucher specimens of all species were preserved and verified by comparison with collections maintained by Agriculture Canada in Ottawa.

Within each 3.6-m radius subplot, vegetation cover was recorded for each species in each stratum. Strata were set at intervals to capture small changes in vegetation at the following heights: 0-5 cm, 5-15 cm, 15-25 cm, 25-50 cm, 50-100 cm, 100-150 cm, 150-200 cm, and 200-400 cm. In order to facilitate comparison between plots we took a synthetic measure of the maximum cover of each species in all strata below 150 cm. In 2002 we compared the synthetic measure to a visual estimate of total cover by species below 150 cm and found the two measures to be nearly identical for each plot. Cover is given here as the percentage of each 3.6-m radius (40 m^2) subplot occupied by vegetation.

Vegetation monitoring began in 1997 and data were obtained from all study plots before the initiation of the first deer cull in September of that year. Monitoring

observations were made annually for six years on Reef Island (1997 to2002), four years on S'Gaang Gwaii (1997, 1999 to2001). Monitoring was repeated at the same time of year (June through mid-July) at each site.

4.4 Control sites

To control for possible ongoing changes in the vegetation of the archipelago as a whole, we selected separate control sites for each experimental island. Control sites were chosen for similarity of climate, forest type, area and topography. Kunga and East Limestone islands were selected as control sites for Reef Island (see Chapter 1, Fig. 1). Both islands occur in Laskeek Bay and, like Reef Island, are included in the submontane wet hypermaritime variant of the coastal western hemlock zone (Green and Klinka 1994). Kunga Island is larger (395 ha) and higher (420 m asl) than Reef Island, but similar in slope. To control for differences in elevation, control plots were located below 150 m asl. East Limestone Island is smaller (41 ha), lower (90 m asl) and has a limestone substrate. We selected 20 interior and 10 shoreline plots on Kunga Island and 10 interior and 9 shoreline plots on East Limestone Island. Vegetation monitoring at these sites was carried out by the same methods as on experimental islands.

Louscoone Point, at the south end of Moresby Island, close to S'Gaang Gwaii was selected as the control site for S'Gaang Gwaii. Like S'Gaang Gwaii, Louscoone Point occurs in the central very wet hypermaritime variant region (Green and Klinka 1994) but rises abruptly to more than 700 m asl. To control for differences in elevation, control plots on Louscoone Point were located below 90 m asl. We selected 10 interior and 5 edge plots on Louscoone Point. Vegetation monitoring at these sites was carried out by the same methods as at Reef Island. Monitoring was repeated at the same time of year

(June through mid-July) at each site on each island in 1997 and 2001 (1998 and 2001 on Louscoone Point).

The three islands without deer in Laskeek Bay, Low, S.Low and Lost Islands (see chapters 1 and 2) were utilized as non-deer controls for Reef Island. No islands without deer could be found in the proximity of S'Gaang Gwaii.

4.5 Exclosures

To assess potential for change on control islands (positive control), three 15- by 15-m exclosures were erected at each control site in the summer of 1998. Exclosures were placed in the interior of each island separated from one another by at least 25 m and at least 100 m from the high-tide line. Sites were chosen for their similarity to interior plots on corresponding islands. Fencing was 3 to 4 m high consisting of stucco wire (5 cm mesh size, welded and galvanized) attached to a cedar 5- by 10 cm (2- by 4-inch) frame on a 10- by 10-cm posts set 50 cm in the ground at 5 m intervals.

All vascular plant species were recorded within each exclosure. Within the central 10 m^2 of each exclosure, a single 3.6-m radius subplot was established around a wooden post to assess cover. Vegetation was sampled in exclosure plots in June of 1999 and again in June of 2001.

4.6 Integrated light measures

Two 20-day measures of average integrated light were made at each plot (interior and edge) on Reef Island in June and July of 2000 using diazo-paper integrating light sensors (Friend 1961, Sullivan and Mix 1983) at three locations within each plot. Each sensor was made of a booklet of 15 layers of diazo paper (Azon number 4516

nonerasasable diazo sepia paper, Azon Corp., Johnson City, New York), approximately 2 by 3 cm, topped with 10 layers of aluminum screen (mesh size 7 cm^{-1}) and a disc made from a double layer of plastic duct tape with two 5-mm holes. Each sensor was encased in a 9-cm diameter plastic petri dish, sealed with electrical tape and affixed with plastic duct tape to the top of one of three 1.5-m posts (plot markers) in each plot. Standard sensors were set out on a rocky knoll with no canopy for the entire 20-day period and a new sensor was added at the beginning and end of each setup and collection day. Setup and collection of sensors was done within a half-day and readings were adjusted using standard sensor readings. Diazo paper is bleached from yellow to white upon exposure to light through the holes in the duct tape disks so upon development (see Friend 1961) the number of developed sheets was counted (see Sullivan and Mix 1983) and averaged for each plot.

4.7 Composition and similarity

Community composition was measured as the summed cover of all species within each response guild (see Chapter 2). Similarity in composition was measured with Czekanowski's index of similarity:

CI=[2 * sum (min(Xj, Yj)] / (sum Xj + sum Yj), for j = 1 to 5 (guilds I-IV and NA).

Czekanowski's index, CI, is calculated as the sum of the minimum between two samples (X and Y) over the sums of the measures for both samples, which is a simple adaptation of Sorenson's index of similarity for use with abundance data (Sokal and Rolf 1995). This is an index in which joint absences are excluded from consideration, and matches are weighted double. Czekanowski's index was calculated for the similarity in guild composition of each plot to the expected average non-deer composition and expected

average control composition. The expected average non-deer composition was taken as the average guild composition of three non-deer islands in Laskeek Bay both for the forest interior and forest edge. The expected average composition of control islands for Reef Island was taken as the average guild composition of Kunga and E.Limestone Islands. The expected average composition of control islands for S'Gaang Gwaii was taken as the average guild composition of Louscoone Point. Although the combining of measures from different islands could be considered a minor case of pseudoreplication (Hurlbert 1984) it does not compromise the statistical tests we conducted. Rather than testing the similarity between the average non-deer composition and the composition of experimental islands we instead tested the difference in this similarity at the beginning and end of our study.

4.8 Analysis

Repeated measures ANOVAs were performed for species richness and cover values from experimental islands (Reef Island and S'Gaang Gwaii) and control islands (Kunga, E. Limestone, Louscoone Point) using data from each year that variables were measured (1997 to 2002 on Reef Island and 1997, 1999 to2001 on S'Gaang Gwaii). Post-hoc Scheffe tests were used to determine the significance of differences between individual years. Paired t-tests were performed to compare species richness and cover values for exclosure plots on control islands (Kunga, Limestone, and Louscoone Point) in 1997 and 2001 (1998 and 2001 on Louscoone Point). Paired t-tests also were used to compare similarity measures (similarity in composition of experimental plots to the average composition of control and non-deer plots) from 1997 with similarity measures at the end of the study (2002 on Reef Island, 2001 on S'Gaang Gwaii). Linear regression

was performed to test the relationship between the change in species richness from 1997 to 2002 and integrated light on Reef Island, and to test the relationship between the change in cover of key species from 1997 to 2002 and integrated light on Reef Island. Multiple regression analysis was performed to test the linear relationship between the change in total cover and two factors: integrated light and initial species richness, on Reef Island.

5 Results

5.1 Species Richness

Species richness of 25-m radius forest interior plots increased an average of 8.2 ± 1.3 species per plot on Reef Island from 1997 to 2002 (Fig. 1, Table 1) and an average of 5.7 ± 1.0 species per plot on S'Gaang Gwaii from 1997 to 2001 (Fig. 2, Table 1). The species richness of Reef Island's interior plots initially changed only slightly but then jumped substantially in 1999, subsequently leveling off from 2000 to 2002. The light study conducted on Reef Island revealed that the increase in species over this period was greater in plots with more light (Fig. 3; linear regression, R^2=0.33, F{1,21}=10.4, p<0.01). On S'Gaang Gwaii, the species richness in interior plots increased most between 1997 and 1999 but continued to increase through 2001 (the last year of sampling on this island). All three control islands experienced a slight increase in species richness in forest interior plots, increasing an average of 2.3 ± 0.40 species on Limestone Island (Fig. 1, Table 1), and 0.90 ± 0.89 species on Kunga Island (Fig. 1, Table 1) between 1997 and 2001 and an average of 0.3 ± 1.2 species on Louscoone Point (Fig. 2, Table 1) between 1998 and 2001.

Species richness of exclosure plots on these islands (Fig. 4) increased almost twice as much as control plots did in the period of 1999 to 2001, with an increase of an average of 4.3 ± 1.8 species on Limestone Island (paired t-test, $t\{4\}= -1.49$, $p=0.21$), 2.7 ± 1.3 species on Kunga Island (paired t-test, $t\{4\}=-0.54$, $p=0.63$) and 2.3 ± 0.67 species on Louscoone Point (paired t-test, $t\{4\}=-1.75$, $p=0.15$).

Species richness of edge plots increased an average of 6.8 ± 0.77 species on Reef Island from 1997 to 2002 (Fig. 5, Table 2) and 6.0 ± 1.2 species on S'Gaang Gwaii from 1997 to 2001 (Fig. 6, Table 2). As per the interior, the species richness of edge plots on Reef Island initially changed little, then experienced a large increase in species in 1999 and then leveled off slightly from 2000 to 2002. The light study conducted on Reef Island revealed that in edge plots the species richness response was unmodified by the availability of light (linear regression, $R^2=0.045$, $F\{1,12\}=0.568$, $p=0.47$). Species richness of edge plots on S'Gaang Gwaii increased gradually from 1997 to 2000 with a small jump between 2000 and 2001. No significant increase in the species richness of forest edge plots occurred on any of the three control islands.

5.2 Cover

Cover of vegetation below 150 cm in 40 m^2 interior plots increased an average of 28 ± 4.5 % (11 ± 1.8 m^2) on Reef Island from 1997 to 2002 (Fig. 7, Table 3) and 5.1 ± 2.4 % (2.0 ± 1.0 m^2) on S'Gaang Gwaii from 1997 to 2001 (Fig. 8, Table 3). The increase in cover in the interior of both islands began slowly but after 1999 increased more rapidly. The light study conducted on Reef Island revealed that the increase in cover in the interior from 1997 to 2002 was greater in plots with more light, and was modified additionally by the initial species richness of the plot (Fig. 9 A and B; multiple

regression, R^2=0.69, BETA{light}=0.68 , BETA{SR}=0.42, F{2,20}=10.4, p<0.001). No significant change in vegetation cover occurred in interior control plots, which increased an average of 0.7 ± 0.6 % (0.29 ± 0.22 m^2) on East Limestone Island (Fig. 7, Table 3), 2.4 ± 1.8 % (1.1 ± 0.64 m^2) on Kunga Island (Fig. 7, Table 3), and decreased 4.2 ± 1.6 % (1.8 ± 0.60 m^2) on Louscoone Point (Fig. 8, Table 3).

No significant change in vegetation cover occurred in 40-m^2 exclosure plots (Fig. 10), which increased an average of 5.4 ± 4.5 % (2.1 ± 1.8 m^2) on Limestone Island (paired t-test, t{4}=-1.49, p=0.21), 15 ± 7.8 % (6.0 ± 3.1 m^2) on Kunga Island (paired t-test, t{4}=-0.54, p=0.63) and 14 ± 12 % (5.6 ± 4.8 m^2) on Louscoone Point (paired t-test, t{4}=-1.75, p=0.15) from 1999 to 2001.

Cover of vegetation below 150 cm in 40-m^2 forest edge plots increased an average of 39 ± 7.3 % (15.6 ± 2.9 m^2) on Reef Island from 1997 to 2002 (Fig. 11, Table 4) and 20 ± 4.5 % (8.0 ± 1.8 m^2) on S'Gaang Gwaii from 1997 to 2001 (Fig. 12, Table 4). In edge plots on Reef Island, increases in cover from 1997 to 2002 were negatively correlated with light (Fig. 13; linear regression, R^2=0.32, F{1,12}=3.99, p<0.05). No clear increase in the cover of edge plots occurred on either Reef Island or S'Gaang Gwaii until 2001, with cover increasing further on Reef Island in 2002. No significant change in the cover of 40-m^2 edge control plots occurred.

5.3 Composition

The composition of species within response guilds (see chapter 2) in Reef Island interior plots (Fig. 14) were more similar to the average guild composition of interior plots on non-deer islands in 2002 than in 1997 (Table 5) and less similar to the average guild composition of interior plots on control islands in 2002 than in 1997 (Table 6).

Reef Island edge plots (Fig. 15) in 2002 also showed greater similarity in guild composition to the average composition of edge plots on non-deer islands than in 1997 (Table 5) and less similarity to the average composition of edge plots on control islands (Table 6). On S'Gaang Gwaii, neither interior plots (Fig. 16) nor edge plots (Fig. 17) showed any significant change in similarity to the average composition on non-deer control islands between 1997 and 2001 (Tables 5 and 6).

The breakdown of cover into individual response guilds showed that the increase in cover of species in guilds III and IV accounted for most of the increase in cover in interior plots on Reef Island (Fig. 14; 78.3 ± 5.2% of total change) and S'Gaang Gwaii (Fig. 16; 67.0 ± 7.7% of total change). Cover of species within guilds I and II increased little in Reef Island interior plots (21.4 ± 2.4 % of total change) but slightly more in S'Gaang Gwaii interior plots (33.0 ± 5.2 % of total change). In Reef Island edge plots (Fig. 15), guild IV species showed relatively little increase (19.2 ± 2.6 % of total change), while guild III species increased substantially (46.7 ± 2.4 % of total change). In S'Gaang Gwaii edge plots (Fig. 17), the cover of species in guilds I and IV increased substantially (30.8 ± 4.8% and 61.7 ± 4.5 % of total change respectively), while the cover of species in guild III showed a reduction (- 3.9 ± 2.5 % of total change).

The increase in cover of Sitka spruce and western hemlock made the major contribution to the increase in the cover of species in guild IV in both the forest interior and edge, while Nootka reedgrass showed no clear trend in either the forest interior or edge on Reef Island (Figs. 18 and 19). Similarly, on S'Gaang Gwaii, the cover of species within guild IV was dominated by the effects of Sitka spruce, however an increase in Nootka reedgrass was also evident in the forest edge plots of this island (Figs. 20 and 21).

6 Discussion

Superficially, the recovery of vegetation after the release from deer browsing shows evidence of a high degree of resilience. Clear increases in species richness and cover, as well as changes in the community composition of the forest understorey of experimental islands, demonstrate a quick response to a release from browse pressure. Some of these changes appear to be reversing the effects of deer impacts on native vegetation. However, several key elements of the post-cull community have either continued to diverge from the deer-free community or have not responded to the culls, suggesting a possible alternate stable-state.

6.1 A Indications of resilience: species richness

The sharp increase in species richness on experimental islands over the period of the study is evidence of the key role of deer in limiting the diversity of the forests of Haida Gwaii. Although certain levels of herbivory can increase the plant species richness of some systems (McNaughton et al. 1979, 1984, Olff and Ritchie 1998), deer herbivory in Haida Gwaii has evidently brought about a large decrease in species richness (see chapter 1). When deer herbivory was subsequently eliminated, many species were able to re-establish, indicating the lack of resource competition at this stage in the recovery of the understory. Several secondary factors also appeared to influence the change in species richness after the cessation of deer browsing, as demonstrated by the substantial noise in the species richness response on the various experimental and control islands. The increase in species richness from 1997 to 2001 on Limestone Island, one of three control islands, provides a pertinent example of this noise.

Variation in species richness may have been affected by stochastic variation in deer-density, rainfall and sunlight. Substantial variation in species abundance and richness due to climatic factors are common (Andrewartha and Birch 1954, Bunnell 1990a, Crawley 1997) and can overwhelm the effects of herbivory. For example, following the removal of exotic European rabbits, goats and donkeys from the San Benito Islands, Mexico, El Nino-related precipitation still dominated vegetation dynamics (Donlan et al. 2002).

Sampling biases are also likely to affect changes to species richness over time. Because many species can be difficult for the beginner to distinguish from one another, an observer becomes less likely to group two species together over time. This may lead to an artificial increase in species richness in both experimental and control plots. Such a bias may be inherent to many time-series plant studies that measure species richness.

On Reef Island, species richness response was also limited by the availability of light in the interior, where levels were relatively low compared to the forest edge. Within the forest interior, light reaches the understorey through gaps in the canopy. Because light is limited within most forest systems, gaps facilitate tree regeneration, and enable herb and shrub species to grow and reproduce within late-successional forests in the temperate rain forest (Eck 1984, Stewart 1984, Taylor 1990, Lertzman 1992). Light levels are known to greatly affect the germination and growth of plants and seed dispersal by animals (Ferguson and Drake 1999, Nomiya 2003). The greater increase in species richness in plots with more available light reflects this general pattern, illustrating the importance of light availability to the resilience of a forested system.

Despite the influence of these secondary factors to the species richness response, the difference between trends observed after the deer culls on Reef Island and S'Gaang Gwaii and those seen at the control sites gives a clear indication that deer heavily suppress the species richness of the deer modified forest. The flush of new species appearing in study plots on Reef Island and S'Gaang Gwaii after the deer culls signals the removal of the chief factor controlling species richness in this system. However, the observed trend of rapidly increasing species richness is likely to be short lived, experiencing a tapering off and possible reversal as plants become established and competition for resources increases.

6.1 B Indications of resilience: cover

The large increase in the cover of vegetation resulting from the release from deer-browse also clearly indicates the termination of suppression by deer. Similar to the species richness response, plots in the forest interior with more available light had greater increases in cover. The response was different in the forest edge, where greater light usually meant less surrounding forest structure and hence more exposure to wind and salt-spray. Wind and salt-spray can be extreme in this region, often stunting the growth of trees and shrubs that occur in highly exposed areas (Calder and Taylor 1968). Furthermore, many edge plots with high amounts of light were initially dominated by dense grasses, which appeared to limit the increase in cover of other species. As such, the cover response at the forest edge was opposite to that in the interior, increasing slower in plots with more light.

The cover response in the forest interior was also modified by initial species richness. Increase in cover was greater in plots with higher initial species richness. As

the increase in cover following a perturbation is a measure of resilience (Ludwig et al. 1997), the relationship between resilience and diversity may be indicative of a stability-diversity relationship (Tilman 2000). Because much of the increase in cover came from only a handful of species (Figs. 18, 19, 20 and 21), the greater increase in species-rich plots can be explained as a specific instance demonstrating the diversity-stability insurance hypothesis, where communities show an increased chance of a positive response with a greater number of species (Naeem and Li 1997). Similarly, De Grandpré and Bergeron (1997) found that areas of the boreal forest with more species tended to contain species that could react quickly to disturbance by increasing their cover. However, the interaction with light in our study makes such an effect impossible to measure without further careful experimentation utilizing a series of carefully measured controls (Tilman 2000).

The large increase in cover in study plots on Reef Island and S'Gaang Gwaii after the deer culls signals the removal of the factor controlling the abundance of standing vegetation in the understorey of this system, but also the high productivity of the coastal temperate rain forest. This forest is extremely productive (Pojar et al. 1991), arguably one of the most productive ecosystems on the planet (Schoonmaker et al. 1997). As such, the observed trend of rapidly increasing cover, like the trend of increasing species richness, is likely to be short lived, experiencing a tapering off as plants become established and competition for resources increases.

6.2 Indications of irreversibility: community composition

Although the community composition on Reef Island showed some indication of reversal, by becoming more similar to non-deer composition after the culls, several key

elements in the community have continued to diverge. Cover of the shrub salal, which makes up the largest component of the understorey in the interior of deer-free islands (see chapters 1 and 2), increased only minimally on both Reef Island and S'Ganng Gwaii over the course of our study. Likewise, guild I, which is dominated by salmonberry, *Rubus spectabilis*, and thimbleberry, *Rubus parviflorus*, makes up nearly a third of the understorey in the interior of deer-free islands (see Chapter 2), but has increased little on either experimental island since the cull. In contrast, guild IV, which includes Sitka spruce and makes up only a small component of the understorey of deer-free islands (see chapter 2), has experienced a large sustained increase since the culls. Community composition on S'Gaang Gwaii showed even less change following the cull than on Reef Island. S'Gaang Gwaii's guild composition showed no more similarity to non-deer guild composition in 2001 than in 1997. Similar to Reef Island, the cover of species on S'Gaang Gwaii in guilds I and II showed little increase after the culls, while the cover of guild IV increased substantially.

Both Reef Island and S'Gaang Gwaii appear to be developing a very different understorey from the type that occurs on deer-free islands. Some of the divergence in recovery may be explained by differences in environmental factors between experimental islands and the non-deer islands to which they are compared. However, because deer have colonized all but a few small outlying islands in the archipelago, no deer-free islands of comparable size to Reef Island and S'Gaang Gwaii exist in Haida Gwaii (Daufresne and Martin 1997). The understorey composition of Reef Island and S'Gaang Gwaii before the arrival of deer may have been quite different from that of the small islands of Laskeek Bay. Interior sites on these small islands subject to wind and salt

spray may more closely resemble edge plots on the larger islands. However, forest site series developed for this region, which take into account edaphic factors as well as vegetation (Pojar et al. 1991, Green and Klinka 1994), indicate that despite probable differences between small and large islands, the missing shrubs, especially salal, are an important component of the understorey of almost all site series. Furthermore, in analogous regions of the coast without heavy deer modification, the shrub layer is generally dense (Green and Klinka 1994). Zonal sites in these regions typically have a well-developed layer of ericaceous shrubs, while alluvial sites usually have a dense layer of salmonberry or devil's club, *Oplopanax horridus* (Pojar et al. 1991). Pojar et al. (1980) reported a 70.6% combined cover of shrubs on the mainland coast compared to only a 29.0% cover on Haida Gwaii. There exists strong historical and circumstantial evidence of a major decline in the shrub layer of Haida Gwaii since the introduction of deer (Pojar et al. 1980). The present lack of a shrub dominated understorey on Reef Island and S'Gaang Gwaii appears to be the result of severe deer modification and a subsequent failure of the shrub species in guilds I and II to regenerate.

6.3 Reversibility of herbivore modification

If a community is to experience a full return to the pre-modified state, species that decreased in the presence of herbivory must increase when released from this pressure, and species that increased in the presence of herbivory must eventually decrease, reversing the process of modification. Several studies have demonstrated reversals of this sort following the removal of a herbivore (Tansley and Adamson 1925, Allen et al. 1984, Woodward et al. 1994, Donlan et al. 2002). In the understorey of old-growth coastal spruce-hemlock forests in Washington, deer and elk herbivory were found to

maintain patches of graminoids that were quickly replaced by ferns and shrubs following herbivore exclusion (Woodward et al. 1994). In New Zealand, in stands browsed by introduced deer, unpalatable tree species were found to dominate regeneration and palatable species were rare, while the opposite was true within 12-17 year-old exclosures (Allen et al. 1984). Tansley and Adamson (1925) found that fenced plots quickly became dominated by a few highly palatable species when rabbits were excluded from areas of the English chalk grasslands. Donlan et al. (2002) recorded a reduction in unpalatable plants and an increase in palatable plants following the eradication of exotic European rabbits, goats and donkeys from the San Benito Islands, Mexico.

Numerous studies have also demonstrated modifications that did not reverse when herbivores were removed from a modified system (Costello 1944, Dublin et al. 1990, Huston 1982, Coughneour 1991). In Yellowstone National Park, species composition of grasslands in 30-year-old exclosures remained nearly identical to the surrounding grazed grassland despite the fact that elk populations grew nearly 6-fold during this period (Huston 1982, Coughenour 1991). In the Great Basin of western North America, sagebrush (various subspecies of *Artemesia tridentate*) grew denser and understorey vegetation was gradually eliminated with heavy grazing but the community did not change over a subsequent 45-year period of livestock exclusion (Anderson and Holte 1981). In the short-grass steppe areas of the Central Great Plains, heavy grazing increased the dominance of blue grama, *Bouteloua gracilis*, which remained dominant after the cessation of grazing (Costello 1944). The continued dominance of a browse-tolerant species after the removal of herbivores represents a system with multiple stable

states (Holling 1973, Noy-Meir 1975, May 1977, Law and Morton 1993, Ludwig et al 1997).

Several deer-modified forest systems have appeared to result in alternate stable states. Areas of the Alegheny Plateau have developed under heavy deer browsing pressure into self-perpetuating glades of ferns (Tilghman 1987). Horsely and Marquis (1983) predicted that these fern glades would persist in the absence of deer browse. In the Great lakes forests of Wisconsin, Minnesota and Michigan, deer have induced shifts from a conifer-dominated forest (eastern hemlock, *Tsuga Canadensis*, white cedar, *Thuja occidentalis*, and Canada yew, *Taxus Canadensis*) to a deciduous forest (Anderson and Loucks 1979, Alverson et al.1988) and have virtually eliminated eastern hemlock regeneration over large areas (Frelich and Lorimer 1985). In West Virginia, deer have suppressed regeneration of balsam fir, *Abies balsamea*, a species seldom browsed in other areas (Graham 1954), leading to red spruce, *Picea rubens*, dominated forests (Michael 1992). White cedar was virtually eliminated from swamps in the New Jersey Pine Region following a large fire and intensive deer browsing (Little and Somes 1965). Each of these changes may represent permanent or long-term stable-states (Stromayer and Warren 1997).

A commonly used conceptual model to explain multiple stable-state systems is that of a ball and troughs (Krebs 1985). In a single stable-state system there is only one trough, a single minimum. When this system is perturbed the ball rises up but always returns to the original state at the bottom of the trough; a global model analogous to the *climax* concept of Clements (1916). In multiple stable-state systems there may be a large number of troughs, the depth of each representing the range of environmental conditions

under which the system is stable. When a multiple stable-state system is perturbed beyond a critical range, the ball passes a threshold and may come to rest in a new trough. When the threshold is crossed, the forces that shape a community are altered, forming a positive feedback that keeps the modification in place. Within this second state, the forces required to perturb the system beyond the critical range will be different than they were in the first state (Ludwig 1997).

The driver for the process of reversal is often competition. Because plant defense against herbivory is usually an expensive adaptation, browse-tolerant species tend to be slow growing and poorly suited for competition with fast-growing undefended species (Grime 1977, Burke and Grime 1996). Hence, in the absence of herbivory, browse-tolerant species are often out-competed (Bryant et al. 1991). Systems where fast-growing, undefended species can rapidly overtake browse-tolerant ones will tend to be resilient. Systems where established browse-tolerant species maintain their advantage enter an alternate stable-state. The threshold in this case is the limit where undefended species are no longer able to overtake the advanced position of browse-tolerant species and the system does not revert to its original state.

6.4 Reversibility in the coastal temperate rain forest

In areas of the coastal forest without severe deer modification, residual shrubs are able to quickly establish themselves after a disturbance (Dryness 1973, Alaback 1984, Haeussler and Coates 1986, Halpern 1989, Bunnell 1990b). The natural succession of the coastal temperate rain forest occurs as a small-scale patch disturbance process from a single tree to several hectares in size often leaving the understorey intact (Lertzman et al. 1996, Alaback and Pojar 1997). While suppressed saplings quickly grow to replace those

killed by the disturbance (Pojar and MacKinnon 1994) early stages of tree development often involve a period of competition with shrub species (Haeussler and Coates 1986, Halpern 1989). Although regenerating trees eventually overtop this shrub layer (Halpern 1989), the patch dynamics of the system allow for the rapid spread of shade-intolerant shrub species to adjacent forest openings (Dryness 1973, Alaback 1982).

Salal can expand rapidly from the rhizomes of residual plants, achieving prominence within three to five years after a disturbance (Dryness 1973). Bunnell (1990b) concluded that 85% of the space that will be occupied by salal after nine years is occupied within three years of a major disturbance. Salal is a vigourous competitor for light aboveground and for moisture and nutrients belowground (Bunnell and McCann 1990). It inhibits mineralization and uptake of nitrogen through the production of tannins, and interferes with the mycorrhizal associations of several trees (McDonald 1990, Boateng and Comeau 2002).

In hemlock -spruce forests of central Oregon, residual salmonberry plants under dense canopy cover can produce dense stands or *brushfields* to dominate a site within six months after the reduction of overstory canopy (Alaback and Herman 1988). Salmonberry brushfields provide formidable competition for conifer seedlings (Ahgren and Ahgren 1960). In many areas, this shrub competes with Sitka spruce and western hemlock regeneration (Ruth 1956). Thimbleberry can also become dominant within two to five years after logging or fire in western forests (Morgan and Neuenschwander 1988) and competes with conifers primarily for light (Boateng and Comeau 1997a). With such a rapidly expanding shrub layer, shade-intolerant Sitka spruce (Klinka et al. 1985) can

require chemical shrub control to regenerate at high densities following a harvest (Krygier et al. 1961, Gratkowski 1978, Boateng and Comeau 1997a, 1997b, 2000, 2002).

Despite the robust nature of the shrub layer in the face of many natural and human-driven disturbance events such as fire, windthrow and logging, key elements of the shrub layer may be extremely sensitive to modification through herbivory. Successive removal of aboveground plant material can exhaust root supplies of many plants in a relatively short period of time. Although salal is generally thought of as a low preference food item (Bunnell 1990a), when other major food sources are absent it can be virtually eliminated (see Chapters 1 and 2). Manual cutting for several consecutive years is known to severely reduce the ability of salal to regenerate (Boateng and Comeau 2002). Salmonberry shows significantly reduced regeneration after two summers of sheep grazing (Leininger and Sharrow 1987) and reduced sprouting ability after numerous successive monthly treatments of manual cutting (Zasada et al. 1979). Thimbleberry can succumb to livestock grazing over a single season, though older woody stems usually prove more resistant (Boateng and Comeau 1997a).

As many shrub species reproduce primarily through vegetative means (Haeussler and Coates 1986), the shrub layer, once removed, may be extremely slow to return. For example, the potential of salal for reproduction from seed is poor under natural conditions in the coastal forest (Halpern 1989). The spread of salal is done primarily through expansion of existing clones, through layering, sprouting of rhizomes (Haeussler and Coates 1986). Initial growth of this understorey dominant is slow, taking two to three years to reach 8-13 cm (Kruckeberg 1982). Viability in the seedbank is also low (Kellman 1970) and seed crops are poor under a dense forest canopy (Haeusller and

Coates 1986). Similarly, salmonberry stems typically develop from perennial rootstocks or aboveground creeping stems (Great Plains Flora Association 1986). Under ordinary circumstances, recruitment of new salmonberry genets through seedling establishment is relatively rare (Kelpsas 1978). Vegetative regeneration is particularly important in perpetuating colonies of salmonberry in shaded understorey habitats (Barber 1976). Likewise, in the absence of soil disturbance, thimbleberry, Nooka rose, *Rosa nutkana*, and most *Ribes* species (e.g. black gooseberry, trailing black currant) regenerate primarily through vegetative means (Stickney 1986, Boateng and Comeau 2000). Devil's club also reproduces vegetatively and seedling growth is slow (Kruckeberg 1982).

In contrast, those shrubs that can reproduce well through the establishment of new seedlings appear to be more resilient to the effects of herbivory. Both red huckleberry, *Vaccinium parvifolium*, and false azalea, *Menziesia ferruginea*, reproduce well through seedling establishment (Vander Kloet 1988). Red huckleberry seed is typically produced in abundance and approximately seven percent of all seed produced eventually develops into vigorous seedlings (Vander Kloet 1988). Although the seeds are readily dispersed by birds and mammals (Hitchcock and Cronquest 1973), red huckleberry seedlings are generally abundant wherever parent plants occur (Kruckeberg 1982). False azalea produces numerous small seeds in capsules, which are dispersed by wind or gravity (Alaback 1982). Both shrubs can also tolerate densely shaded conditions (Calder and Taylor 1968). Consequently, both shrubs have shown substantially increased cover since the culls with numerous seedlings on both Reef Island and S'Gaang Gwaii.

With the exception of a few seedling-producing species, the resilience of the shrub layer in the coastal forest is based largely on the presence of an established shrub

layer. After severe reduction of this layer, the resilience of this system appears to be greatly reduced. Although it is too early to know at this stage whether understorey communities on Reef Island and S'Gaang Gwaii have been knocked into an alternate stable-state (Connell and Sousa 1983), the degree of modification incurred from deer browsing on these islands will likely continue to affect the recovery and succession long after the deer have been removed.

6.5 Prospects for recovery in the future

In heavily deer-modified Haida Gwaii forests, the shrub layer is neatly removed while Sitka spruce growth is merely slowed down. (Vila et al. 2001). Even if the deer are eliminated, the competitive balance may be tipped in the favour of Sitka spruce because it is already established. In deer-modified forests, growth of this tree is not limited by a shrub layer, as it is in the unmodified forest, and a cohort of accumulated trees is able to grow up unimpeded in a dense single-aged stand. The resultant dense canopy coverage can then become a positive feedback loop to maintain this imbalance by impeding the development of the shrub layer (Haeussler and Coates 1986, Halpern 1989, Bunnell 1990b). Once regeneration has reached full canopy closure, understorey production may be greatly reduced for at least the next 100 years (Hanley and McKendrick 1985). As deer population is likely to recover before this occurs (Reimchen in press), shrub regeneration may continually be kept in check. Even a low population of deer may limit recovery if these shrubs are high preference forage.

To examine the prospects for the intermediate recovery of the understorey we revisited the data and looked at the increase in cover of different species in all measured strata in the forest interior and edge. In the interior, we discovered a marked difference in

the response patterns of Sitka spruce, salal, red huckleberry and guild I shrubs in the upper strata of the interior (Fig. 22). Sitka spruce, which possessed significant initial cover in all strata, showed a clear increase in cover in each stratum, including the 100-150 cm stratum, while the response of salal and the guild I shrubs was concentrated below the height of 100 cm. The substantial increase in red huckleberry cover was also concentrated below 100 cm, but a moderate increase in cover occurred above this level as well, indicating that the shade-tolerant shrub is re-growing quickly. However, because of the rapid expansion of tree cover immediately above that of the emerging shrubs, the future interior of these islands appears to exclude a fast recovery of shade-intolerant shrubs. Increased cover by tree species in the ensuing years is likely to preclude further shrub recovery and may shade out many of the newly established plants in the understorey.

At the forest edge, greater initial cover of shade-intolerant shrubs has translated into greater absolute increases in cover for these species (Fig. 23). Sitka spruce still showed rapid expansion immediately above these shrubs, however competition for light is likely to be less important at the forest edge with little to no canopy interception and greater transverse light penetration and is therefore unlikely to preclude further shrub development.

Although increases in the amount of cover of most shrub species in the interior has been small relative to the initial cover in 1997, proportional increases in cover have been quite large for salal, red huckleberry, salmonberry, and false azalea (Gaston et al. in press). However, these increases have contributed little to the total cover of vegetation, and, of these species, only red huckleberry has shown an absolute increase in interior

cover greater than 1% over the duration of our study (Fig. 22). The absolute change in cover of these shrubs at the forest edge has been far more substantial (Fig. 23). The largest change once again, has been the increase in cover of red huckleberry. Similarly, Sitka spruce, which showed little reduction due to deer (chapters 1 and 2), has been able to expand rapidly in both the forest interior and edge.

6.6 The importance of salal

Salal is one of the most common forest understorey plants in the western coastal forest, often forming impenetrable thickets (Pojar and Mackinnon 1994). This broadleaved evergreen spreads quickly into areas with newly formed canopy gaps (Calder and Taylor 1968) by expanding vegetatively from existing individuals (Bunnell 1990b). While *relict* individuals exisiting under dense canopy are capable of expanding rapidly when the opportunity arises (Dryness 1973), initial establishment usually occurs at a time when canopy cover is low (Bunnell 1990b). Hence the continued persistence of salal on a landscape scale requires its presence in many patches across the landscape.

Salal is well suited for use as a ground cover on erosive banks, coastal dunes, roadcuts, highway right-of-ways, and other types of disturbed or reclaimed ground (Kruckeberg 1982). The roots of salal form *ericoid mycorrhizae* that facilitate the mineralisation of nutrients and metallic elements in acidic environments (Xiao and Birch 1996). On some sites in western Washington, the presence of salal, and its associated fungi, has been shown to actually increase the nutrient availability of the soil (Klinka et al. 1989).

Before European contact, salal berries were the most plentiful and important fruit for aboriginal peoples in many places along the coast (Turner 1995). The berries are

readily eaten by many species of birds and small mammals (Hitchcock et al. 1959, Bunnell 1990b). In some areas, blue grouse, *Dendragapus obscurus fuliginosus*, exhibit a marked preference for salal fruit, with both chicks and adults consuming large quantities during July and August (King and Bendell 1982). Hummingbirds regularly feed from salal flowers (Pojar 1975).

6.7 Implications for management

Severe deer-modification has the capability of shifting the forests of Haida Gwaii into a permanent or semi-permanent state lacking key shrub species such as salal. The failure of these shrub species to establish quickly after the cessation of browsing may lead to an extremely long delay in their establishment as Sitka spruce develops abundant closed canopy stands. A threshold appears to have been crossed when the shrub layer was virtually eliminated by deer browsing. Beyond this threshold, the ability of the shrub layer to expand through vegetative reproduction was compromised. Closed-canopy stands, which have started to develop, may serve to lock this change into place. However, elimination of deer before this threshold is crossed is likely to radically change the community response. Remnant shrubs would then be able to expand vegetatively, which would then likely halt the development of dense closed-canopy stands of spruce.

In order to work towards restoration of herbivore-modified systems we need to be able to understand the thresholds that may lead to alternate states and the factors that can hold a community in those states. The elimination of the shrub layer serves merely as one pertinent example of such a threshold. Mass wasting, fires, clear-cut logging and the introduction of exotic plant species are all potential factors that may act to prevent a community from re-crossing a threshold.

Within the forests of Haida Gwaii, strategies that may act to facilitate the speedy recovery of deer-modified regions can and should be employed. Action should be taken before the shrub layer has been eliminated. As we have demonstrated previously (Chapter 2), the shrub layer can persist for a relatively long period of time (20 years), even under intense deer modification. Measures to prolong this period even further can be utilized until such a time as a reduction in deer density is possible. Deer exclosures can be erected to maintain browse-sensitive species during periods of intense deer herbivory. Following a reduction in browsing pressure, these exclosures can then act as seed sources to recolonize the deer-modified landscape. Several exclosures of various sizes have been erected on Graham Island as well as the 225 m^2 exclosures utilized in this study. Among these, the exclosures with adequate light penetration have experienced large increases in shrub cover, while those under dense tree canopy have shown little change. To encourage vegetative recovery of the shrub layer, further exclosures could be erected in areas without dense canopies. The use of exclosures to generate advanced stands of vegetatively reproducing shrubs should also be used as a prelude to deer population reduction efforts.

Increased hunting pressure evidently benefits the recovery of the understorey, but hunting should be directed to areas with some existing shrub layer. If deer culls could be directed to these areas before the elimination of the shrub layer, many shrub species could quickly recruit stems above the browse limit. In addition to the recovery projects on Reef Island and S'Gaang Gwaii, Haida hunters have intensively hunted the Juskatla area of Graham Island over the last decade and recruitment of browse-sensitive western redcedar is noticeably higher in this area (pers. obs.). Less intense methods might also

suffice to facilitate the recovery of some areas. The Spirit Lake area, located close to the town limits of Skidegate, possesses many species that are highly palatable to deer (pers. obs.). This area is frequently visited by people throughout the year and is frequently used to exercise dogs. The high level of human and canine traffic may force deer to move before they can consume a large portion of any standing plant.

Similar strategies to facilitate the recovery of the forest understorey by targeting or creating areas capable of responding quickly to a release from deer pressure should be employed in Haida Gwaii. A well-designed adaptive management program could potentially result in large areas with a functional forest understorey as well as adequate recruitment of commercial tree species and a healthy population of deer. An ideal target for sustainable limits to the deer population density would allow populations of deer to consume only equal to or less than the new growth of palatable understorey species (highly sensitive species may still need exclosures). Such an arrangement might balance the desires of forestry, the hunting community, users of traditional plants and conservationists. Monitoring such a level would be reasonably simple, involving the measurement of new growth retained on browsed plants at several times of the year and a subsequent effort to direct hunting to overbrowsed areas. Conversely, failure to take into account the potential for the forest understorey to enter an alternate stable-state may render conservation efforts ineffectual. Reducing deer densities in areas without the capability to recover will likely result in much wasted time and effort and a permanently altered forest understorey.

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Table 1: Changes to species richness in forest interior plots (25-m radius) on experimental and control islands as determined by repeated measures ANOVA.

Island (plots)	Type	Degrees of freedom	F	Significance [1]
Reef (23)	Experimental	5, 110	27.2	***
S'Gaang Gwaii (12)	Experimental	3,33	20.1	***
E.Limestone (10)	Control	1,9	6.61	*
Kunga (20)	Control	1,19	1.02	0.33
Louscoone (10)	Control	1,9	0.0592	0.81

1 Significance levels of $p<0.001$ given as ***, $p<0.01$ as **, $p<0.05$ as *.

Table 2: Changes to species richness in forest edge plots (10-m radius) on experimental and control islands as determined by repeated measures ANOVA.

Island (plots)	Type	Degrees of freedom	F	Significance [1]
Reef (14)	Experimental	5,65	32.4	***
S'Gaang Gwaii (5)	Experimental	3,12	12.8	***
E. Limestone (9)	Control	1,8	0.229	0.65
Kunga (10)	Control	1,9	0.0957	0.76
Louscoone (5)	Control	1,4	0.0476	0.84

1 Significance levels of $p<0.001$ given as ***, $p<0.01$ as **, $p<0.05$ as *.

Table 3: Changes to cover of vegetation in forest interior plots (average of two 3.6-m radius subplots for each plot) on experimental and control islands as determined by repeated measures ANOVA.

Island (plots)	Type	Degrees of freedom	F	Significance [1]
Reef (23)	Experimental	5, 110	50	***
S'Gaang Gwaii (12)	Experimental	3,33	7.4	***
E.Limestone (10)	Control	1,9	1.04	0.33
Kunga (20)	Control	1,19	0.33	0.57
Louscoone (10)	Control	1,9	3.0	0.12

1 Significance levels of $p<0.001$ given as ***, $p<0.01$ as **, $p<0.05$ as *.

Table 4: Changes to cover of vegetation in forest edge plots (3.6-m subplot) on experimental and control islands as determined by repeated measures ANOVA.

Island (plots)	Type	Degrees of freedom	F	Significance [1]
Reef (14)	Experimental	5,65	15.1	***
S'Gaang Gwaii (5)	Experimental	3,12	13.3	***
E. Limestone (9)	Control	1,8	1.17	0.33
Kunga (10)	Control	1,9	0.88	0.37
Louscoone (5)	Control	1,4	2.16	0.22

1 Significance levels of $p<0.001$ given as ***, $p<0.01$ as **, $p<0.05$ as *.

Table 5: Similarity of composition of species within response guilds between experimental and non-deer islands, measured with Czekanowski's index of similarity. Similarity measures for the *first* (1997) and the *last* year of measurement (2002 for Reef, 2001 for S'Gaang Gwaii) were compared using a paired t-test.

Island	Average similarity first ± SE	Average similarity last ± SE	Degrees of freedom	t	Significance[1]
Reef interior	0.034 ± 0.003	0.12 ± 0.01	22	-6.94	***
Reef edge	0.076 ± 0.006	0.16 ± 0.01	13	6.20	***
S'Gaang Gwaii interior	0.041 ± 0.01	0.066 ± 0.02	11	1.29	0.22
S'Gaang Gwaii edge	0.10 ± 0.04	0.15 ± 0.04	4	-0.783	0.48

1 Significance levels of $p<0.001$ given as ***, $p<0.01$ as **, $p<0.05$ as *.

Table 6: Similarity of composition of species within response guilds between experimental and control islands, measured with Czekanowski's index of similarity. Similarity measures for the *first* (1997) and the *last* year of measurement (2002 for Reef, 2001 for S'Gaang Gwaii) were compared using a paired t-test.

Island	Average similarity first ± SE	Average similarity last ± SE	Degrees of freedom	T	Significance[1]
Reef interior	0.25 ± 0.03	0.12 ± 0.01	22	4.37	***
Reef edge	0.31 ± 0.06	0.24 ± 0.06	13	3.96	**
S'Gaang Gwaii interior	0.28 ± 0.07	0.30 ± 0.07	11	-1.91	0.08
S'Gaang Gwaii edge	0.14 ± 0.07	0.13 ± 0.06	4	1.69	0.08

1 Significance levels of $p<0.001$ given as ***, $p<0.01$ as **, $p<0.05$ as *.

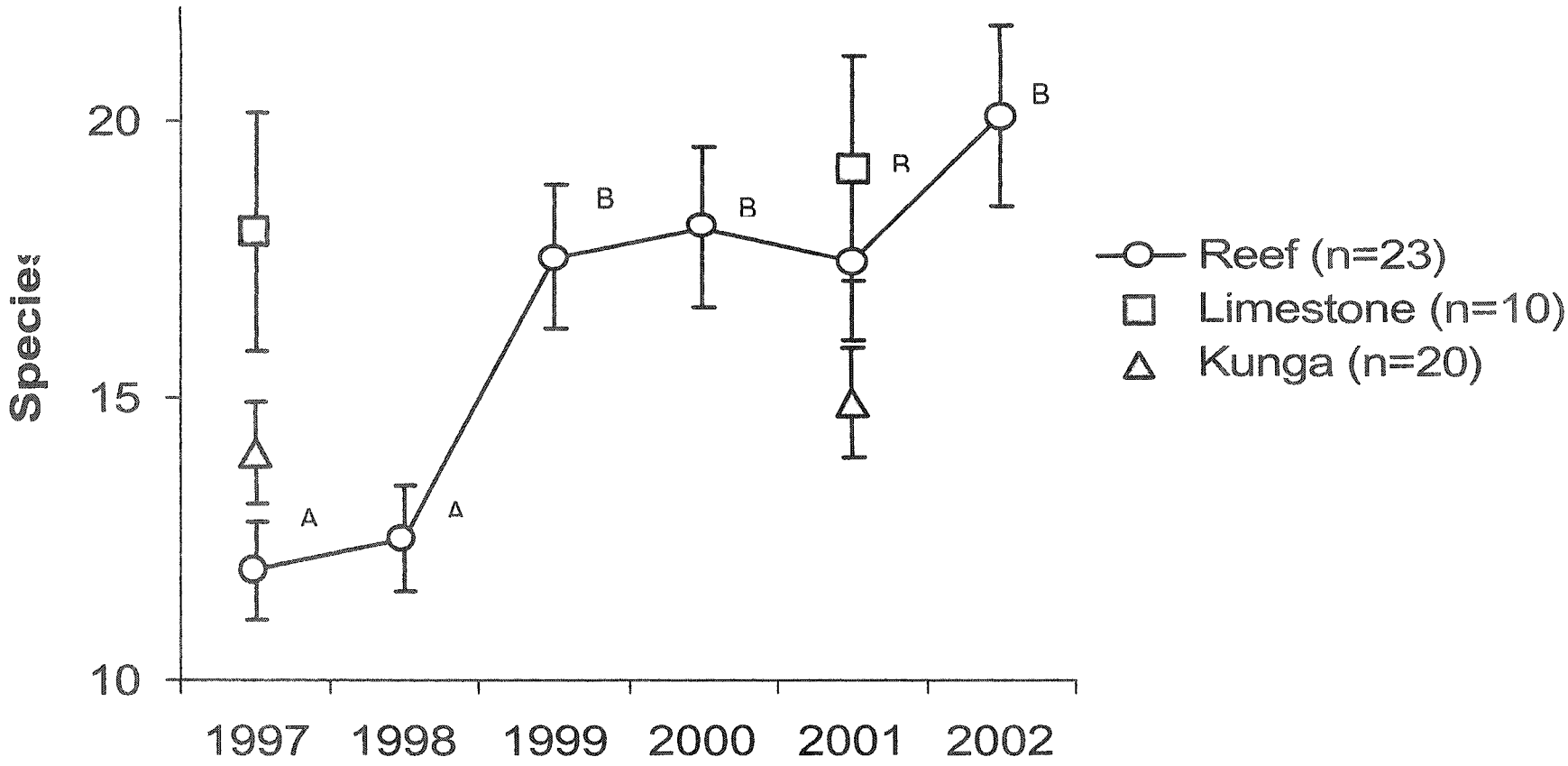

Figure 1: Average species richness (± SE) of forest interior plots on Reef (n=23), Limestone (n=10) and Kunga (n=20) islands 1997 to 2002, showing a large increase in species on Reef Island following the culls of 1997 and 1998. Levels significantly different from one another (as determined through post-hoc Scheffe tests) are denoted with different letters.

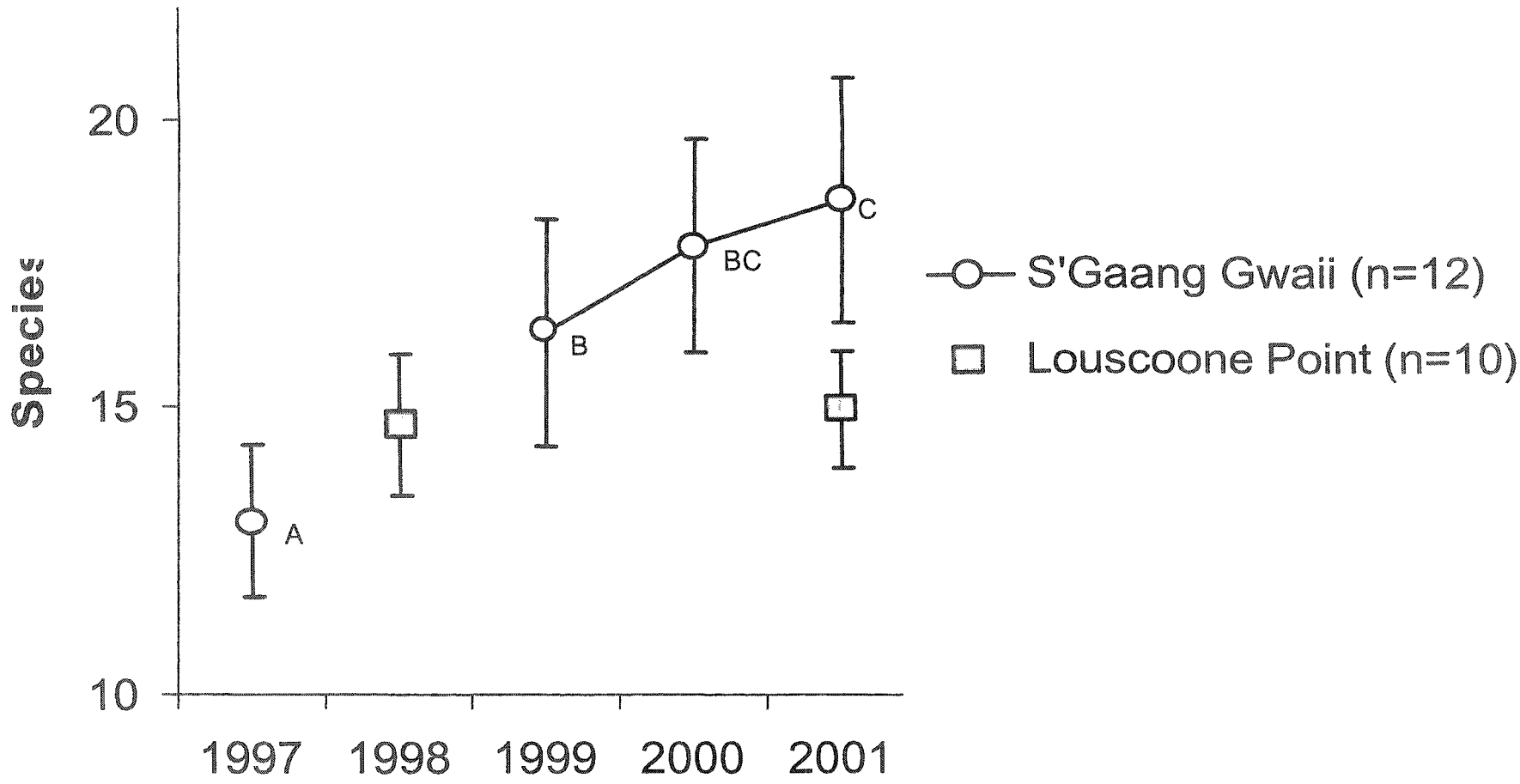

Figure 2: Average species richness (± SE) of forest interior plots on S'Gaang Gwaii (n=12), and Louscoone Point (n=10) 1997 to 2001, showing a large increase in species on S'Gaang Gwaii following the culls of 1997 and 1998. Levels significantly different from one another (as determined through pos-hoc Scheffe tests) are denoted with different letters.

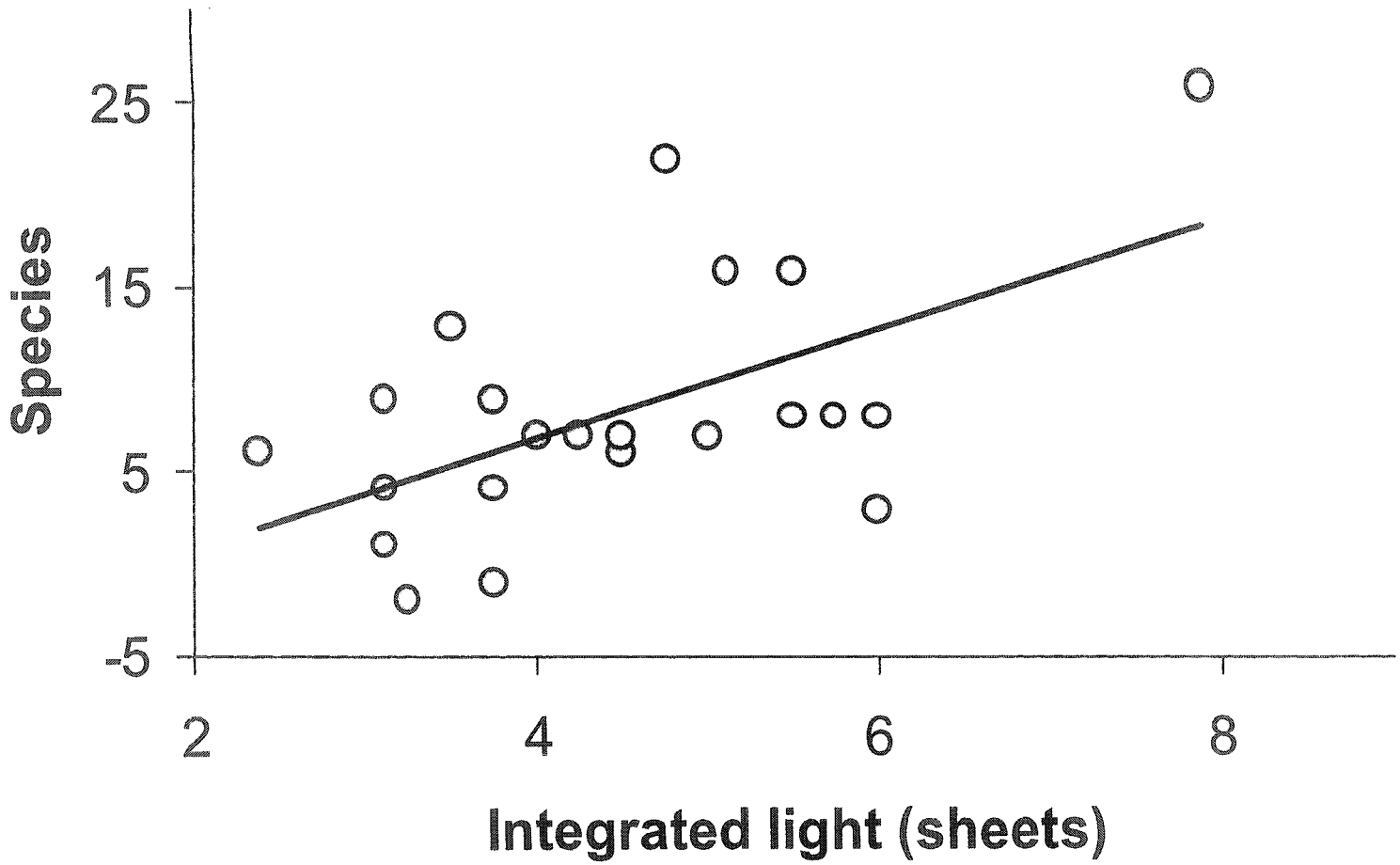

Figure 3: Change in species richness as a function of light in the forest interior, showing the change in species richness between 1997 and 2002 and integrated light as determined by pinhole cameras (Sullivan and Mix 1984) for 23 forest interior plots on Reef Island.

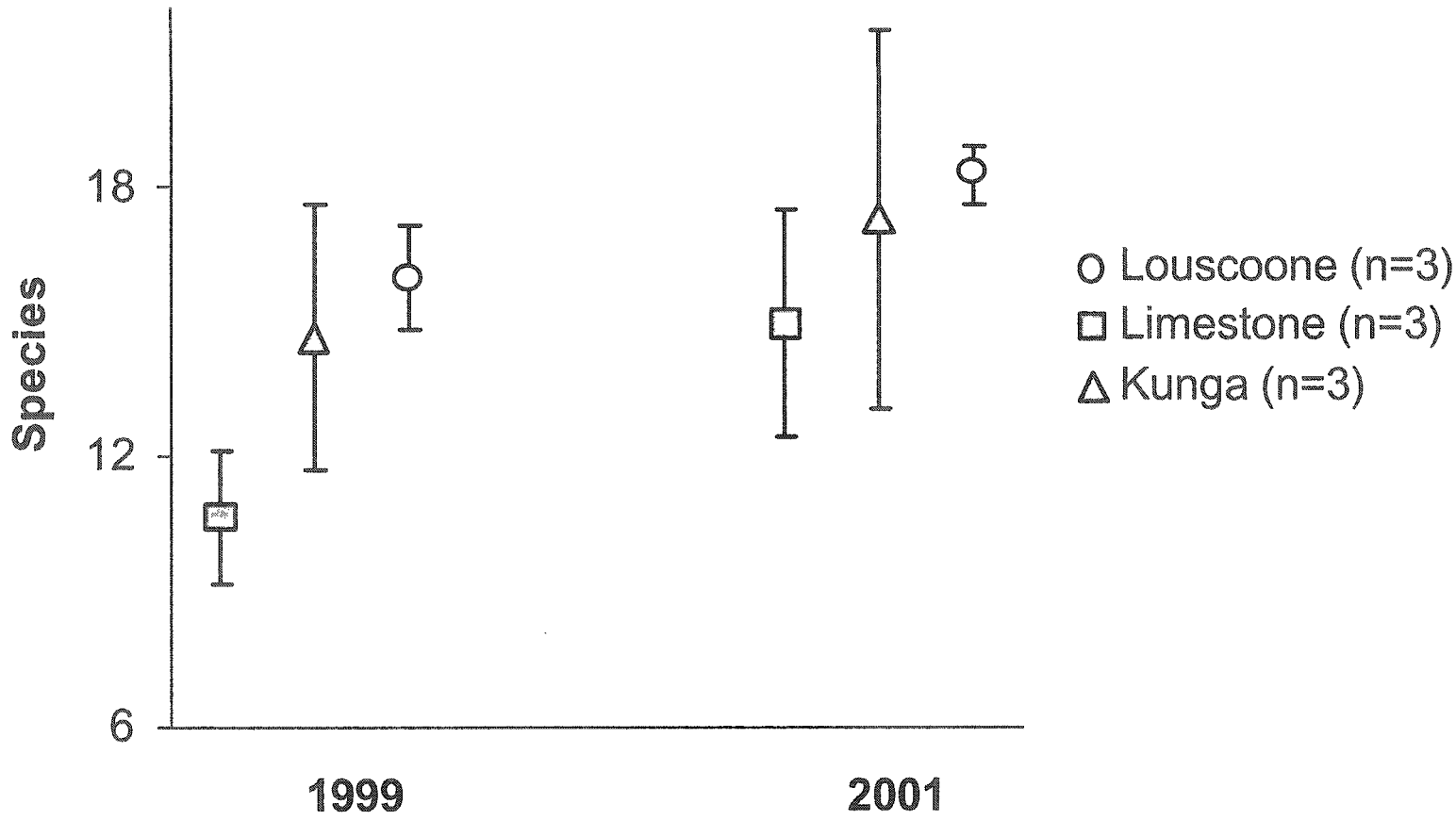

Figure 4: Average species richness (± SE) of exclosure plots on Limestone Island (n=3), Kunga Island (n=3) and Louscoone Point (n=3) in 1999 and 2001, showing an increase in average species richness at each site. Exclosures were erected in 1998.

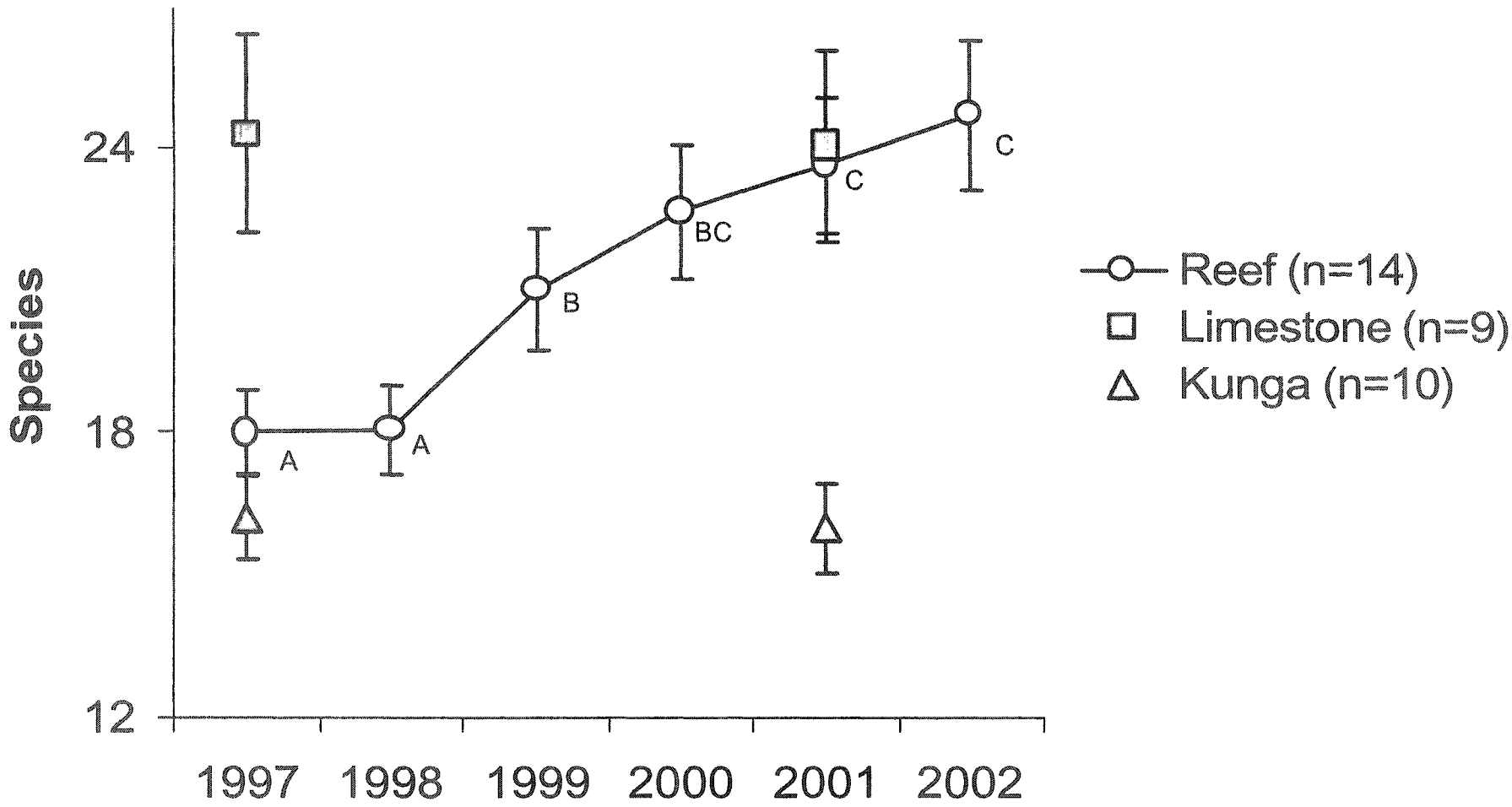

Figure 5: Average species richness (± SE) of forest edge plots on Reef (n=14), Limestone (n=9) and Kunga (n=10) islands 1997 to 2002, showing a large increase in species on Reef Island following the culls of 1997 and 1998. Levels significantly different from one another (as determined through post-hoc Scheffe tests) are denoted with different letters.

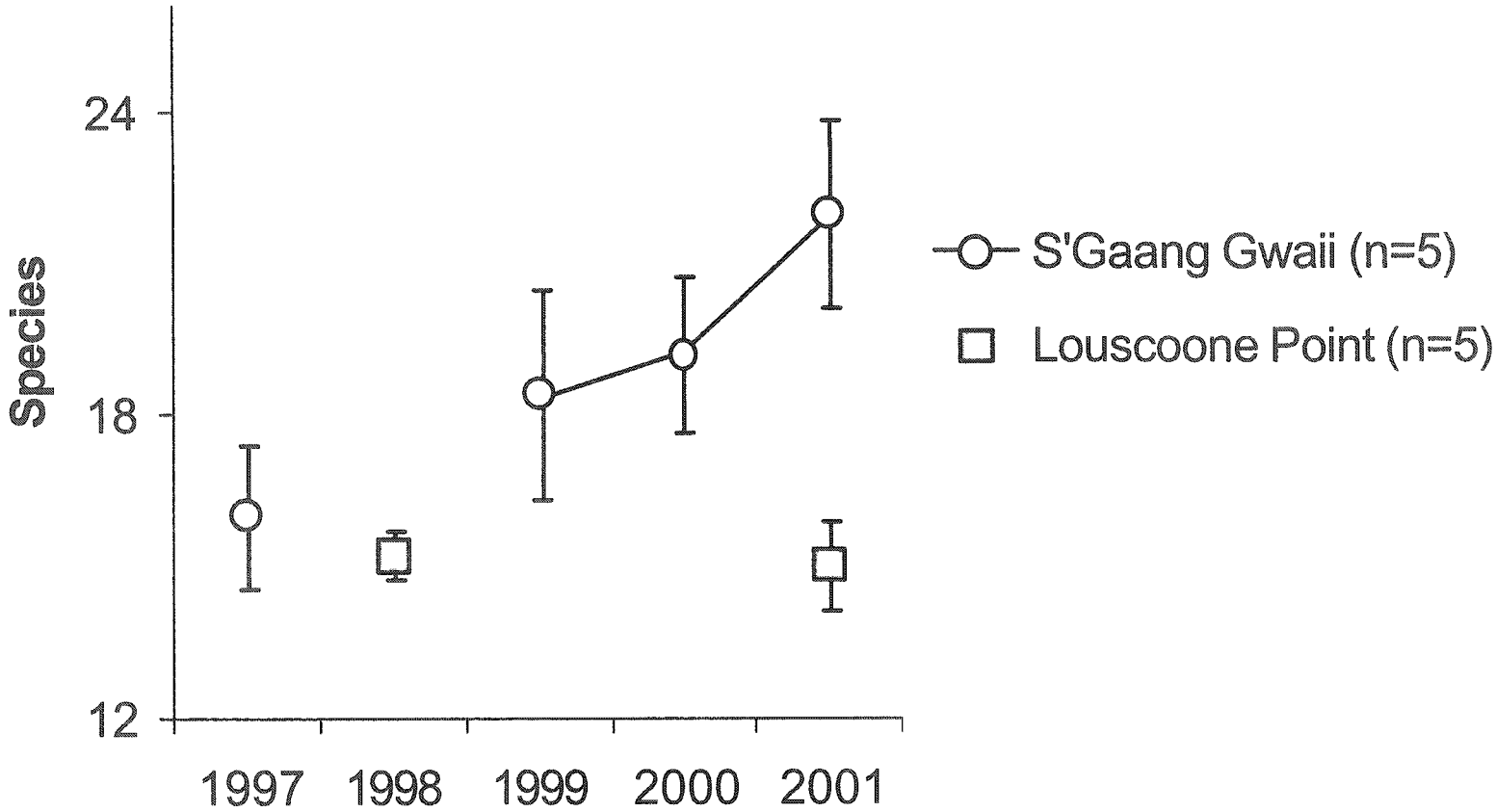

Figure 6: Average species richness (± SE) of forest edge plots on S'Gaang Gwaii (n=5) and Louscoone Point (n=5) 1997 to 2001, showing a large increase in species on S'Gaang Gwaii following the culls of 1997 and 1998. Levels significantly different from one another (as determined through post-hoc Scheffe tests) are denoted with different letters.

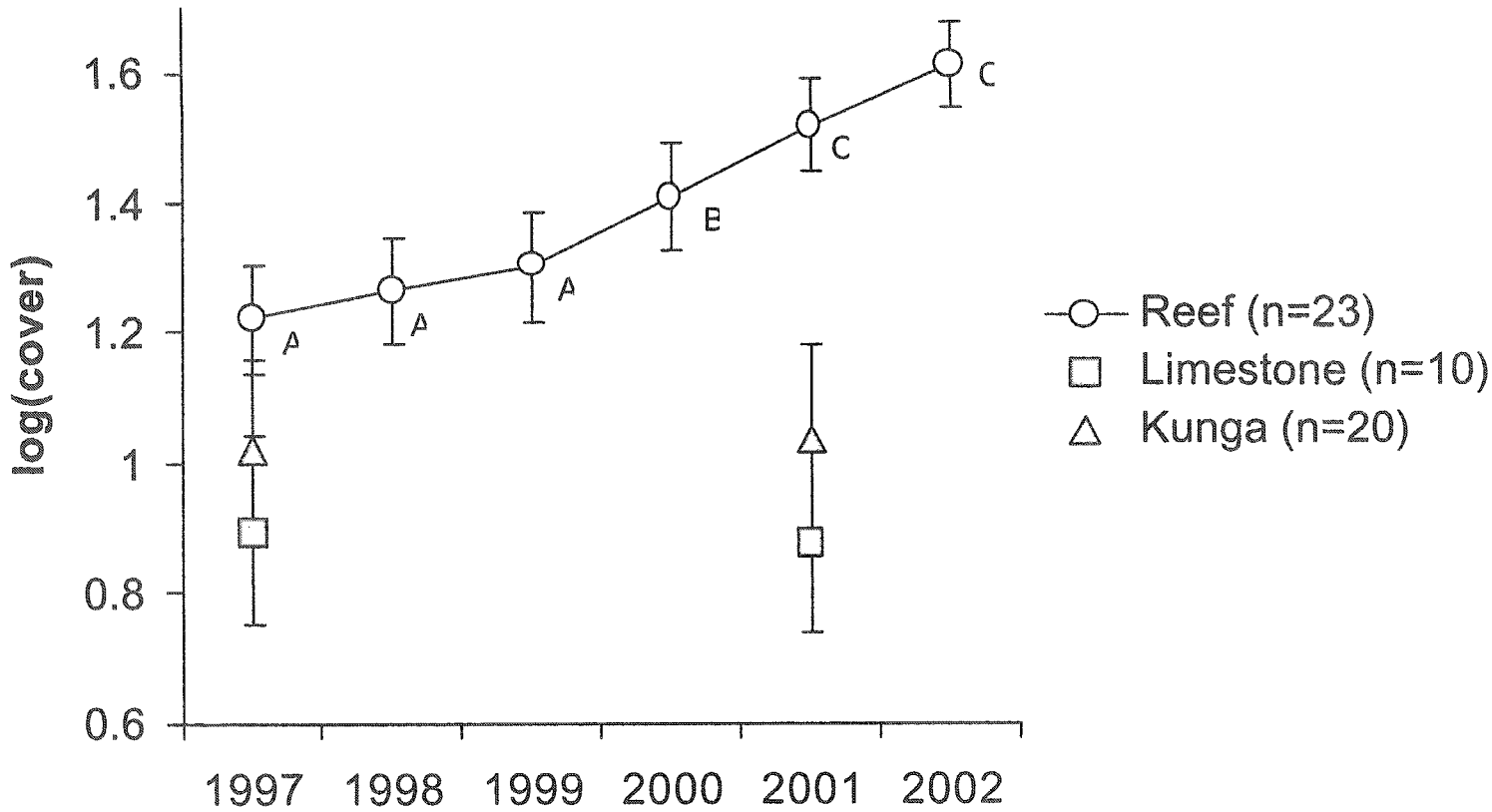

Figure 7: Average cover of vegetation (log tansformed ± SE) of forest interior plots on Reef (n=23), Limestone (n=10) and Kunga (n=20) Islands 1997 to 2002, showing a large increase in cover on Reef Island following the culls of 1997 and 1998. Levels significantly different from one another (as determined through post-hoc Scheffe tests) are denoted with different letters.

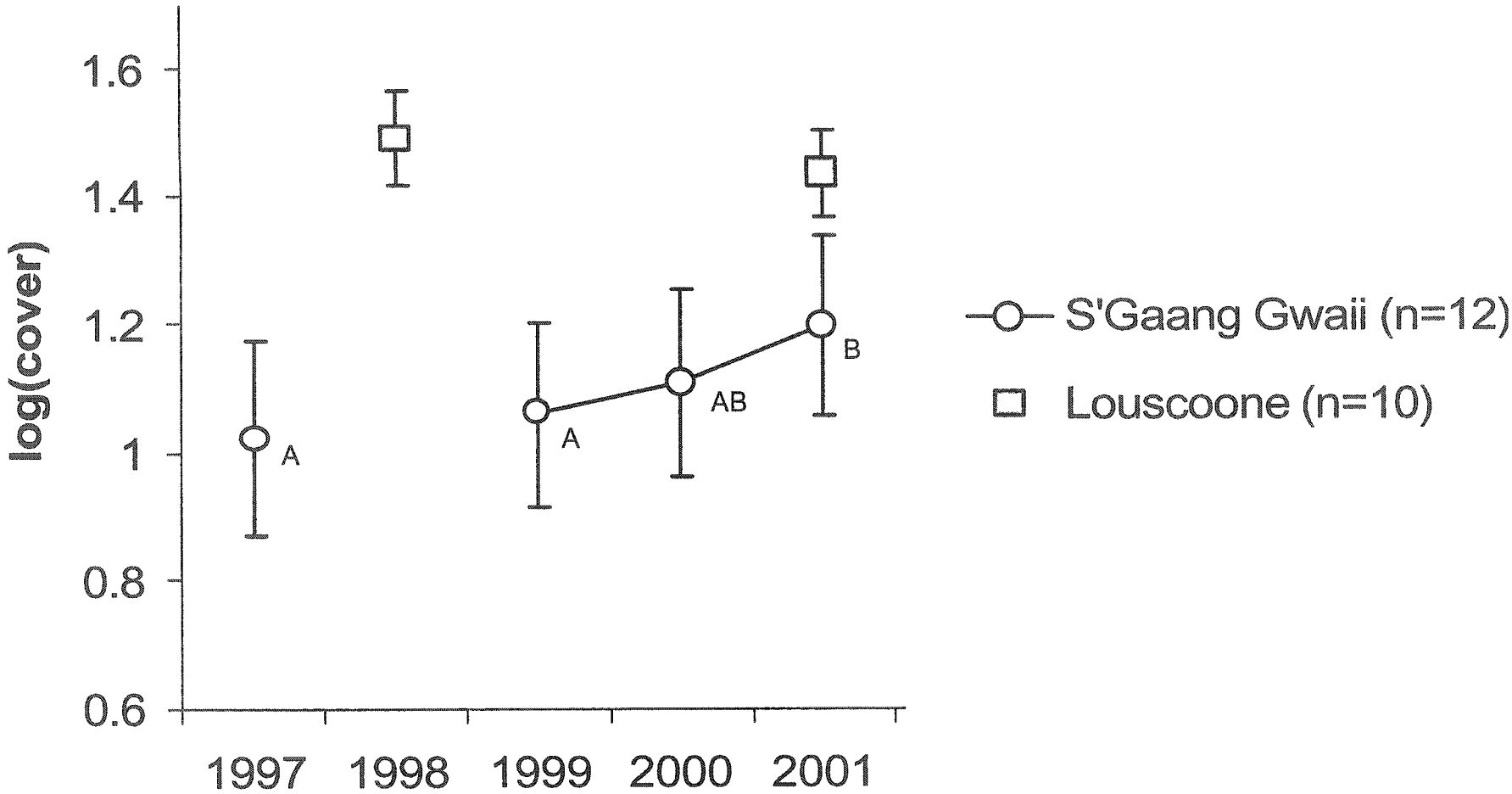

Figure 8: Average cover of vegetation (log tansformed ± SE) of forest interior plots on S'Gaang Gwaii (n=12) and Louscoone Point (n=10) 1997 to 2001, showing an increase in cover on S'Gaang Gwaii following the culls of 1997 and 1998. Levels significantly different from one another (as determined through post-hoc Scheffe tests) are denoted with different letters.

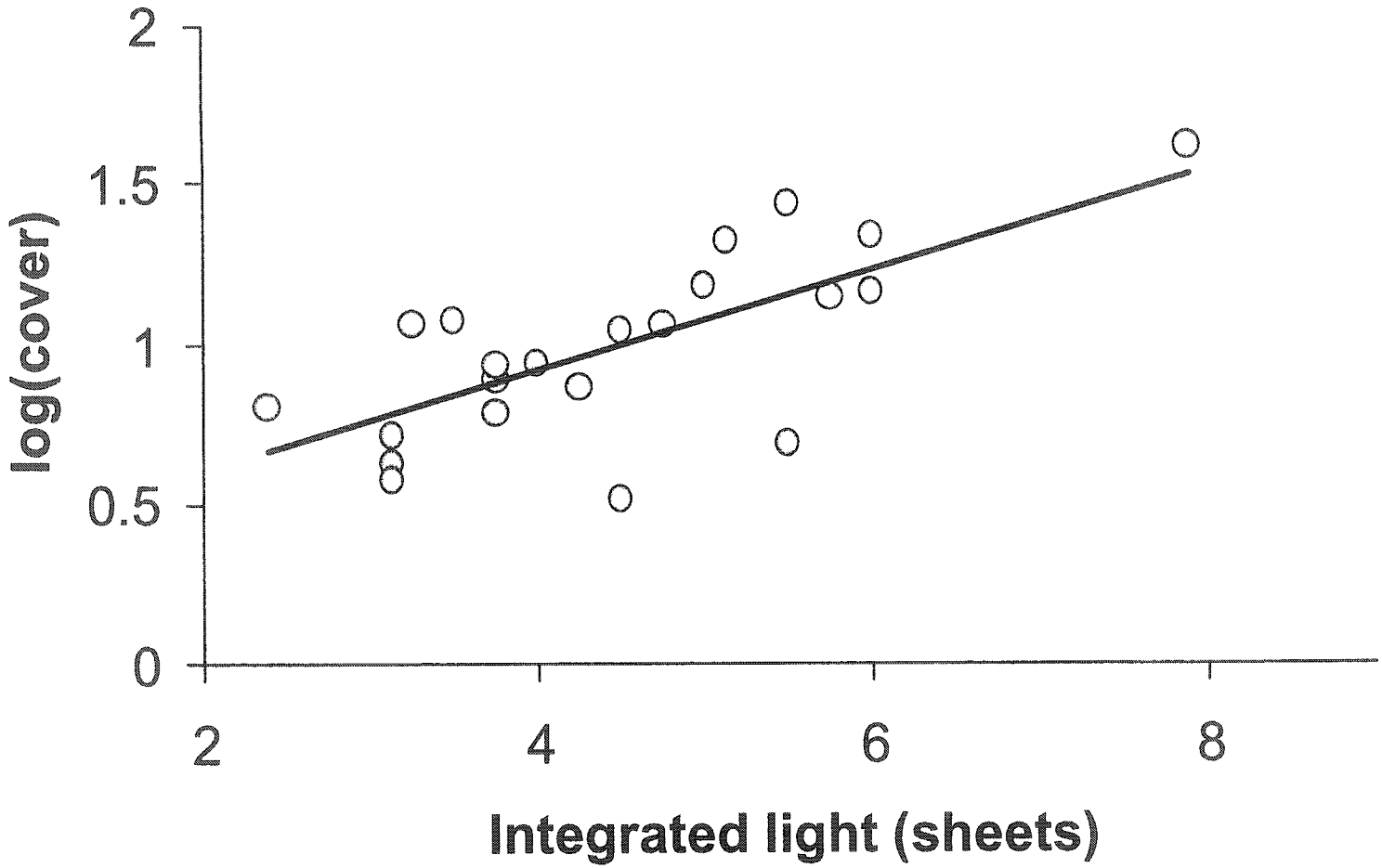

Figure 9 A: Change in the cover of vegetation as a function of light in the forest interior, showing the change in cover below 150 cm between 1997 and 2002 and integrated light as determined by pinhole cameras (Sullivan and Mix 1984) for 23 forest interior plots on Reef Island.

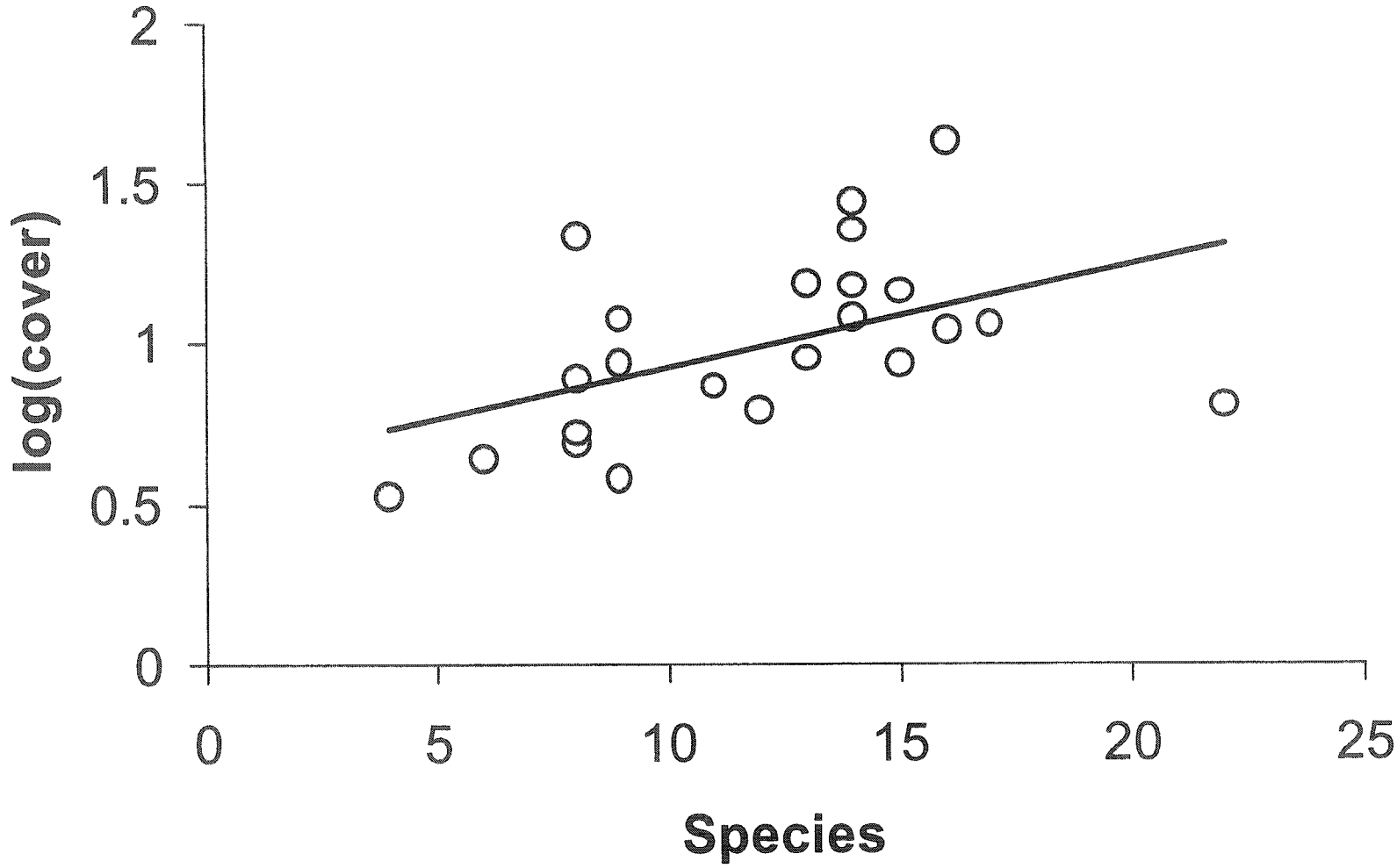

Figure 9 B: Change in the cover of vegetation as a function of species richness in the forest interior, showing the change in cover below 150 cm between 1997 and 2002 and the species richness measured in 1997 for 23 forest interior plots on Reef Island.

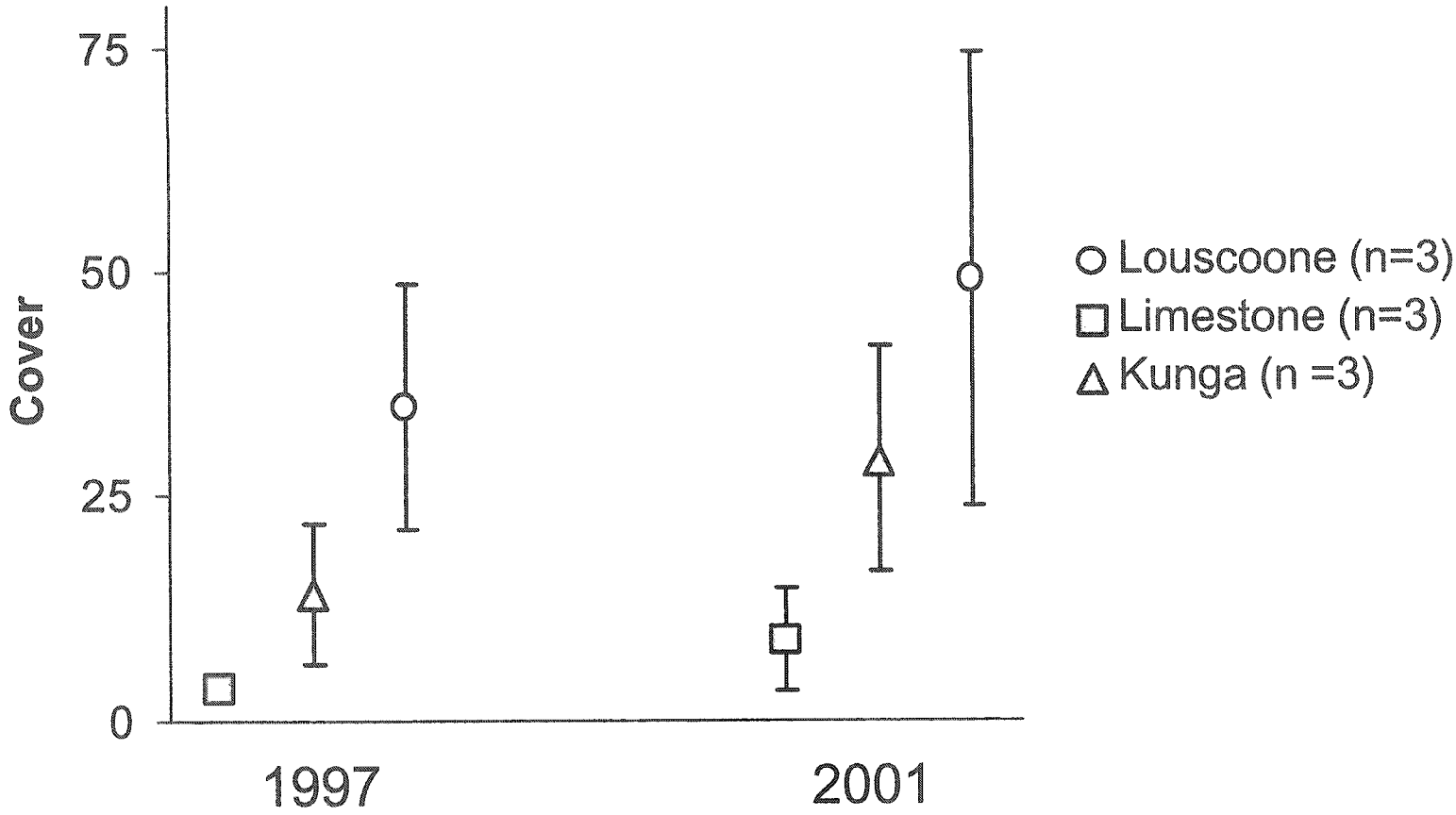

Figure 10: Average cover of vegetation (m2/100m2 ± SE) of exclosure plots on Limestone Island (n=3), Kunga Island (n=3) and Louscoone Point (n=3) in 1999 and 2001, showing an increase in average species richness at each site. Exclosures were erected in 1998.

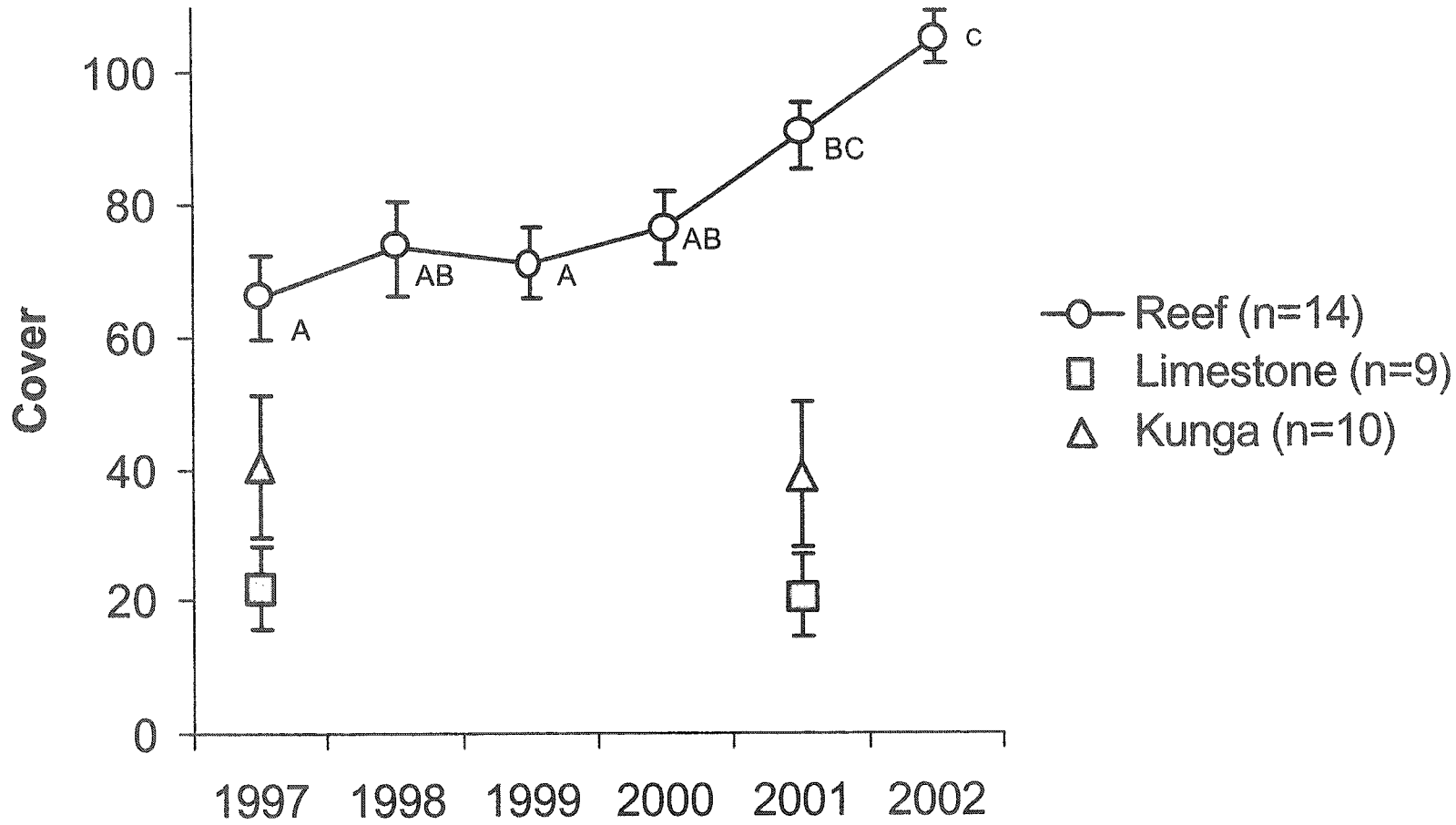

Figure 11: Average cover of vegetation (± SE) of forest edge plots on Reef (n=14), Limestone (n=9) and Kunga (n=10) islands 1997 to 2002, showing a slow increase in cover on Reef Island following the culls of 1997 and 1998. Levels significantly different from one another (as determined through post-hoc Scheffe tests) are denoted with different letters.

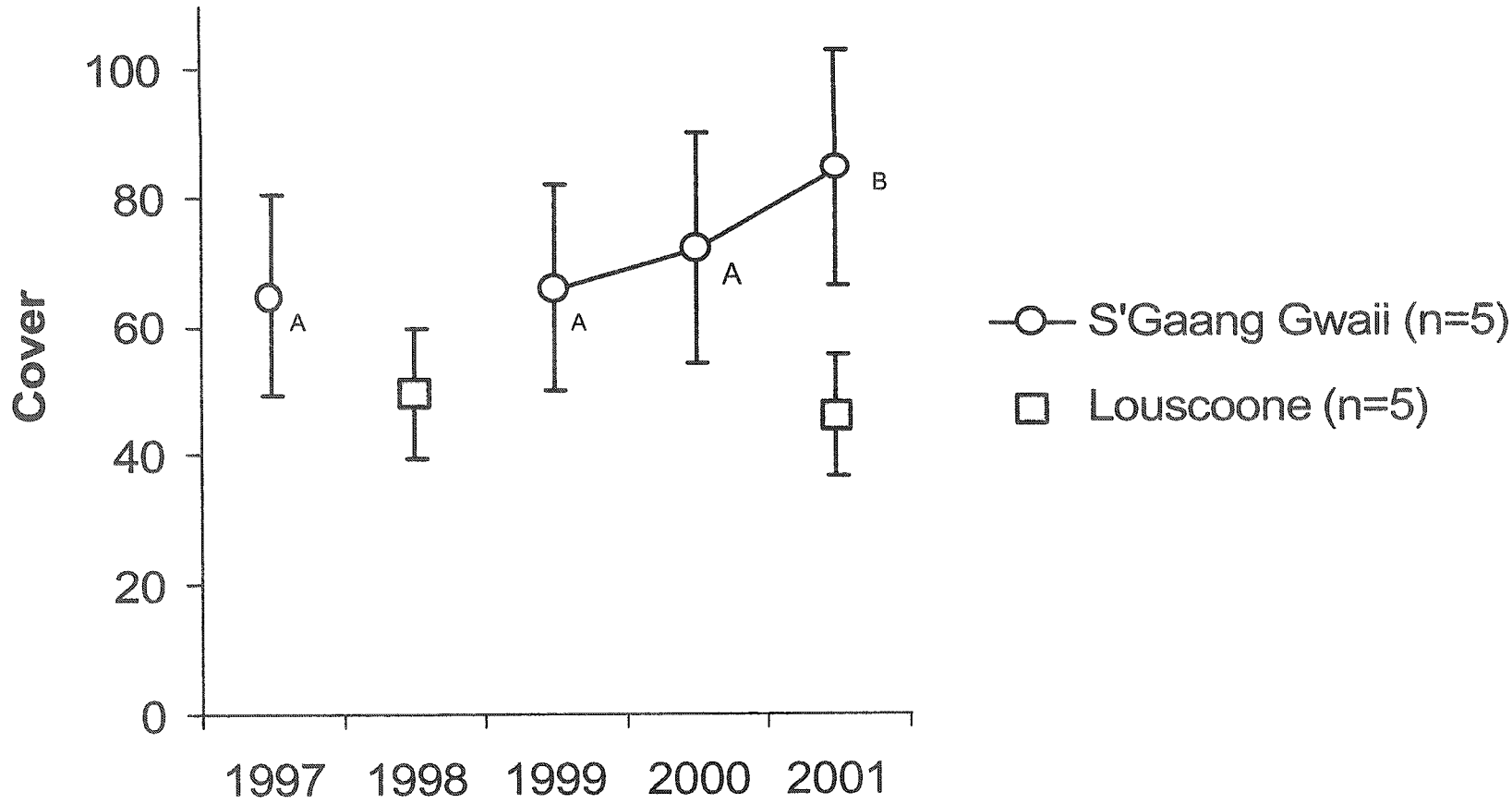

Figure 12: Average cover of vegetation (± SE) of forest edge plots on S'Gaang Gwaii (n=5) and Louscoone Point (n=5) 1997 to 2001, showing a slow increase in cover on S'Gaang Gwaii following the culls of 1997 and 1998. Levels significantly different from one another (as determined through post-hoc Scheffe tests) are denoted with different letters.

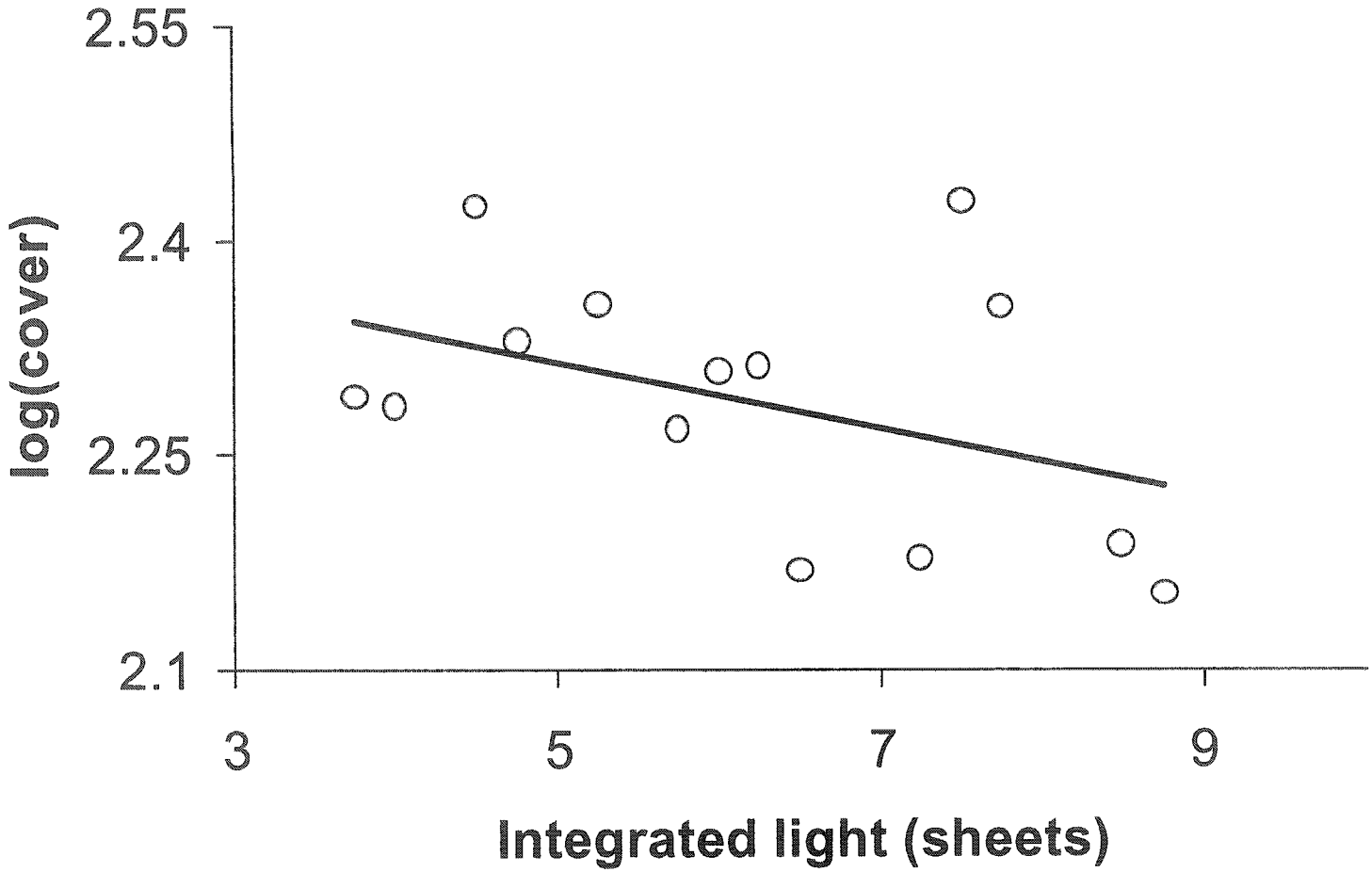

Figure 13: Change in the cover of vegetation as a function of light in the forest edge, showing the change in cover below 150cm between 1997 and 2002 and integrated light as determined by pinhole cameras (Sullivan and Mix 1984) for 14 forest edge plots on Reef Island.

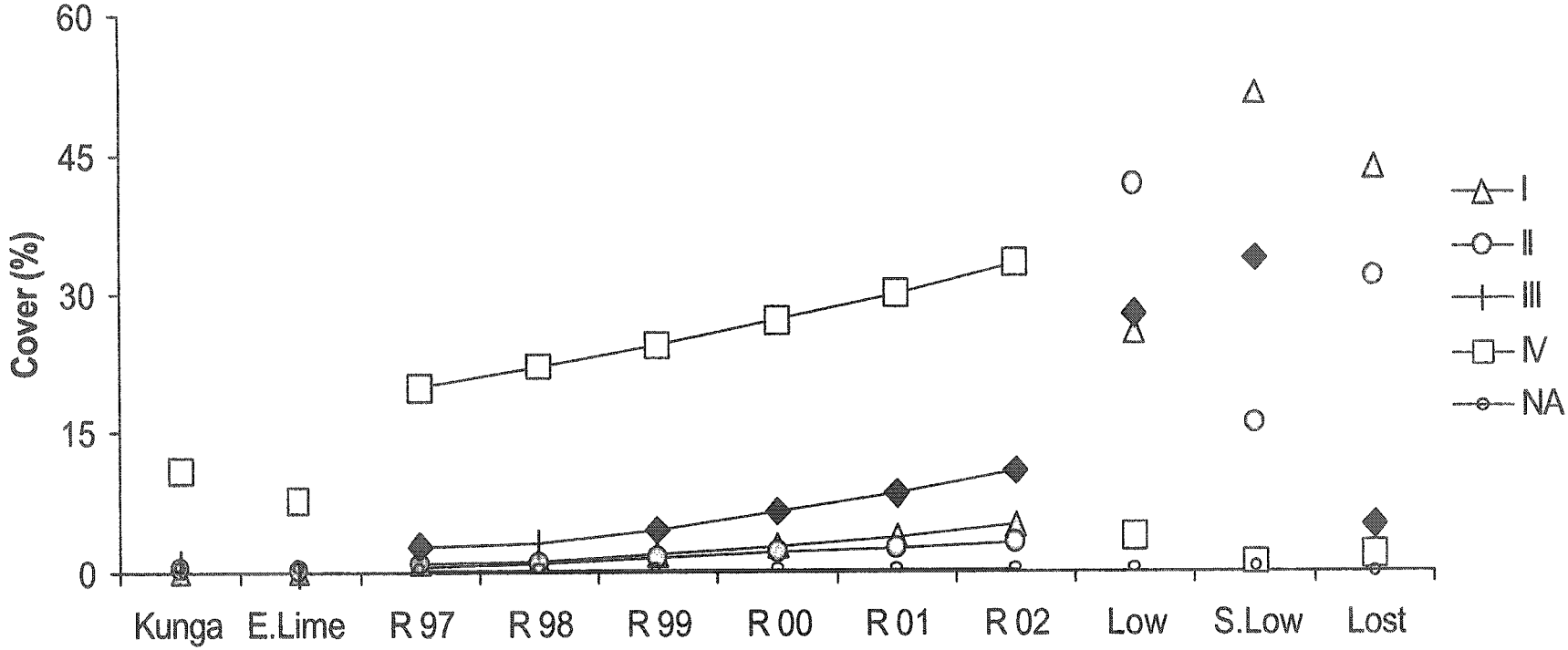

Figure 14: Average cover of vegetation in forest interior plots below 150 cm grouped by response guilds for control islands, Kunga (n=20) and E.Limestone (E.Lime; n=10); experimental island Reef 1997 to 2002 (R 97 to R 02; n=23); as well as on no-deer islands, Low (n=5), S.Low (n=5) and Lost (n=5). Response guilds were assembled based on the response of each species to deer modification. Measures are for 1997 on Kunga and E.Limestone Islands and 2000 for Low, S.Low and Lost Islands.

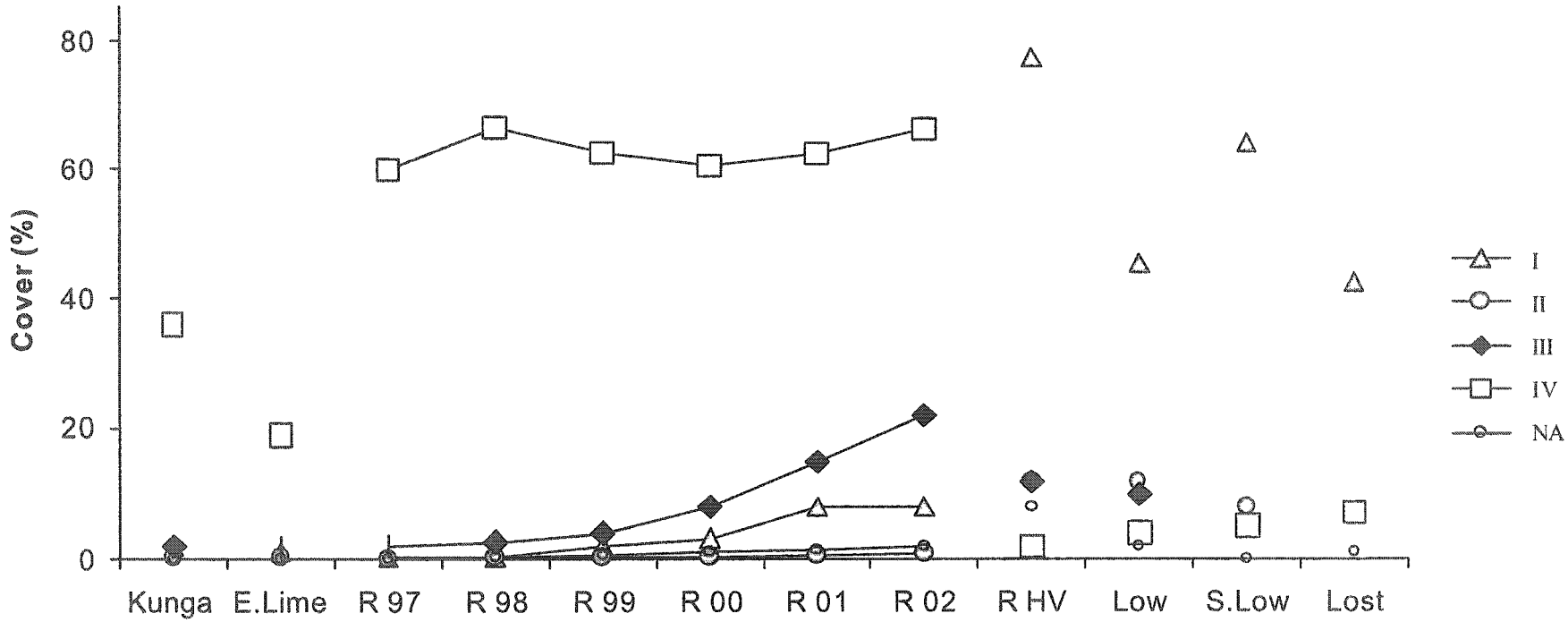

Figure 15: Average cover of vegetation in forest edge plots grouped by response guilds for control islands, Kunga (n=10) and E.Limestone (E.Lime; n=9); experimental island, Reef 1997 to 2002 (R 97 to R 02; n=14); natural exclosure, Reef *Hidden Valley* (R HV; n=1); as well as on no-deer islands, Low (n=10), S.Low (n=10) and Lost (n=10) in 2000. Response guilds were assembled based on the response of each species to deer modification. Measures are for 1997 on Kunga and E.Limestone Islands; 2000 for Low,

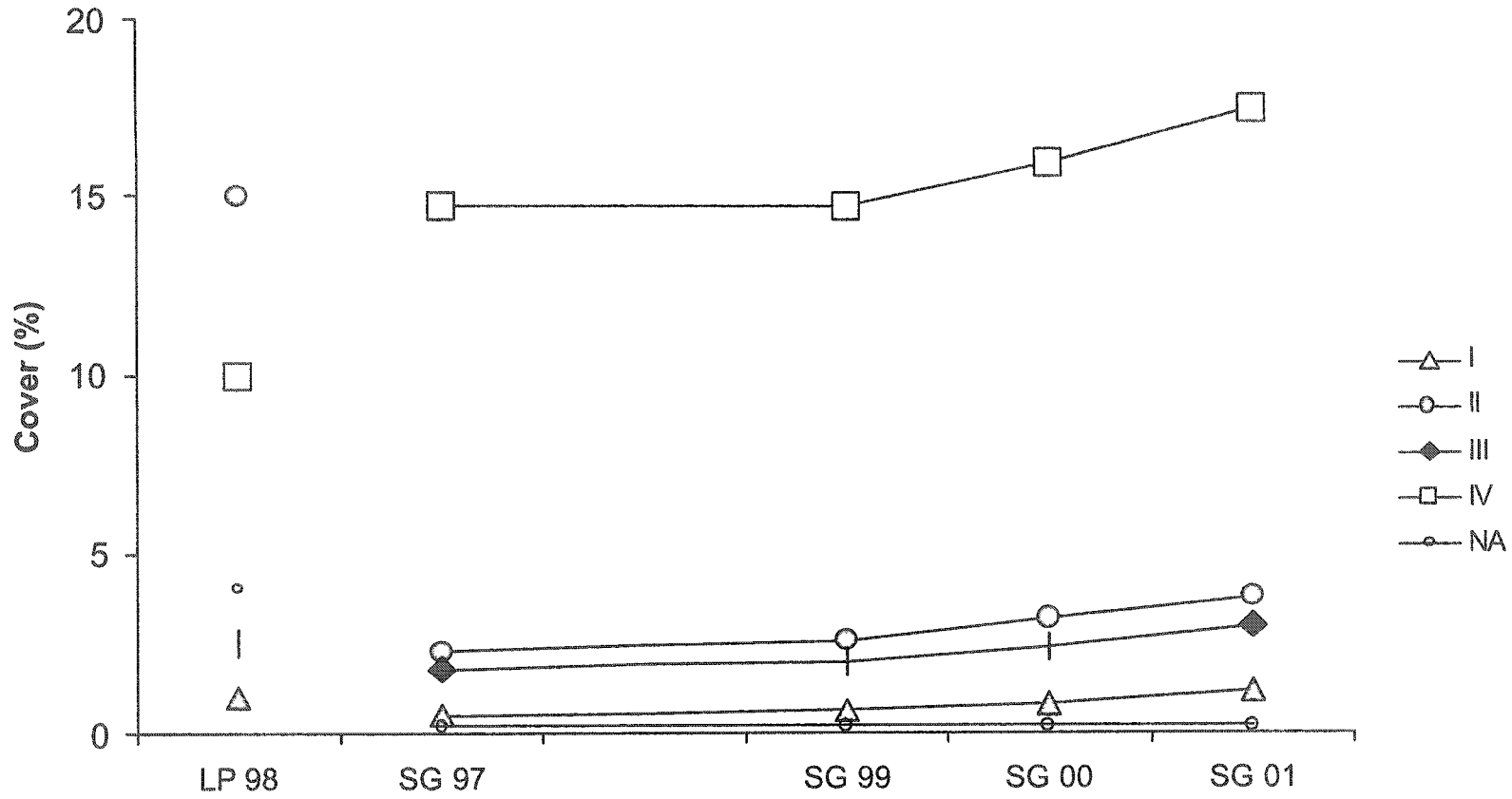

Figure 16: Average cover of vegetation in forest interior plots grouped by response guilds for control site, Louscoone Point in 1998 (LP 98; n=10); and experimental island, S'Gaang Gwaii from 1997 to 2001 (SG 97 to SG 01; n=12). Response guilds were assembled based on the response of each species to deer modification.

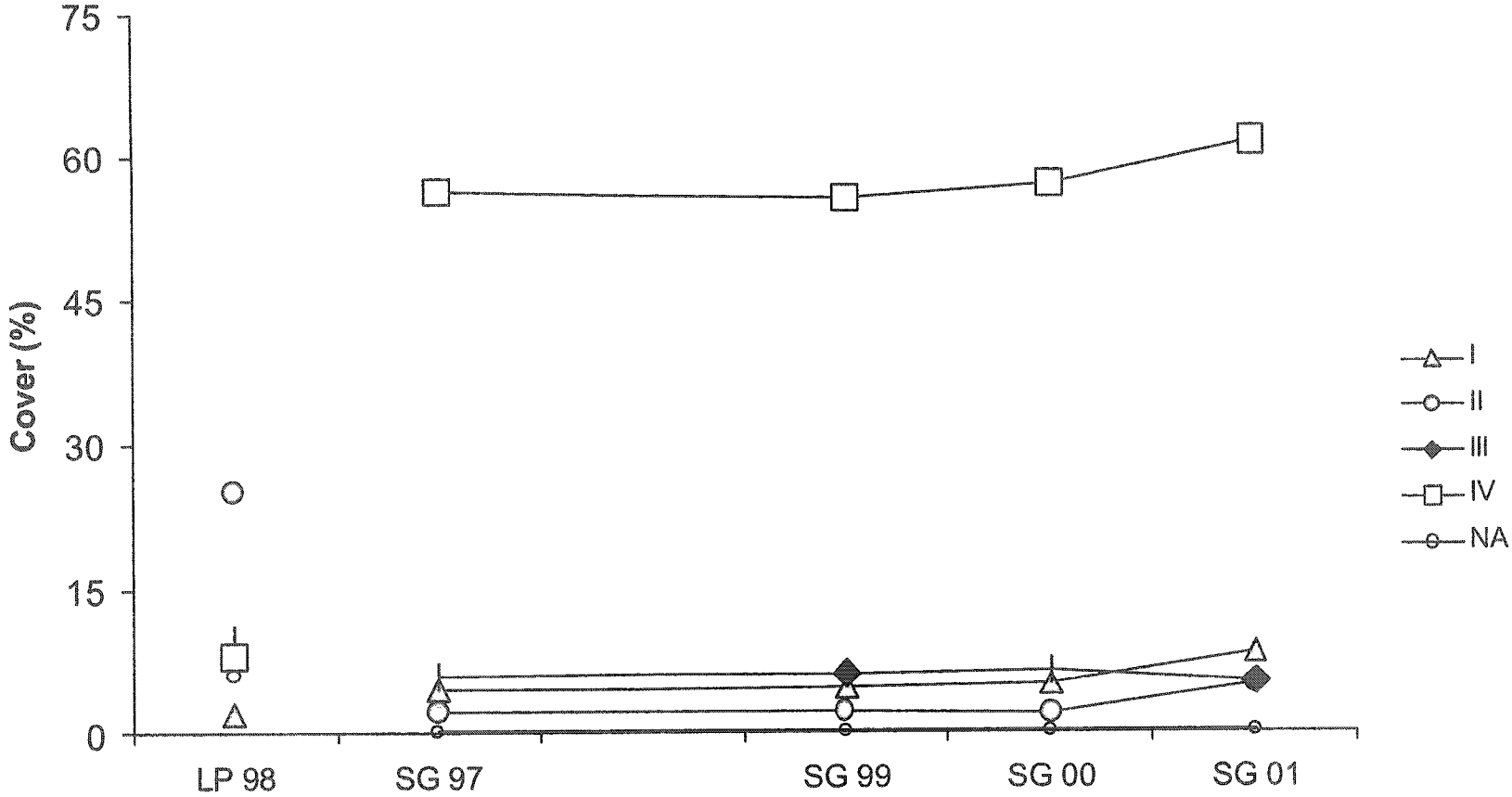

Figure 17: Average cover of vegetation in forest edge plots grouped by response guilds for control site, Louscoone Point in 1998 (LP 98; n=5); and experimental island, S'Gaang Gwaii from 1997 to 2001 (SG 97 to SG 01; n=5). Response guilds were assembled based on the response of each species to deer modification.

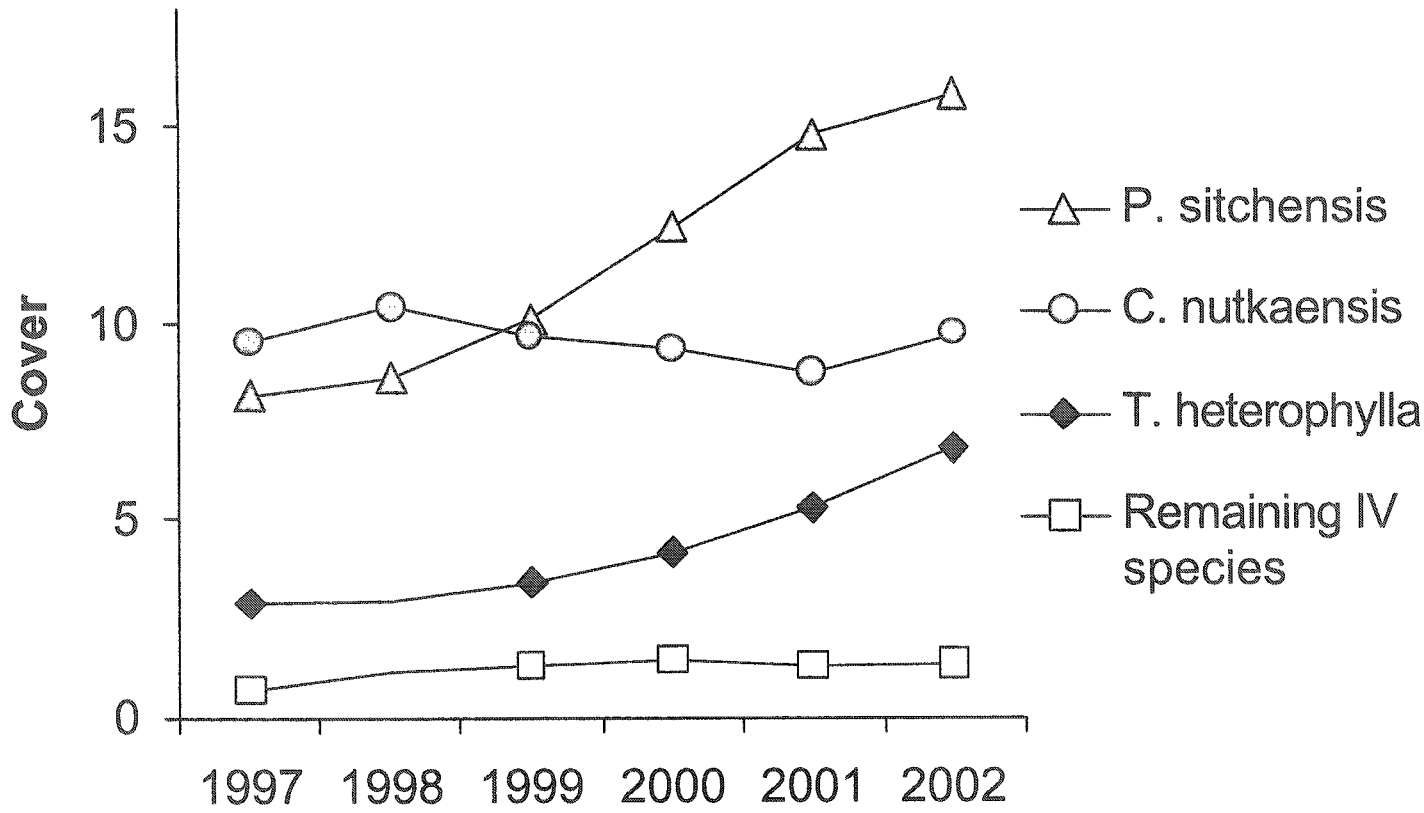

Figure 18: The composition of guild IV in the forest interior of Reef Island, showing the average cover of *Picea sitchensis*, *Calamagrostis nutkaensis*, *Tsuga heterophylla* and the summed cover of the 13 remaining species in guild IV, occurring in 23 forest interior plots on Reef Island from 1997 to 2002.

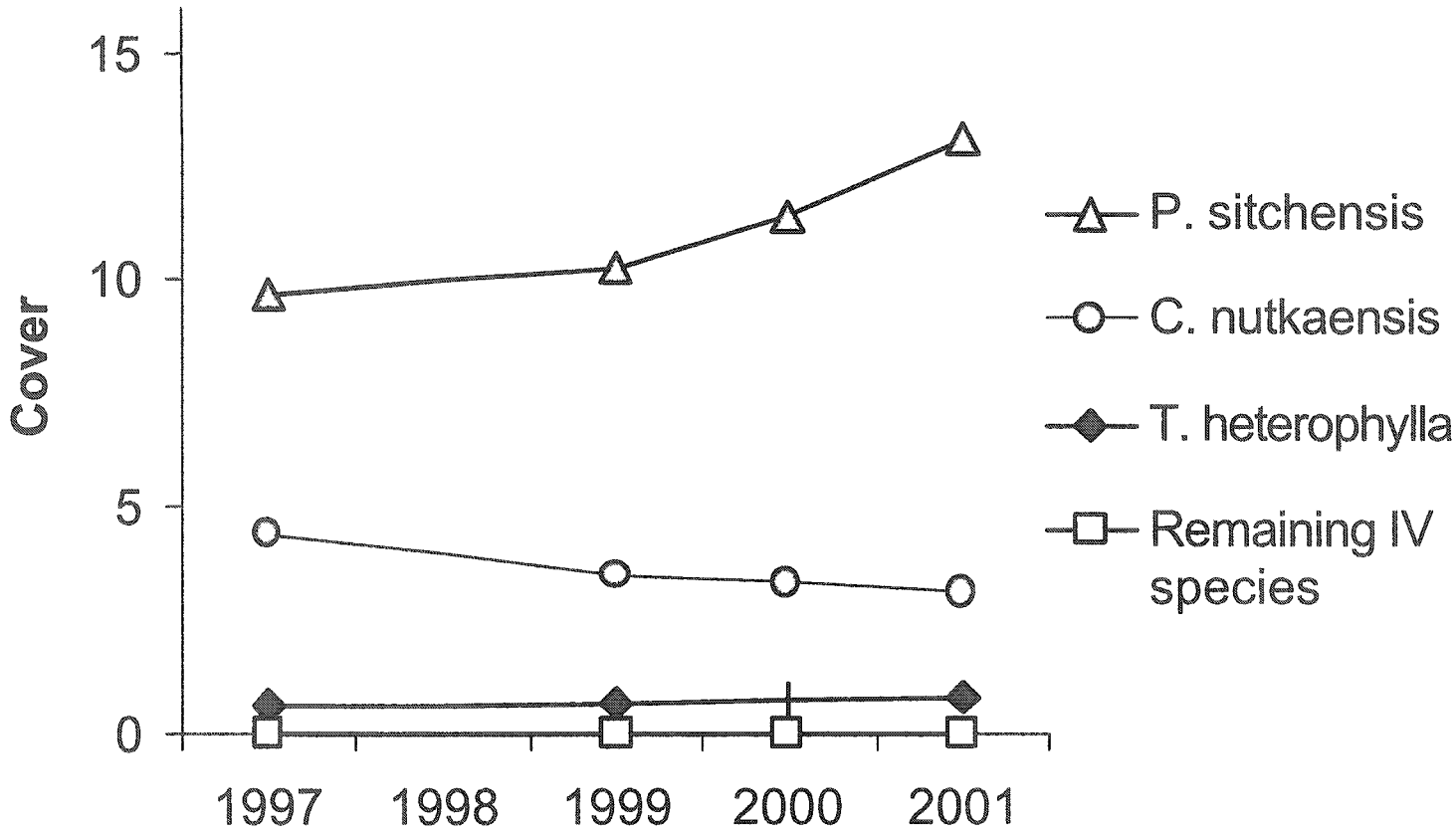

Figure 19: The composition of guild IV in the forest edge of Reef Island, showing the average cover of *Picea sitchensis*, *Calamagrostis nutkaensis*, *Tsuga heterophylla* and the summed cover of the 13 remaining species in guild IV, occurring in 14 forest edge plots on Reef Island from 1997 to 2002.

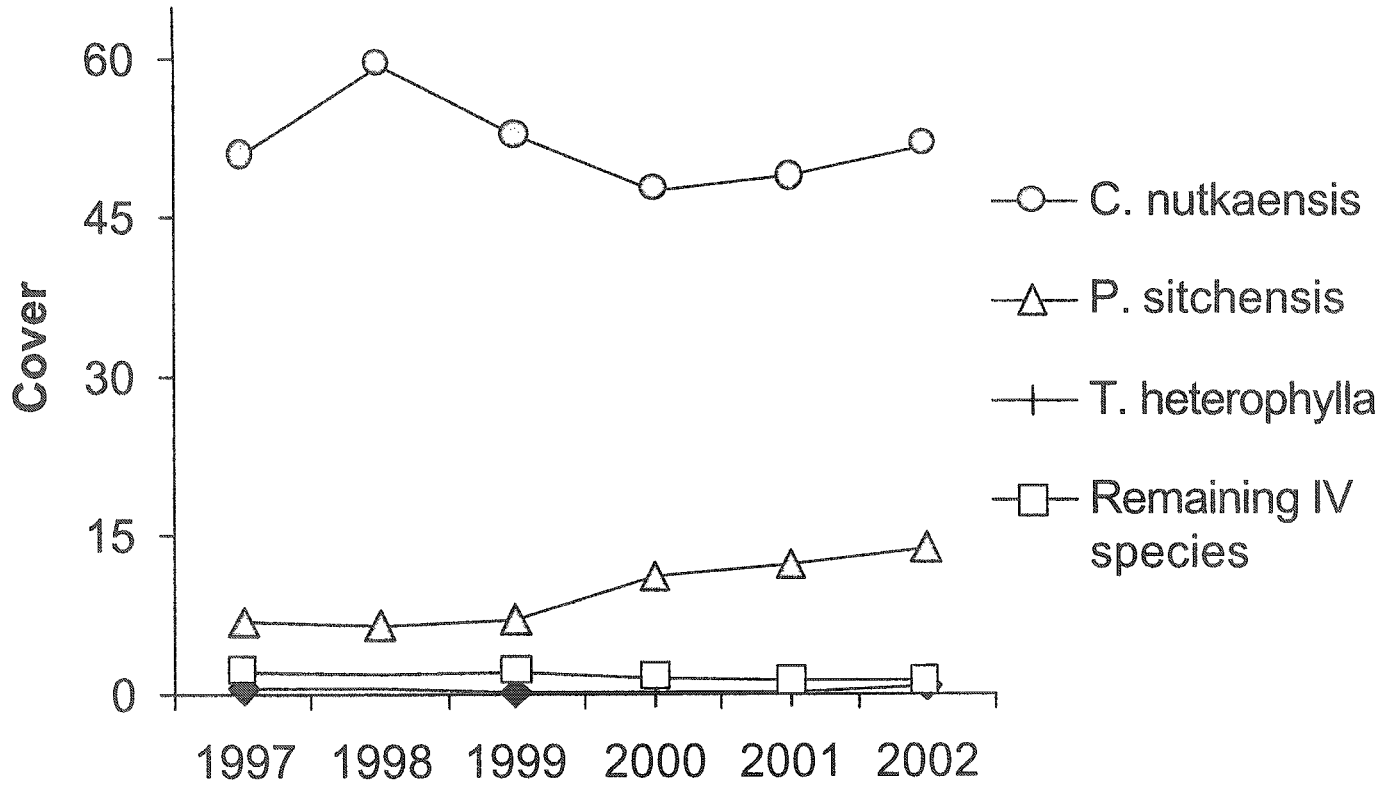

Figure 20: The composition of guild IV in the forest interior of S'Gaang Gwaii, showing the average cover of *Calamagrostis nutkaensis*, *Picea sitchensis, Tsuga heterophylla* and the summed cover of the 13 remaining species in guild IV, occurring in 12 forest interior plots on S'Gaang Gwaii from 1997 to 2001.

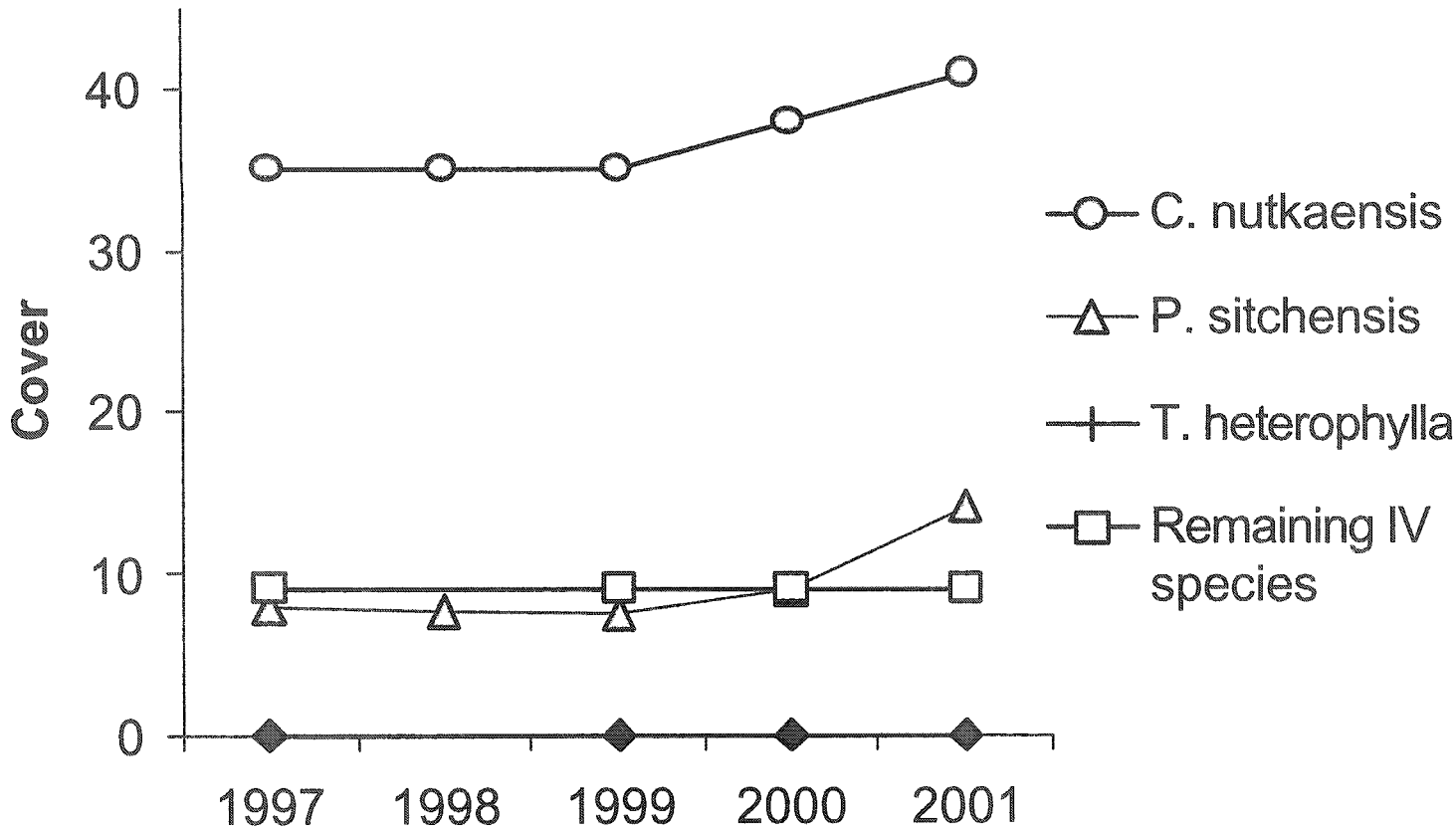

Figure 21: The composition of guild IV in the forest edge of S'Gaang Gwaii, showing the average cover of *Calamagrostis nutkaensis, Picea sitchensis, Tsuga heterophylla* and the summed cover of the 13 remaining species in guild IV, occurring in 5 forest edge plots on S'Gaang Gwaii from 1997 to 2001.

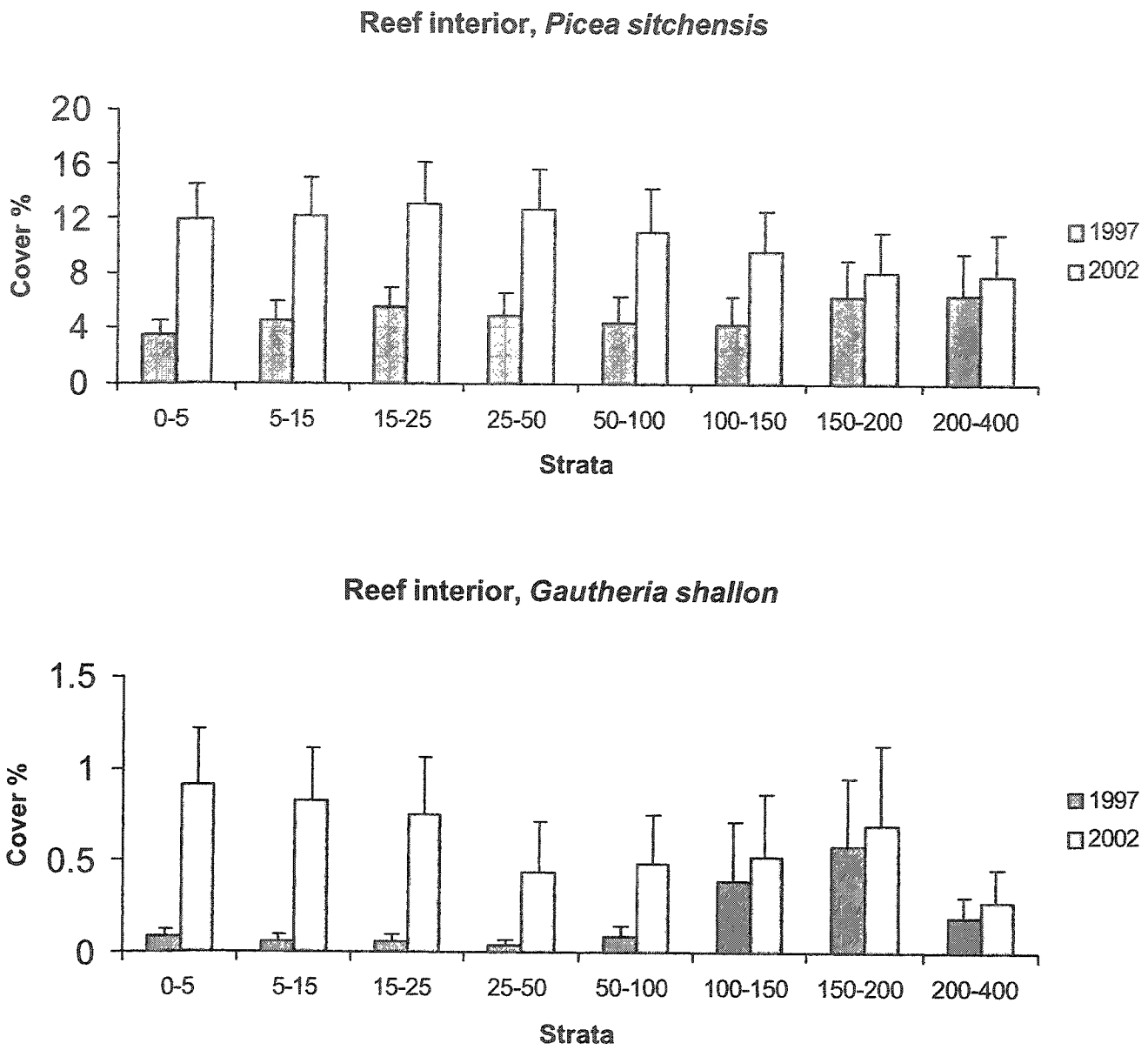

Figure 22 A and B: Average increase in cover of *Picea sitchensis* and *Gaultheria shallon* in interior plots by strata for Reef Island (n=23).

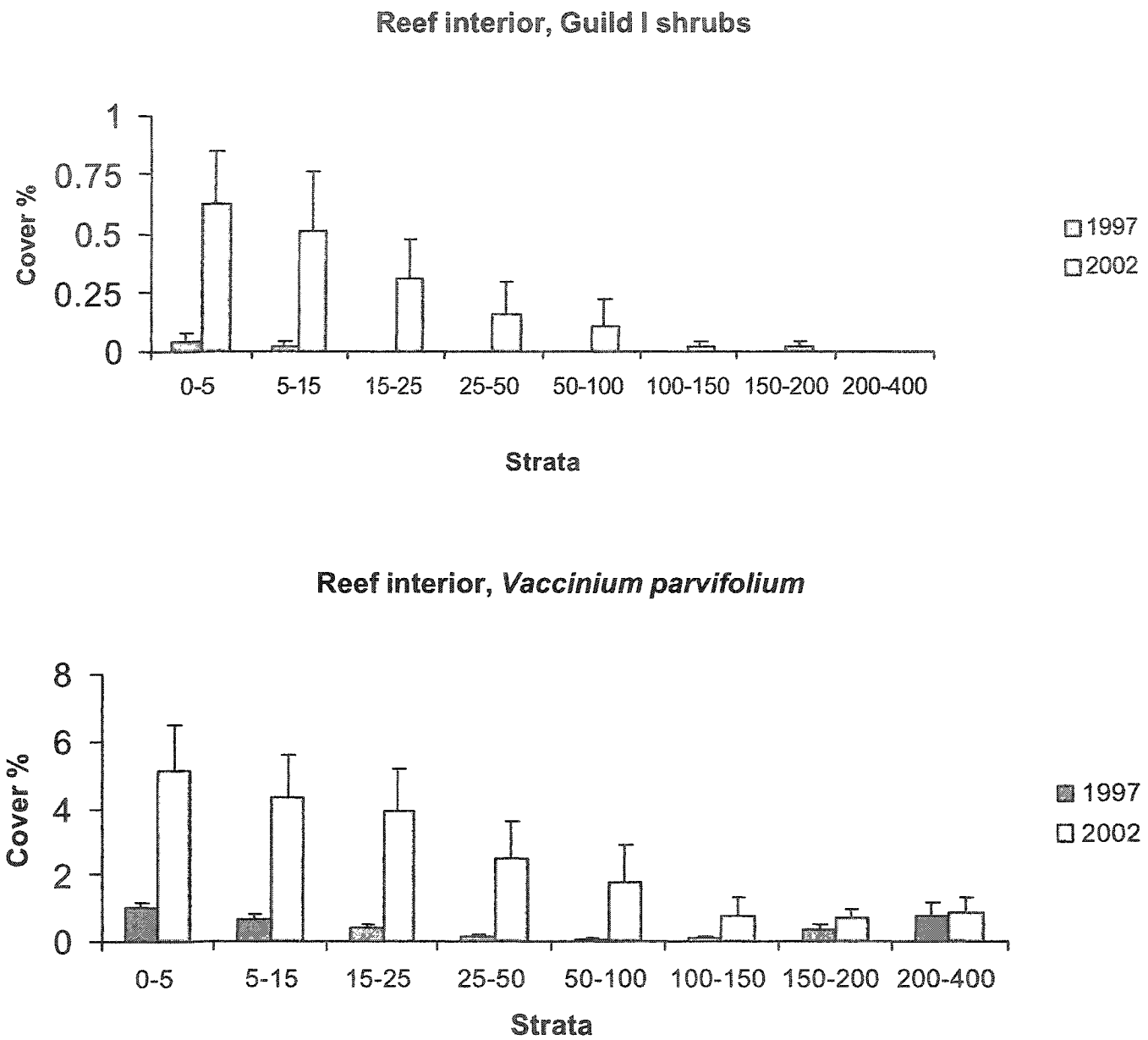

Figure 22 C and D: Average increase in cover of Guild I shrubs and *Vaccinium parvifolium* in interior plots by strata for Reef Island (n=23).

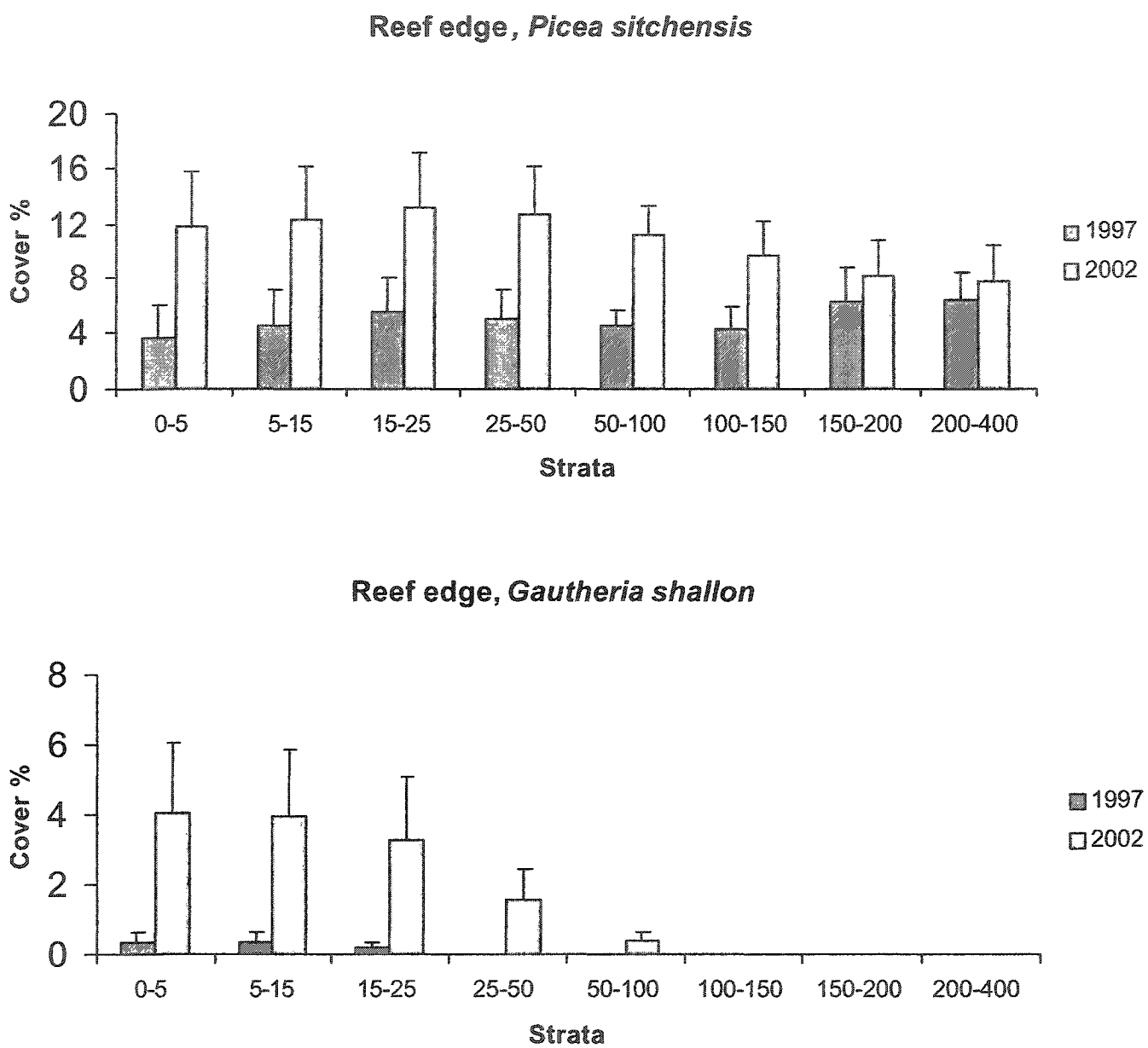

Figure 23 A and B: Average increase in cover of *Picea sitchensis* and *Gaultheria shallon* in edge plots by strata for Reef Island (n=14).

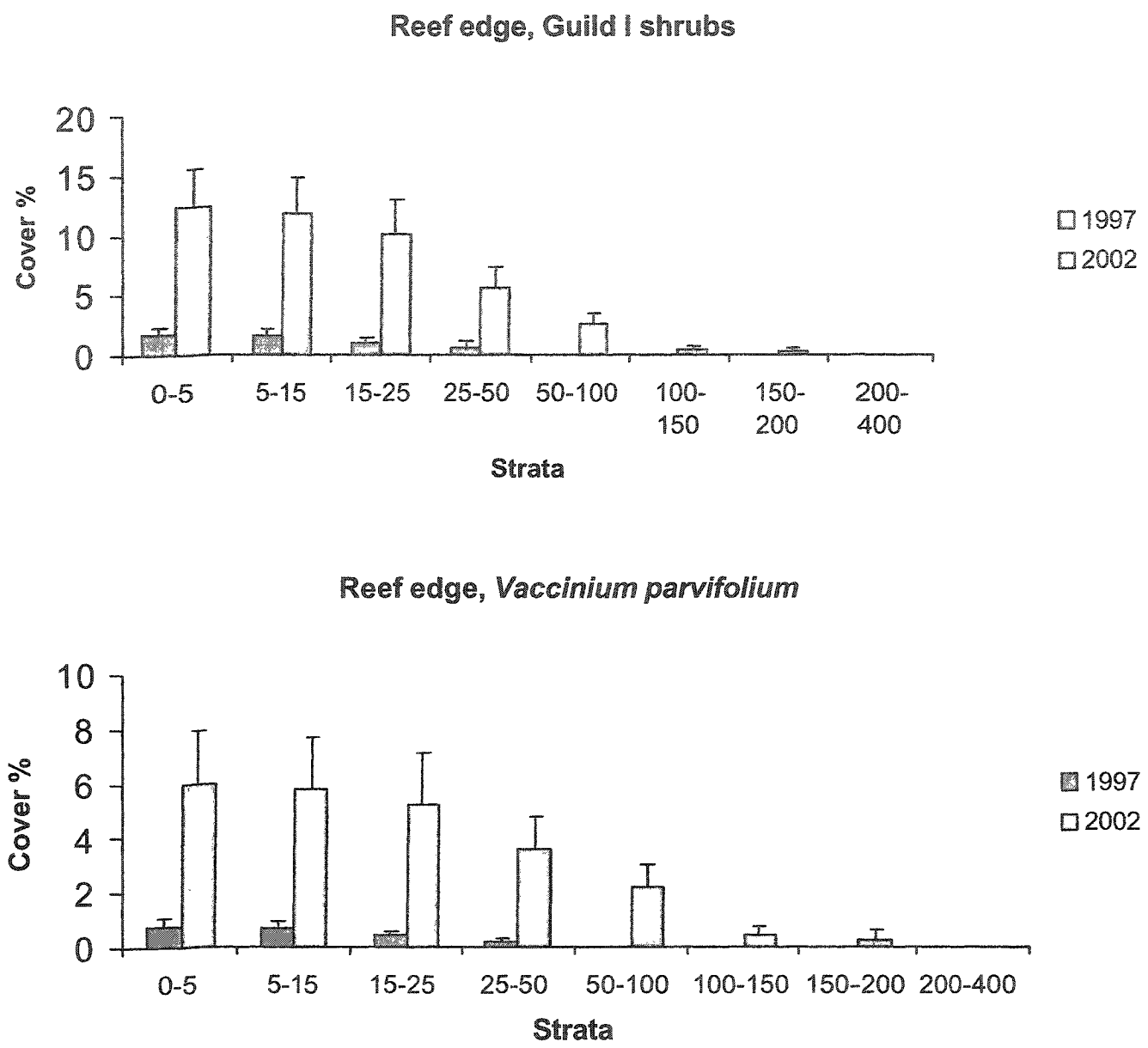

Figure 23 C and D: Average increase in cover of Guild I shrubs and *Vaccinium parvifolium* in edge plots by strata for Reef Island (n=14).

General Discussion and Conclusion

Are Sitka black-tailed deer: a keystone species?

Sitka black-tailed deer effect dramatic changes to the forests of Haida Gwaii. Unconstrained populations of these deer have greatly modified the forest understorey, reducing species richness and cover (Chapter one), and altering the community composition to one dominated by grass and tree seedlings (Chapter two). Some of these changes may be permanent (Chapter three).

The potential of these deer to modify the forest on this archipelago begs the question; are Sitka black-tailed deer a keystone species in the temperate rain forest? The term keystone species was first used by Paine (1969) to describe the role of the starfish *Pisaster ochracues* in the rocky intertidal community of the Pacific Northwest. Paine (1966) found that the removal of the starfish caused a decline from 15 to 8 species in this intertidal community. According to Paine (1992), the role of a keystone species is to reduce competitive exclusion and therefore increase species richness. More specifically, keystone species are predator species that control the density of primary consumers, which would otherwise exclude other species from the community through competition or predation (Mills et al. 1993). A wider definition includes any species that exerts strong effects on its community structure despite a low biomass (Power 1990).

Examples of keystone species have been reported in a wide range of ecosystems and for a wide range of organisms. In the Eel River in California, Power (1990) noted that steelhead trout, *Oncorhhyncus mykiss*, and California roach, *Hsperoleuces symmetricus*, controlled the abundance of river invertebrates, which in turn controlled the abundance of algae. In a terrestrial system in Sweden, Atlegrim (1989) noted increased

insect damage to bilberry, *Vaccinium myrtillus*, after the exclusion of insectivorous birds. In tide pools in the northwest Atlantic, Lubchenko (1978) noted that the absence of the intertidal snail, *Littorina littorea*, lead to the competitive exclusion of red algae, *Chondrus crispa*, by green algae, *Enteromorpha spp.* Upon re-examination Menge (1978) found that the green crab, *Carcinus maenus*, controlled snail populations in these pools and was protected from bird predation by the presence of green algae. The white-tailed deer has been suggested as a keystone species in the eastern hardwood forests of North America (McShea and Rappole 1992, Waller and Alverson 1997). However, missing predators (e.g. wolves, *Canis lupus* L., and cougars, *Puma concolor* L.) leading to overabundant deer, may represent the real keystone species in this system (Waller in press).

In view of the deer modification of the forests in Haida Gwaii, a similar role could be suggested for Sitka black-tailed deer and/or their predators in the temperate rain forests of North America. However, by singling out a keystone species, caution must be taken not to view this role out of the context of its system and food web (Mills et al. 1993, Waller and Alverson 1997). Deer management in the temperate rain forest of North America must take into consideration the whole community, including the role of humans in the modification of this system. Silvacultural practices in particular have greatly altered the availability of forage for deer in this region. Black-tailed deer often form large feeding aggregations on favourable clearcuts (Bunnell 1990). The resultant patchwork landscape created by these cuts generally provides food and beneficial habitat for deer (Leopold 1933, Alverson et al. 1988, Kremsater and Bunnell 1992) allowing deer populations to increase (Schoen and Kirchoff 1985, Sharpe 1999). However, as dense

regeneration of trees gradually retake these cuts, the understorey vegetation becomes effectively shaded out and deer are forced to seek forage in the surrounding forests. In some regions, this boom and bust cycle is augmented by nearby agricultural fields, which provide seasonal availability of high-quality forage (Alverson et al. 1988).

The preceding papers demonstrate that the role of the Sitka black-tailed deer in the temperate rain forest is extremely important. This may be a critical point in time to conserve the existing biodiversity of the temperate rain forest biome. With continued development and large-scale habitat modification in this region, managing deer populations at acceptable levels in the coming years, with or without natural control mechanisms, may prove an extremely difficult task. Consideration of the effects of deer on the forest understorey may help direct conservation efforts to maintain ecological integrity in this region.

Lessons learned from the islands

Lessons learned in the simplified system of our natural laboratory may be broadly applicable across Haida Gwaii, and the temperate rain forest. The old-growth forest in our natural laboratory, with no hunting or predators, little to no snow-pack, and few introduced plant species, neatly isolates the interaction of deer and plant. Historical influences, geology, climate and plant communities differ substantially across the forest of the southern half of the archipelago (Banner et al. 1989). However, the response of the understorey vegetation to the release from deer on opposite ends of this region (Reef Island to the northeast and S'Gaang Gwaii to the southwest) was similar in many respects (see chapter 3). Similar deer effects were encountered on 20 small islands in Skincuttle Inlet and Juan Perez Sound in 2001 (Stockton unpublished data). The nature of these

sites, small islands with large edge-to-interior ratios, may serve to make the effect more acute (Vila 2002). However, similar changes to the understorey of this region have been observed within the large tracts of unbroken forest occurring on the archipelago's largest islands: Moresby and Graham Islands (Pojar et al. 1980, Englestoff 2001).

The results of our study indicate that the direct threat of deer to forest understorey plant diversity at a regional scale is not great (many species persist as scattered relict individuals), but secondary effects, such as the introduction of invasive deer-resistant plants, would likely prove devastating. However, because our study is based on small remote islands, which usually possess low species richness (MacArthur and Wilson 1967), the loss of species may be much larger than we have detected. Unfortunately, there remain no deer-free areas on the large islands in Haida Gwaii for comparison.

The direct effect of deer on the plant diversity of subalpine areas, where most of the endemic plant species on Haida Gwaii are known to occur (Oglivie 1994), is unknown at present. The potential danger to these endemics has been noted for over two decades (Pojar et al. 1980). However, nothing has been done to forestall their potential extinction.The threat of deer to rare plants with limited distribution is exemplified by the effect of deer on plant diversity in Laskeek Bay at the scale of individual islands (see chapter one). During a plant inventory on Hotsprings Island in July of 2002, three of the four located individuals of Gmelin's sedge, *Carex gmeleni*, a provincial blue-listed sedge (Douglas et al. 1998) had been partially eaten by deer (pers. obs.), highlighting the threat deer browsing poses to rare plants. The effect of deer on individual plant species in Haida Gwaii demonstrates a real and present threat to regional and global plant diversity.

The effect of deer on plant communities and vegetation structure may be equally dangerous. Severely modified habitats like the ones encountered in Haida Gwaii may be subject to a host of secondary deleterious effects. These include pollinator failure (Cox and Elmqvist 2000), seed dispersal problems (Ferguson and Drake 1999), reduced plant litter and soil nutrient availability (Pastor et al. 1993), increased soil erosion and reduced *mycorrhizae*-facilitated mineral availability (Pojar 1999). Changes to the structure of vegetation also threaten to alter food and habitat availablity in the food chain (Martin and Daufresne 1999). The effect of deer in Laskeek Bay has been to eliminate most of the ecological function of the forest understorey (Martin and Daufresne 1999).

Recommendations for management

Careful steps must be taken to rehabilitate the forest understorey in Haida Gwaii and to ensure that unaffected areas remain that way. In order to provide refuge for rare species sensitive to the effects of deer browsing and to provide seed stores for future restoration efforts, the islands in Haida Gwaii without deer at present should be monitored. Deer colonizing these islands should be immediately eliminated. To reduce chances of the introduction of new species, a comprehensive plan for the entire archipelago should be developed (*sensu* Simberloff in press). Hunting regulations, specific to Haida Gwaii, should be developed. Potential options include communal and commercial hunting and programs which target does, such as the *earn-a-buck* program (Waller in press). Hunting should be directed to areas selected in coordination with silvacultural operations and hunter access should be facilitated. Hunters should be actively involved in collecting tissue samples to assist with monitoring. In national parks and protected areas, where hunting is prohibited, systematic culls should be conducted

and alternative strategies such as reproductive blockers should be employed where possible. Exclosures should be erected several years in advance of directed hunting or culls and also in areas where rare and endangered plants can be protected. Hunting pressure on experimental islands (Reef Island and S'Gaang Gwaii) should be maintained and further vegetation monitoring should be conducted to better understand the process of recovery. Vegetation monitoring should also be conducted over wide areas of the archipelago on an annual basis. Facilitating the recovery of the understorey on these islands will be a long and involved process necessitating the long-term collaboration of community members, resource managers and researchers.

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Appendices 1 to 5

Appendix 1

Progress

Since the Research Group on Introduced Species (RGIS) conference held in Queen Charlotte City in October of 2002, several steps have been initiated in response to the problems posed by introduced species to Haida Gwaii (Golumbia 2003). A local community group to oversee corrective actions was initiated on October 30th of 2002. Immediate actions included: creating a traveling road show of the results from the RGIS conference to show at schools and communities in Haida Gwaii, and applying for a permit for communal hunting. The Council of Haida Nations has created a draft document to discourage the introduction of exotic species. Events have been conducted in both 2002 and 2003 to eliminate invasive plants (Scotch broom, *Cytisus scoparius*, and Japanese knotweed, *Polygonum cuspidatum*). Local hunters have begun to lobby for an extended doe season and to develop information sheets for hunters to collect data on body conditions (pregnancy rates, etc.). A local environmental youth team, Haida Forest Guardians, will work in 2003 to expand exclosures built in 2001 to preserve traditional medicinal plants.

Appendix 2

Operational definitions

Fraying scar: Male deer will often use small trees to rub the dead skin from their antlers during the rutting season. This rubbing causes characteristic *fraying scars* on the trees where bark is scraped off. These scars can be identified and dated through analysis of the annual growth rings of affected trees. Vila et al. (submitted) have made extensive use of this technique to date the advent of deer to specific islands in Haida Gwaii.

Guild: a functional guild is usually defined as a group of species that exploit the same class of environmental resources in a similar way (Simberloff and Dayan 1991) i.e. species which have similar growth, reproductive and metabolic characteristics and perform the same ecological function. By extension, a response guild is a group of species that share a similar response to a given perturbation. Wilson (1999) gives an extensive review of various types of guild classification.

Hysteresis: A reaction is said to experience *hysteresis* when a continuous change in the control variable (e.g. herbivore density) has discontinuous effects on the response variable (e.g. plant density; May 1977). A system is said to experience *hysteresis* if, even after a long time, the state of a system is partly determined by its history. i.e. the system is still affected by the herbivore even after the herbivore is removed (Ludwig et al 1997).

Keystone species: Although there is considerable debate on the proper usage of this term (see Afterword), we use it to mean a predator species that control the density of primary

consumers, which would otherwise exclude species from the community through competition or predation (Mills et al. 1993).

Multiple stable-states: A community with multiple stable states can be fixed at one of two or more distinct compositions and these states can each exist within the same physical setting (Ludwig et al., 1997).

Relict species: A term used for species that persist in areas removed from the effects of a major perturbation e.g. cliff dwelling plant species, which are removed from direct consumption by herbivores.

Species richness: species richness was measured as the number of species within a set area. Gotelli and Colwell (2001) have suggested the term *species density* for this type of measurement to distinguish it from the measure of the number of species per individual.

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Appendix 3

Guild membership

Guild membership and plant type (T = tree, S = shrub, F = forb, G = graminoid, or E = fern) of 94 vascular plant species occurring on seven small islands (Lost, Low, S. Low, S. Skedans, W. Skedans, W. Limestone, and Haswell islands) in Laskeek Bay

Common name (Plant type)	Latin name	Guild
Alaska alkali grass (G)	*Puccinellia nutkaensis*	III
Alaska brome (G)	*Bromus sitchensis*	III
Alaska saxifrage (F)	*Saxifraga ferruginea*	I
Arctic rush (G)	*Juncus arcticus*	III
Beach pea (F)	*Lathyrus japonicus*	I
Bearded fescue (G)	*Festuca subulata*	NA
Bird vetch (F)	*Vicia cracca*	NA
Black gooseberry (S)	*Ribes lacustre*	NA
Black lily (F)	*Fritillaria camschatcensis*	I
Black twinberry (S)	*Lonicera involucrata*	I
Bracken fern (E)	*Pteridium aquilinum*	I
Bull thistle (F)	*Cirsium vulgare*	IV
Cleavers (F)	*Galium aparine*	I
Coastal pearlwort (F)	*Sagina maxima*	IV
Coastal strawberry (F)	*Fragaria chiloensis*	I
Common harebells (F)	*Campanula rotundifolia*	I
Cow's parsnip (F)	*Heracleum lanatum*	I
Crisp sandwort (F)	*Stellaria crispa*	I
Curled dock (F)	*Rumex crispus*	NA
Dandelion (F)	*Taraxicum officinale*	NA
Dewey's sedge (G)	*Carex deweyana*	NA
Douglas aster (F)	*Aster subspicatus*	I
Dunegrass (G)	*Elymus mollis*	I
Early hairgrass (G)	*Aira praecox*	III
Fairyslipper (F)	*Calypso bulbosa*	NA
False azalea (S)	*Menziesia ferruginea*	NA
False lily-of-the-valley (F)	*Maianthemum dilatatum*	I
few-seeded bittercress (F)	*Cardimine oligasperma*	NA
Field chickweed (F)	*Cerastium arvense*	I
Fireweed (F)	*Epilobium angustifolium*	I
Fringecup (F)	*Tellima grandiflora*	I
Giant vetch (F)	*Vicea gigantea*	I
Goosetongue (F)	*Plantago maritima juncoides*	I
Hairy rockcress (F)	*Arabis hirsuta*	I
Heart-leaved twayblade (F)	*Listera cordata*	NA
Kinnikinnik (S)	*Arctostaphylos uva-ursi*	I
Lady fern (E)	*Athyrium filix-femina*	I
Licorice fern (E)	*Polypodium glycyrrhiza*	III

Many-headed woodrush (G)	*Luzula multiflora*	IV
Marsh cudweed (F)	*Gnaphalium uliginosum*	IV
Meadow barley (G)	*Hordeum brachyantherum*	III
Menzies' pipsissewa (F)	*Chimaphila menziesii*	NA
Merten's sedge (G)	*Carex mertensii*	NA
Monkeyflower (F)	*Mimulus guttatus*	I
Nootka lupine (F)	*Lupinus nootkatensis*	I
Nootka reedgrass (G)	*Calamagrostis nutkaensis*	IV
Nootka rose (S)	*Rosa nutkana*	I
Northwestern twayblade (F)	*Listera caurina*	NA
Pacific crabapple (T)	*Malus fusca*	I
Pacific draba (F)	*Draba hyperborea*	NA
Pacific hemlock parsley (F)	*Conioselinum pacificum*	I
Pretty shootingstar (F)	*Dodecatheon pulchellum*	NA
Purple willowherb (F)	*Epilobium ciliatum*	III
Rattlesnake plantain (F)	*Goodyera oblongifolia*	NA
Red alder (T)	*Alnus rubra*	III
Red columbine (F)	*Aquilegia formosa*	I
Red elderberry (S)	*Sambucus racemosa pubens*	I
Red fescue (G)	*Festuca rubra*	III
Red huckleberry (S)	*Vaccinium parvifolium*	III
Salal (S)	*Gaultheria shallon*	II
Salmonberry (S)	*Rubus spectabilis*	I
Saskatoonberry (S)	*Amelanchier alnifolia*	I
Scouler's willow (S)	*Salix scouleriana*	I
Seabeach sandwort (F)	*Honkenya peploides*	I
Seablush (F)	*Plectritis congesta*	I
Seawatch (F)	*Angelica lucida*	I
Shield fern (E)	*Dryopteris expansa*	I
Shore blue-eyed-grass (F)	*Sisysinchium littorale*	III
Shorepine (T)	*Pinus contorta var. contorta*	NA
Siberian miner's lettuce (F)	*Claytonia sibirica*	I
Single delight (F)	*Moneses uniflora*	NA
Sitka alder (S)	*Alnus crispa sinuata*	I
Sitka mountain-ash (S)	*Sorbus sitchensis*	NA
Sitka sedge (G)	*Carex sitchensis*	III
Sitka spruce (T)	*Picea sitchensis*	IV
Slender hawkweed (F)	*Hieracium gracile*	NA
Small-flowered woodrush G)	*Luzula parviflora*	NA
Small-leaved montia (F)	*Montia parvifolia*	NA
Snowberry (S)	*Sympohoricarpos albus*	I
Spreading stonecrop (F)	*Sedum divergens*	I
St. Barbara's cress (F)	*Barbarea orthoceras*	I
Sweet-scented bedstraw (F)	*Galium triflorum*	IV
Sword fern (E)	*Polysticum munitum*	III
Thimbleberry (S)	*Rubus parviflorum*	I

Trailing black currant (S)	*Ribes laxiflorum*	I
Unalaska paintbrush (F)	*Castilleja unalaschcensis*	I
Villous cinquefoil (F)	*Potentilla villosa*	I
Western buttercup (F)	*Ranunculus occidentalis*	I
Western coralroot (F)	*Corallorhiza maculata mertensiana*	NA
Western hemlock (T)	*Tsuga heterophylla*	IV
Western rattlesnake root (F)	*Prenanthes alata*	I
Western redcedar (T)	*Thuja plicata*	I
Wood groundsel (F)	*Senecio sylvaticus*	IV
Yarrow (F)	*Achillea millefolium*	I

Appendix 4

Vascular Plant Species found in Laskeek Bay

Vascular plant species identified on Reef Island (RI), E. Limestone Island (ELI), Kunga Island (KI), seven small islands in Laskeek Bay (Haswell, Lost, Low, S. Low, S. Skedans, W.Limestone, W.Skedans; LB7), Louscoone Point (confined to 200 m of sample plots; LP), and S'Gaang Gwaii (SG).

Species	RI	ELI	KI	LB7	LP	SG
Achillea millefolium	x	x	x	x	x	x
Adiantum pedatum	x	x	x			x
Agrostis sp.					x	
Aira praecox	x	x	x	x	x	x
Alnus crispa ssp. sinuata	x	x	x	x	x	x
Alnus rubra	x	x	x	x	x	x
Ambrosia chamissonis	x			x		x
Amelanchier alnifolia	x	x		x		x
Anaphalis margaritacea	x					
Anemone multifida		x				
Angelica lucida	x	x	x	x		x
Anthyrium filix-femina	x	x	x	x	x	x
Aquilegia formosa	x	x	x	x		x
Arabis hirsuta	x	x	x	x		x
Arceuthobium campylopodum	x				x	
Arctostaphylos uva-ursi	x	x	x	x	x	x
Arnica spp.		x				
Aruncus dioicus	x					
Asplenium trichomanes		x				
Aster subspicatus	x	x	x	x		x
Barbarea orthoceras			x	x		
Blechnum spicant	x	x	x		x	x
Boschniakia hookeri	x				x	x
Bromus sitchensis	x			x		
Cakile edentula						x
Calamagrostis canadensis					x	
Calamagrostis nutkaensis	x		x	x	x	x
Calypso bulbosa	x	x	x	x	x	x
Campanula rotundifolia	x	x	x	x	x	x
Cardamine occidentalis	x		x			
Cardamine oligasperma	x	x	x	x		x
Carex deweyana	x	x	x	x	x	x
Carex laeviculmis		x				

Species	RI	ELI	KI	LB7	LP	SG
Carex lyngbyei	x				x	x
Carex mertensia	x			x		
Carex obnupta					x	
Carex pauciflora					x	
Carex sitchensis	x			x	x	x
Carex spp.						
Castilleja unalaschcensis	x	x		x	x	x
Cerastium arvense	x	x	x	x		x
Chamaecyparis nootkatensis		x			x	x
Chimaphila menziesii	x	x		x		
Cinna latifolia	x					
Cirsium arvense	x	x	x			
Cirsium edule	x	x	x			
Cirsium vulgare	x	x	x	x	x	
Claytonia sibirica	x	x	x	x	x	x
Clintonia uniflora		x				
Cochlearia officinalis	x					x
Collinsia parviflora	x	x		x		
Conioselinum pacificum	x	x	x	x		x
Coptis asplenifolia					x	
Corallorhiza maculata ssp. mertensiana	x	x	x	x		
Cornus canadensis	x				x	x
Cornus stolonifera			x			
Cryptogramma crispa	x					x
Danthonia californica		x				
Deschampsia elongata	x	x				
Dodecatheon pulchellum		x	x	x	x	
Draba hyperborea	x	x	x	x		x
Drosera rotundifolia					x	
Dryopteris expansa	x	x	x	x	x	x
Elymus glaucus	x					x
Elymus mollis	x	x	x	x		x
Empetrum nigrum					x	x
Epilobium angustifolium	x	x	x	x		x
Epilobium ciliatum	x	x	x	x		x
Equisetum sp.	x		x		x	
Eriophorum sp.					x	
Fauria crista-galli	x				x	
Festuca occidentalis	x		x			
Festuca rubra	x	x	x	x	x	x
Festuca subulata	x	x	x	x	x	x
Fragaria chiloensis	x	x	x	x		x
Fritillaria camschatcensis	x	x	x	x	x	x

Species	RI	ELI	KI	LB7	LP	SG
Galium aparine	x	x	x	x		x
Galium trifidum	x	x	x			x
Galium triflorum	x	x	x	x		x
Gaultheria shallon	x	x	x	x	x	x
Gentiana douglasiana					x	
Gentiana platypetala		x				
Geranium richardsonii		x				
Gnaphalium uliginosum	x		x	x		
Goodyera oblongifolia	x	x		x		
Grindelia integrifolia				x		
Gymnocarpium dryopteris	x					x
Heracleum lanatum	x	x		x	x	x
Heuchera chlorantha	x	x				
Hieracium triste				x		
Honkenya peploides				x		
Hordeum brachyantherum	x		x	x		
Hypopitys monotropa	x				x	
Isopyrum savilei		x				
Juncus arcticus	x	x	x	x		
Juncus bufonius					x	
Juncus effusus	x		x			x
Juncus falcatus	x					
Kalmia microphylla ssp. occidentalis					x	
Lactuca muralis	x	x	x			
Lathyrus japonicus	x			x		
Ledum groenlandicum					x	
Ligusticum scoticum				x		
Listera caurina	x	x	x	x	x	x
Listera cordata	x	x	x	x	x	x
Lloydia serotina					x	
Lonicera involucrata	x	x	x	x	x	x
Lupinus nootkatensis	x			x		x
Luzula multiflora	x	x	x	x		
Luzula parviflora	x	x	x	x	x	x
Luzula piperi	x		x			x
Lycopodium clavatum			x		x	
Lycopodium selago	x					
Lysichiton americanum	x	x			x	x
Maianthemum dilatatum	x	x	x	x	x	x
Malus fusca	x	x	x	x	x	x
Menthes arvensis		x				
Menziesia ferruginea	x	x	x	x	x	x
Mimulus guttatus	x	x	x	x		x

Species	RI	ELI	KI	LB7	LP	SG
Minuartia tenella		x				
Moneses uniflora	x	x	x	x	x	x
Montia parvifolia	x	x	x	x	x	x
Oenanthe sarmentosa	x	x				x
Oplopanax horridus			x			
Oxycoccus oxycoccus					x	
Picea sitchensis	x	x	x	x	x	x
Pinguicula vulgaris					x	
Pinus contorta var. contorta	x			x	x	x
Plantago maritima ssp. juncoides	x	x	x	x	x	x
Plectritis congesta	x			x		
Poa sp.		x			x	
Polemonium pulcherrimum		x				
Polypodium glycyrrhiza	x	x	x	x	x	x
Polypodium scouleri						x
Polystichum munitum	x	x	x	x	x	x
Potentilla anserina						x
Potentilla villosa	x	x	x	x		x
Prenanthes alata	x	x	x	x	x	x
Prunella vulgaris		x			x	
Prunus emarginata			x			
Pteridium aquilinum	x			x		
Pterophyte spp.	x					
Puccinellia nutkaensis				x		
Ranunculus occidentalis	x	x	x	x	x	x
Ranunculus repens	x					
Ranunculus uncinatus	x					
Ribes bracteosum	x		x		x	
Ribes lacustre	x	x	x	x		
Ribes laxiflorum	x	x	x	x	x	x
Rosa nutkana	x	x	x	x	x	x
Rubus parviflorus	x	x	x	x	x	x
Rubus spectabilis	x	x	x	x	x	x
Rumex acetosella				x		
Rumex crispus	x	x		x	x	x
Rumex occidentalis						x
Sagina maxima	x	x	x	x	x	x
Salicornia virginica						x
Salix scouleriana	x	x	x	x	x	x
Salix sitchensis	x	x				
Sambucus racemosa ssp. pubens	x	x	x	x	x	x

Species	RI	ELI	KI	LB7	LP	SG
Sanguisorba sp.					x	
Saxifraga caespitosa				x		
Saxifraga ferruginea	x	x	x	x		x
Sedum divergens	x	x	x	x		x
Sedum integrifolium						x
Selaginella wallacei	x		x		x	x
Senecio sylvaticus	x	x	x	x		
Sisyrinchium littorale	x	x		x	x	x
Solanum tuberosum	x					
Solidago canadensis	x					
Sonchus asper	x		x			
Sorbus sitchensis				x		
Stachys cooleyae	x					x
Stellaria crispa	x	x	x	x	x	x
Streptopus amplexifolius	x		x		x	x
Symphoricarpos albus	x	x	x	x	x	x
Taraxacum officinale				x		
Taxus brevifolia			x			x
Tellima grandiflora	x	x	x	x	x	x
Thelypteris phegopteris	x					
Thuja plicata	x	x	x	x	x	x
Tiarella trifoliata	x	x	x		x	x
Tofieldia glutinosa					x	
Trientalis arctica					x	
Trisetum sp.					x	
Tsuga heterophylla	x	x	x	x	x	x
Tsuga mertensiana					x	
Urtica dioica	x	x	x		x	x
Vaccinium alaskaense	x	x	x		x	x
Vaccinium caespitosum					x	
Vaccinium parvifolium	x	x	x	x		x
Vaccinium uliginosum					x	
Veratrum viride					x	
Veronica beccabunga ssp. americana	x	x			x	x
Vicia cracca				x		
Vicia gigantea	x		x	x		x
Viola sp.	x					
Species recorded	135	106	96	100	94	102

Appendix 5

Note submitted to *Canadian Field-Naturalist*

Menzies' pipsissewa *Chimaphila menziesii*: a widespread but previously overlooked species on Haida Gwaii (Submitted to Canadian Field-Naturalist)

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Abstract: Since 1998, four new records of *Chimaphila menziesii* on Haida Gwaii (Queen Charlotte Islands, British Columbia) suggest that this previously overlooked forest plant is potentially widespread on this archipelago. However, the repeated browsing of this plant by introduced black-tailed deer *Odocoileus hemionus sitkensis* hampers its growth and subsequent identification.

Key Words: Menzies' pipsissewa, *Chimaphila menziesii*, introduced species, Sitka black-tailed deer, *Odocoileus hemionus sitkensis*, Haida Gwaii, Queen Charlotte Islands, British Columbia, Canada, vascular plants.

On July 13, 2001, Menzies' pipsissewa *Chimaphila menziesii* was recorded blooming in the forest interior of Reef Island (52° 52' N, 131° 31' W). On August 6, 2001, it was recorded blooming on Graham Island, in the forest interior on the "Golden Spruce Trail" (53° 41' N, 132° 11' W), nearly 120 km north of previous records. These occurrences are the third and fourth records, respectively, for this species in Haida Gwaii and bear out earlier predictions that this species is widespread in the archipelago (Smith & Buttler 1999, Stockton & Buttler 2001). While only four and three individuals were found on Reef Island and Graham Island respectively, several hundred individuals were observed on Haswell Island (52° 52' N, 131° 41' W) on July 21, 2001 (Stockton, S., unpubl. data). Only 16 individuals of *C. menziesii* have previously been detected on Haida Gwaii, eight on East Limestone Island (52°54' N 131°36' W; Smith & Buttler 1999, Lomer & Douglas 1999), and eight on Haswell Island (Stockton & Buttler 2001), both in Laskeek Bay. Prior to 1998, *C. menziesii* was not known to occur on Haida Gwaii (Calder and Taylor 1968). These new records of *C. menziesii* demonstrate a substantial increase in the known range and the number of individuals of this species on Haida Gwaii.

In most instances, the habitat in which *C. menziesii* was found was largely consistent with that on Limestone Island: a thick bed of moss, primarily *Rhytidiadelphus squarrosus*, within a mature Sitka spruce *Picea sitkensis* and western hemlock *Tsuga heterophylla* forest (Smith & Buttler 1999). However, several individuals grew in *P. sitkensis* or *T. heterophylla* needle litter, where moss was absent (Fig. 1). Given the ubiquitous nature of these habitats in the archipelago, the occurrence of this species is expected on other islands.

The vegetation on Reef Island, East Limestone Island and Haswell Island, has been radically modified by Sitka black-tailed deer *Odocoileus hemionus sitkensis* (Daufresne & Martin 1997), and indeed throughout most of the entire archipelago (Pojar 1996). The large number of *C. menziesii* individuals found on Haswell Island in 2001 is likely the consequence of a recent decrease in the intensity of deer browsing on that island. Since June 22, 1999, when Haswell Island was first surveyed, the vegetation has experienced a small recovery. Many plants that are highly susceptible to deer browse, for example Western redcedar *Thuja plicata* and red huckleberry *Vaccinium parvifolium* (Pojar 1996), had by the summer of 2001 grown several centimeters above the thick moss layer of this island (Stockton, S., unpubl. data). Browsed individuals of *C. menziesii* are thought to be present beneath the moss layer throughout large areas of Haida Gwaii but may have been overlooked due to a lack of identifiable leaves and flowers. As anticipated by Smith and Buttler (1999), browsing of *C. menziesii* by deer appears to constitute a major impediment to the successful identification of this small and inconspicuous plant species.

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Figure 1: Menzies' pipsissewa *Chimaphila menziesii* growing amongst the needle litter of western hemlock *Tsuga heterophylla* in the forest interior of Reef Island. The individual in the foreground is approximately 12 cm tall. Photo: S.A. Stockton, July 13, 2001.