THE UPS AND DOWNS OF ECOSYSTEM ENGINEERING BY BURROW-NESTING SEABIRDS ON TRIANGLE ISLAND, BRITISH COLUMBIA

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ABSTRACT

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Some plant communities develop as a result of chemical and physical perturbations by burrowing seabirds and are affected when those activities are reduced. Declines in burrow density and population size of Cassin's Auklets *Ptychoramphus aleuticus* at their largest breeding colony on Triangle Island, British Columbia, from 1989 to 2009, have been associated with decreases in tufted hairgrass *Deschampsia cespitosa* and increases in salmonberry *Rubus spectabilis* cover. These habitat changes may inhibit population recovery because Cassin's Auklets prefer tufted hairgrass and tend to avoid tall salmonberry for nesting. Surveys conducted in 2014 suggested a reversal in the population trend and provided an opportunity to compare vegetation changes during periods of increasing and decreasing burrow density. We hypothesized that decreased burrowing by seabirds allows salmonberry to invade and outcompete grass as the dominant cover and that increased burrowing reverses those trends. We related changes in vegetation composition to trends in burrow numbers within permanent plots established to monitor Cassin's and Rhinoceros *Cerorhinca monocerata* auklets on Triangle Island over a 25-year period. Trends in salmonberry cover and burrow numbers were negatively related. Decreases in salmonberry cover were directly correlated to increases in burrow numbers within plots, but, as found previously, increases in salmonberry cover were not directly correlated with decreasing numbers of burrows. There was no corresponding increase in grass cover with increasing burrow numbers. Vegetation damage and reduction due to seabird activities is probably more immediately apparent than establishment, spread or recovery of vegetation following seabird impacts. Our results confirm that biopedturbation by burrow-nesting seabirds negatively affects and reduces percent cover of woody shrubs, but only when burrow densities are increasing or high. At lower or declining burrow densities, seabird activities are inadequate to halt what may be the natural succession to mainly salmonberry cover on this non-forested island.

Key words: burrow nesting, Cassin's Auklet, ecosystem engineer, habitat selection, island restoration, population recovery, Rhinoceros Auklet, seabird

INTRODUCTION

Burrow-nesting seabirds were recognized as ecosystem engineers (Gillham 1956a,b, Furness 1991) before the concept was formalized (Jones *et al*. 1994, 1997, Wright & Jones 2006). Since then, the dynamic role they play in shaping island habitats where they nest has received considerable study (Bancroft *et al*. 2005a,b, Ellis 2005, McKechnie 2006, Roberts *et al*. 2007). They modify habitats through marine-to-land nutrient transfer, which can increase soil nitrogen, phosphorus levels, and soil acidity, and through physical impacts of burrowing, trampling, and uprooting, which can change soil structure and moisture, damage roots and leaves, and increase carbon levels in soil through digging-in of surface organic material (Durrett & Mulder 2011, Mulder *et al.* 2011, Smith *et al.* 2011). In cool, temperate climates, nutrient inputs and frequent physical disturbance by burrowing seabirds damage woody plants and generally favor fast-growing, short-lived plant species (Bancroft *et al*. 2005b, Ellis 2005, Ellis *et al*. 2011).

These plant communities that develop as a result of chemical and physical perturbations by burrowing seabirds are therefore affected when the activities of nesting birds are reduced or eliminated. When introduced predators reduce seabird populations and thus remove seabird inputs and perturbations, changes in vegetation have been observed (Croll *et al*. 2005, Fukami *et al.* 2006, Russell 2011). Such habitat changes may not be fully reversible, and the quality of the habitat for nesting seabirds may be compromised even following successful removal of alien predators and efforts to restore the ecosystem (Mulder *et al*. 2009, Grant-Hoffman 2010). Concern has also been raised that declines in seabird populations due to oceanographic factors may similarly cause irreversible changes in vegetation composition (Hipfner *et al*. 2010).

Hipfner *et al*. (2010) documented decreases in tufted hairgrass *Deschampsia cespitosa* and increases in salmonberry *Rubus spectabilis* cover that were concurrent with declines in Cassin's Auklets *Ptychoramphus aleuticus* on Triangle and Sartine islands, British Columbia. These islands support the majority of the world's Cassin's Auklet breeding population (Rodway 1991). The reduction in available grass habitat and the expansion of salmonberry cover may have reduced the carrying capacity of these colonies because Cassin's Auklets tend to avoid tall salmonberry and to nest at much lower densities under short salmonberry than under tufted hairgrass (Vermeer *et al*. 1979, Rodway *et al*. 1992). Vegetation changes could thus inhibit potential recovery of breeding populations even if oceanographic conditions improve (Hipfner *et al.* 2010).

Hipfner *et al.* (2010) considered factors other than seabird inputs that may have contributed to vegetation changes on Triangle Island. Introduced European Rabbits *Oryctolagus cuniculus* were ruled out as agents of change on Triangle Island because similar vegetation changes were observed on the adjacent, rabbit-free Sartine Island colony. Climate records revealed that summers had become warmer and drier over the period of study, and Hipfner *et al.* (2010) speculated that climate change may also have influenced vegetation changes on Triangle Island, as they have elsewhere (Donlan *et al.* 2003, Chapuis *et al.* 2004). Salmonberry and tufted hairgrass grow under similar soil moisture and nutrient regimes (Klinkenberg 2014), and it is difficult to predict how climate changes will affect the interaction of these two species. On the Pacific coast of British Columbia, salmonberry tends to increase with increasing precipitation (Klinka *et al.* 1989), in contrast to what was observed by Hipfner *et al.* (2010).

Vegetation trends may reverse if burrowing seabird populations increase and, with them, nutrient transfer and biopedturbation. Evidence of this was observed on Great Island, Newfoundland, where Atlantic Puffin *Fratercula arctica* breeding populations have been recovering from hunting-induced declines (Rodway *et al.* 2003). On that colony, woody vegetation was stunted or eliminated and grassy habitat expanded in perimeter areas where burrowing by puffins had increased. Such ecosystem engineering by burrowing puffins on Great Island revealed a dynamic relationship between vegetation structure and burrow density, suggesting that the process of habitat selection can be much more interactive (e.g., Barker & Derocher 2010) than typically portrayed (Morris *et al.* 2008, McClary 2014).

Most studies investigating vegetation changes associated with seabird inputs have been comparative, contrasting areas with and without nesting seabirds (summarized in Ellis 2005, Ellis *et al.* 2011). Few studies have documented changes in vegetation structure over time within seabird colonies in relation to changes in nesting density and population size. The population trends in Cassin's Auklets on Triangle Island provided an opportunity to do this: the declining trend continued from 1989 through 2009 (Rodway & Lemon 2011), but surveys conducted in 2014 suggested a reversal in the population trend and provided an opportunity to compare vegetation changes during periods of increasing and decreasing burrow density.

Rhinoceros Auklets *Cerorhinca monocerata*, which also nest on Triangle Island and are sometimes intermingled with Cassin's Auklets, exhibit similar habitat preferences for burrowing as Cassin's Auklets (Rodway *et al.* 1992) and have been monitored over the same period using permanent plots. Trends in Rhinoceros Auklet burrow densities have been more variable than Cassin's Auklets (Rodway & Lemon 2011), and vegetation changes associated with changes in their burrow densities have not been investigated.

Therefore, we investigated changes in all Cassin's and Rhinoceros auklet permanent plots that have been surveyed at five-year intervals over a 25-year period (1989–2014) and focused, in more detail, on changes during the five-year interval 2009–2014 when Cassin's Auklet burrow numbers increased. We hypothesized that decreased breeding activity of seabirds would allow salmonberry to invade and outcompete grass as the dominant cover and that increased breeding activity reverses those trends. If the data support our hypothesis, then concern about the impacts of expanded salmonberry cover on recovery of Cassin's Auklet nesting populations would be diminished.

Hipfner *et al.* (2010) considered only grass and salmonberry cover, as these are the predominant vegetation types within colony areas on Triangle Island. Less abundant cover types, including ferns (predominantly lady fern *Athyrium felix-femina*), forbs (most commonly *Maianthemum dilatatum*, *Claytonia perfoliata*, *Epilobium latifolium*, *Heracleum* spp., and *Saxifraga* spp.), and sedges and rushes (*Carex* spp. and *Juncus* spp.), and the proportion of area lacking vegetation cover (bare ground) may also respond to changes in seabird activity. Although most of these species share similar ecological characteristics (Klinka *et al.* 1989, Klinkenberg 2014), salmonberry is shade-tolerant and often dominant in early seral communities, where it hinders natural regeneration and growth of shade-intolerant species (Klinka *et al.* 1989). Lady fern is also shade-tolerant and occasionally dominant in non-forested communities on water-receiving sites. We thus predicted that salmonberry and perhaps lady fern would displace shade-intolerant species such as tufted hairgrass on Triangle Island in the absence of biopedturbation by burrowing seabirds. If Cassin's and Rhinoceros auklet numbers increase, we expected that they would preferentially select grass and other herbaceous cover over salmonberry and fern (Rodway *et al.* 1992). Because the amount of grassy habitat is limited and has been reduced, we expected that burrow numbers under salmonberry and fern cover would also increase, effectively pushing back the spread of those species and allowing grass to re-establish within the colony. Increased traffic and erosion caused by burrowing seabirds would also be expected to increase the percentage of bare ground and affect fragile species such as *Maianthemum dilatatum* and *Claytonia perfoliata*, thus decreasing the percent cover of forbs.

METHODS

Study area

Triangle is a monumental island perched 46 km off the northwest tip of Vancouver Island, British Columbia. With a total area of 144 ha, it rises steeply to a maximum elevation of 194 m. Except for a few stunted, wild crabapple *Pyrus fusca*, the windswept island is treeless, with most of the undulating, plateau-like top of the island covered with wind-pruned salmonberry up to 2 m high (Carl *et al.* 1951). The thick mantle of salmonberry on top gives way to some open, peat-like patches covered with forbs and ferns along the upper ridge-crest, and to some open, grassy (mainly *Calamagrostis nutkaensis*) areas towards the northern and southeastern sides of the island (Rodway *et al.* 1990). Tufted hairgrass grows on steep, perimeter slopes and, in many places, especially where burrowing seabirds are nesting, extends several meters onto the gentler top of the island. Salmonberry thicket surrounds open slopes of tufted hairgrass and extends down to the shoreline in many areas (Hipfner *et al.* 2010). Extensive areas of dense lady fern are found only on northern slopes; small patches of sedges and rushes occur primarily on steep southern slopes; and mixed forbs intermingle with other vegetation types over most of the island.

The island is home to the largest concentration of breeding seabirds in the northeast Pacific south of Alaska (Rodway 1991). When last surveyed in 1989, it supported an estimated 550 000 pairs of Cassin's Auklets and 42 000 pairs of Rhinoceros Auklets (Rodway *et al.* 1992). Between 1989 and 2009, the Cassin's Auklet population may have declined by as much as 40%, while Rhinoceros Auklet burrow numbers showed an erratic but overall increasing trend, and their colony area expanded (Rodway & Lemon 2011). Cassin's Auklets are

abundant on all perimeter slopes with enough soil to support burrows as well as in more open interior areas. They even burrow sporadically under the 2 m high salmonberry thicket across the top of the island. Rhinoceros Auklets nest in similar habitat, but only on the southern and eastern sides of the island (Rodway *et al.* 1990). Substantial populations of other seabird species nest on Triangle Island (Rodway *et al.* 1992), but there is almost no overlap of their nesting areas with Cassin's and Rhinoceros auklet colony areas monitored in this study. Thus, possible inputs by other nesting seabirds that might influence vegetation changes can safely be ignored.

Survey methods

Permanent monitoring plots (10 × 10 m) were established on Triangle Island for Cassin's and Rhinoceros auklets in the 1980s (details in Rodway & Lemon 2011). Six plots were established for Rhinoceros Auklets in 1984, and 15 plots were established for Cassin's Auklets in 1989. Plots were placed along transects laid out to survey populations at that time and to sample colony areas around the entire island. Most plots have been re-surveyed at five-year intervals since 1989. One Rhinoceros Auklet plot was lost to erosion sometime between 1989 and 1994. That plot was re-established, and two additional plots were set up, to sample expanded areas of Rhinoceros Auklet colony in 2009. All established Cassin's and Rhinoceros auklet plots were surveyed in 1989, 2004, 2009, and 2014. We were unable to survey four and five Cassin's Auklet plots in 1994 and 1999, respectively. Plots were surveyed during the following periods: 1 July–16 August 1989, 2–24 June 1994, 31 July–19 August 1999, 10 June–25 August 2004, 23 July–6 August 2009, and 12–24 July 2014.

During each survey, burrows were counted, identified to species, and coded as to the type of ground cover in which the burrow entrance was found. To avoid disturbing nesting birds, burrows were not explored all the way to their ends. Signs near the front of the burrow, including feces, feathers, and regurgitated or dropped food, as well as burrow size, were used to distinguish species. Cassin's Auklet burrows are generally smaller than Rhinoceros Auklet burrows, but burrow sizes do overlap (Rodway *et al.* 1990). Plots established for a particular species contained predominantly burrows of that species. In Cassin's Auklet plots, 0.3% (in 1989; $n = 3132$) to 3.7% (in 2009; $n = 1904$) of burrows were identified as Rhinoceros Auklet. In Rhinoceros Auklet plots, 5.2% (in 2009; $n = 880$) to 25.0% (in 1989; $n = 679$) of burrows were identified as Cassin's Auklet.

Ground cover was classified into seven vegetation categories: grass, salmonberry, fern, forb, salal, sedge, and bare ground. Cover in each plot was mapped using a 1 × 1 m grid, and percent cover for each category was estimated within four 25 m² (1989 to 2004) or eight 12.5 m² (2009 and 2014) subsections of each plot. Data from adjacent 12.5 m² subsections surveyed in 2009 and 2014 were combined to match 25 m² samples used in previous years for comparisons across all years. Cover estimates were likely accurate to within 5% for dominant cover types and 1% for less common types.

Analyses

We used the totals of all burrows (both Cassin's and Rhinoceros auklets) in a plot for analyses because: (1) we predicted the same trends in vegetation cover due to inputs from either species;

(2) changes in vegetation in a plot were likely due to the activities of all birds nesting there; and (3) combining burrows of both species increased our sample size. Correlation analyses were first performed on data from all plots of both species combined, and then data from plots established for each species were analyzed separately to investigate whether vegetation trends in relation to changes in burrow numbers were, in fact, similar for each species. The mix of species' burrows within plots was a confounding factor for these latter analyses, especially for Rhinoceros Auklet plots that had substantial numbers of Cassin's Auklets nesting within them.

Pearson correlations were used to determine associations between changes in burrow numbers and changes in vegetation cover over five-year intervals from 1989 to 2014. These analyses considered changes in the number of burrows and vegetation cover from one survey year to the next, not the actual number of burrows or percent vegetation cover in a particular year. Changes were calculated from T1 (n) to T2 ($n + 5$), where n is year.

We could use paired *t*-tests to analyze changes in vegetation cover between 2009 and 2014 because percent cover was a repeated measure in the fixed plots. We could not use a repeated-measures analysis for changes in burrow numbers in relation to a particular vegetation cover type because the amount of different cover types changed from year to year. Changes between 2009 and 2014 in (1) the number of burrows in a plot subsection under different vegetation types and (2) the density of burrows within each vegetation type, were analyzed using generalized linear models (GLMs), including year as a fixed factor and plot as a random factor, to control for differences among plots. The first analysis revealed changes in the overall number of burrows in a plot that were in a particular cover type, which could be due to expansion or contraction of that particular cover type or due to changes in burrow density within that cover type. The second analysis revealed whether the density of burrows within a cover type had changed. Because percent ground cover, especially of fragile plant species, can change over the seabird-nesting season (Rodway *et al.* 1990), a preliminary analysis was performed to determine whether timing of surveys might have affected proportions of different cover types across years. No effect of date was apparent, and date was excluded from all final analyses. One-tailed tests of significance were used because we had clear directional predictions. Statistical significance was set at 5% Type I error for all tests.

RESULTS

Changes in vegetation cover in relation to changes in burrow numbers from 1989 to 2014

Numbers of burrows in permanent plots varied over the 25 years of this study, showing declines and increases over five-year intervals (Figs. 1, 2). Within Cassin's Auklet plots, the only decrease in salmonberry cover over a five-year interval was from 2009 to 2014 (-5.3%), and this was associated with an increase in burrow numbers (Fig. 1). The greatest percentage increase in salmonberry cover was from 1994 to 1999 (17.1%), concurrent with the largest decrease in burrow numbers seen during the 25 years of monitoring (Fig. 1). However, salmonberry cover also increased between 1999 and 2004 (12.9%), when burrow numbers showed some increase.

Within Rhinoceros Auklet plots, the greatest percentage increase in salmonberry cover over a five-year interval was from 1999 to 2004

(26.3%), concurrent with a decrease in burrow numbers, although not the largest decrease recorded (Fig. 2). The largest decrease in burrow numbers occurred between 1989 to 1994, concurrent with a 5% increase in salmonberry cover. The greatest decrease in salmonberry cover was from 2004 to 2009 (-8.7%), and this was associated with increasing burrow numbers. However, salmonberry cover also increased between 1994 and 1999 (16.9%), when burrow numbers showed an increase.

There were significant correlations between changes in numbers of burrows and changes in percent cover of different vegetation types over five-year intervals. Data from all plots of both species revealed that changes in burrow numbers were negatively related to changes in salmonberry cover ($r = -0.17$, $n = 270$, $P = 0.003$) and fern cover ($r = -0.28$, $n = 103$, $P = 0.002$), and positively related to changes in bare ground ($r = 0.13$, $n = 236$, $P = 0.023$) and sedge ($r = 0.34$, $n = 39$, $P = 0.016$). The negative relationship between changes in burrow numbers and changes in salmonberry cover held up when burrow numbers increased ($r = -0.18$, $n = 130$, $P = 0.019$), but not when they decreased ($r = 0.02$, $n = 128$, $P = 0.40$). The positive relationship between changes in burrow numbers and changes in bare ground was strongest when burrow numbers increased ($r = 0.42$,

$n = 100$, $P < 0.001$) and was not apparent when burrow numbers decreased ($r = -0.11$, $n = 125$, $P = 0.11$). Relationships related to fern and sedge cover were not significant when samples were split between increasing and decreasing burrow numbers ($P_s > 0.05$).

By seabird species, the negative relationship between changes in burrow numbers and changes in salmonberry cover was apparent within Cassin's Auklet ($r = -0.14$, $n = 166$, $P = 0.040$) and Rhinoceros Auklet ($r = -0.26$, $n = 104$, $P = 0.004$) plots. The positive relationship between changes in burrow numbers and changes in bare ground was apparent within Cassin's Auklet ($r = 0.16$, $n = 148$, $P = 0.026$) but not Rhinoceros Auklet ($r = 0.02$, $n = 88$, $P = 0.43$) plots. Fern cover was uncommon in Rhinoceros Auklet plots (Table 1), and the negative relationship between changes in burrow numbers and changes in fern cover was only apparent in Cassin's Auklet plots ($r = -0.22$, $n = 82$, $P = 0.022$). Similarly, sedge cover was uncommon in Cassin's Auklet plots (Table 1), and the positive relationship between changes in burrow numbers and changes in sedge cover was apparent only in Rhinoceros Auklet plots ($r = 0.39$, $n = 33$, $P = 0.013$). In addition, changes in burrow numbers were negatively related to changes in forb cover within Rhinoceros Auklet plots ($r = -0.43$, $n = 56$, $P < 0.001$).
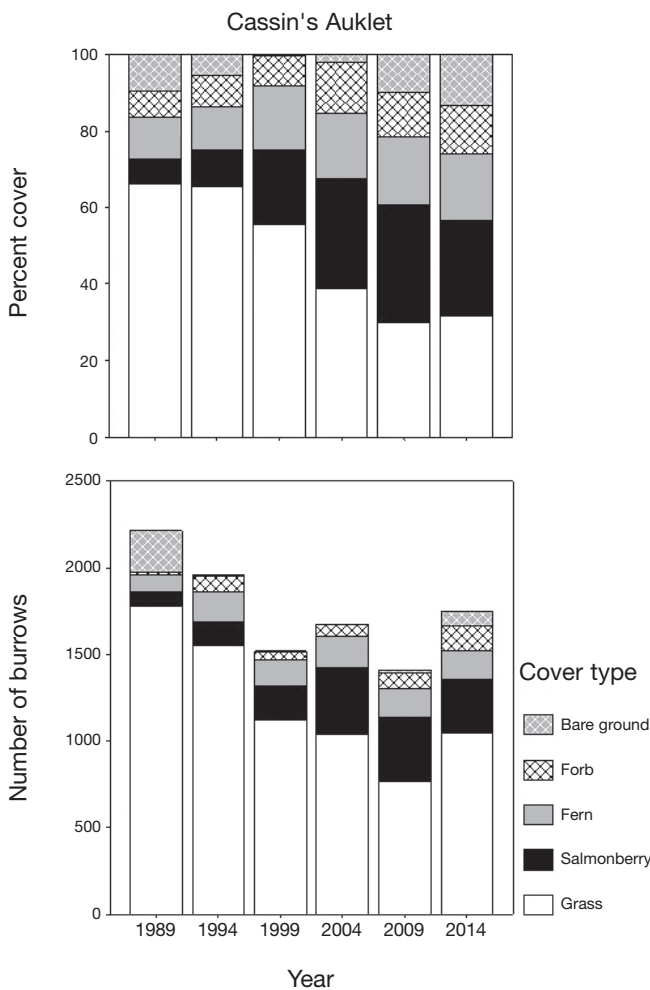

Fig. 1. Changes in vegetation cover and total numbers of burrows counted within Cassin's Auklet permanent plots on Triangle Island, British Columbia between 1989 and 2014. Only plots that were surveyed every five years are included.
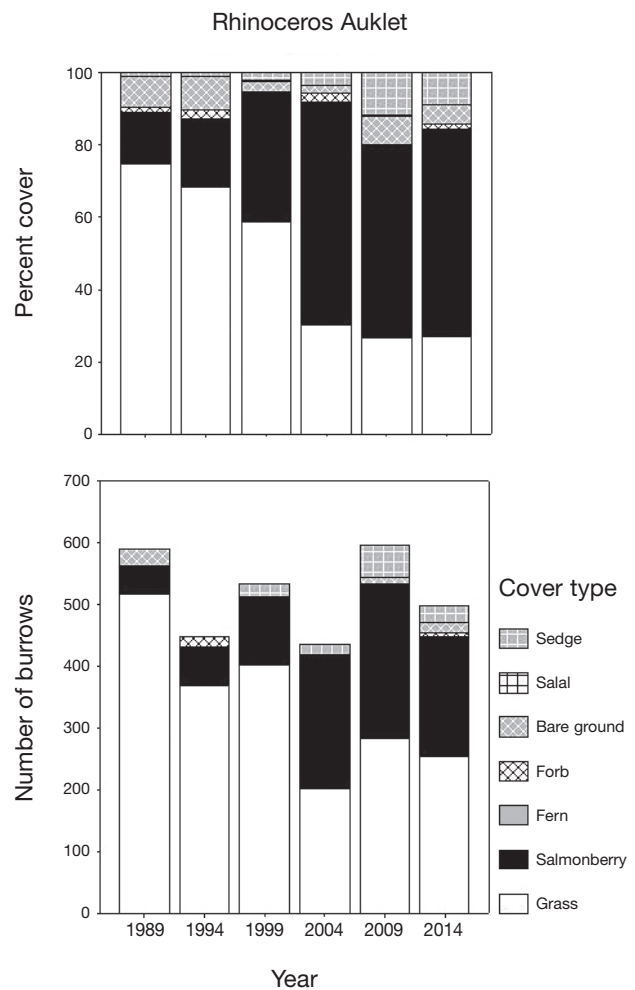
Fig. 2. Changes in vegetation cover and total numbers of burrows counted within Rhinoceros Auklet permanent plots on Triangle Island, British Columbia between 1989 and 2014. Only plots that were surveyed every five years are included.

Changes between 2009 and 2014

Paired *t*-tests comparing percent cover of different vegetation types between 2009 and 2014 indicated an overall decrease in salmonberry, an increase in bare ground, and no significant change in other cover types within Cassin's Auklet plots, and an increase in fern, a decrease in bare ground, and no significant change in other cover types within Rhinoceros Auklet plots (Table 1).

The total number of burrows of both species combined increased within Cassin's Auklet plots and showed no change within Rhinoceros Auklet plots between 2009 and 2014 (Table 2). Density of Cassin's Auklet burrows within Cassin's Auklet plots increased from (mean ± standard error) 1.22 ± 0.06 to 1.56 ± 0.08 burrows/m^2 ($F_{1,238} = 11.17$, $P = 0.001$), while density of Rhinoceros Auklet burrows within Rhinoceros Auklet plots decreased from 1.13 ± 0.06 to 0.93 ± 0.06 burrows/m^2 ($F_{1,110} = 5.91$, $P = 0.017$) between 2009 and 2014. Numbers of Cassin's Auklet burrows within Rhinoceros Auklet plots also increased ($F_{1,110} = 8.49$, $P = 0.004$), while no change was found in numbers of Rhinoceros Auklet burrows within Cassin's Auklet plots ($F_{1,110} = 0.68$, $P = 0.41$). The concurrent increase in Cassin's Auklet and decrease in Rhinoceros Auklet burrows resulted in no significant change in total burrow numbers within Rhinoceros Auklet plots (Table 2).

Burrow numbers did not change uniformly across cover types between 2009 and 2014. Within Cassin's Auklet plots, the number of burrow entrances in grass and bare ground increased, but the number of burrow entrances under salmonberry or other cover types showed no change (Table 2). The density of burrows within grass and bare ground also increased, but did not change in other cover types (Table 3). Increases in the number of burrows in grass and bare ground were thus due not only to increases in the percent cover

of those vegetation types, but also to increases in burrow density within those cover types (Table 1).

Within Rhinoceros Auklet plots, the number of burrow entrances under salmonberry and sedge cover decreased, the number under ferns increased, and no change was detected under other cover types (Table 2). The density of burrows decreased within salmonberry cover but did not change within other cover types (Table 3). The increase in the number of burrows under fern cover matched the increase in percent cover of fern (Table 1), while the decrease in burrows in salmonberry was at least partially due to changes in nesting density within that vegetation type.

DISCUSSION

The relationship between burrowing seabirds and their nesting habitat is dynamic and interactive. Previous research on Triangle Island had shown that woody shrub cover expanded, displacing preferred grassy nesting habitat, during a period (1989–2004) when the population of Cassin's Auklets declined (Hipfner *et al.* 2010). We found a reversal in the trend for salmonberry shrub cover when numbers of nesting Cassin's and Rhinoceros auklets increased, and evidence that the decrease in salmonberry was directly related to increased numbers of burrowing seabirds. In agreement with Hipfner *et al.* (2010), we found no correlation between changes in salmonberry cover and changes in numbers of burrows when nesting populations were declining, and also conclude that vegetation changes were thus not driving population declines. There are likely time lags due to factors such as growth rate and climate that affect the spread of salmonberry when seabird inputs are reduced.

Results supported our hypothesis and indicate that Cassin's and Rhinoceros auklets are effective allogenic ecosystem engineers (Jones *et al.* 1994) that modify the vegetation community in

TABLE 1
Changes in percent cover of different ground cover types within Cassin's Auklet (N = 120) and
Rhinoceros Auklet (N = 56) permanent plot sections between 2009 and 2014 on Triangle Island, British Columbia

Plot type	Cover type	Year				Paired *t*-test	
		2009		2014			
		Mean	SE	Mean	SE	*t*	*P*
	Grass	31.4	2.8	30.3	2.1	0.59	0.55
	Salmonberry	33.9	3.2	28.6	2.5	3.62	<0.001
	Fern	14.7	2.8	14.6	2.8	0.12	0.91
Cassin's Auklet	Forb	10.7	1.9	12.0	1.6	-1.25	0.21
	Bare ground	7.1	1.3	12.4	1.4	-4.72	<0.001
	Salal	1.7	0.8	1.4	0.6	0.95	0.34
	Sedge	0.6	0.3	0.7	0.3	-0.99	0.32
	Grass	34.7	4.1	37.7	4.0	-1.07	0.29
	Salmonberry	48.0	4.6	48.6	4.5	-0.29	0.77
	Fern	0.8	0.3	1.5	0.5	-2.79	0.007
Rhinoceros Auklet	Forb	0.0	0.0	0.9	0.5	-1.91	0.06
	Bare ground	8.0	1.3	4.7	0.7	2.40	0.020
	Salal	0.1	0.1	0.2	0.2	-0.81	0.42
	Sedge	8.5	2.9	6.5	2.2	1.67	0.10

the areas where they nest. Their effects, however, are density-dependent. We can conclude that biopedturbation by burrow-nesting seabirds reduces the percent cover of woody shrubs, as found in other studies conducted at cool, temperate latitudes (Bancroft *et al.* 2005b, Ellis 2005). However, effects were only apparent at high or increasing burrow densities. Direct evidence of this was noted in 1989, when Cassin's Auklet burrow density was at the highest recorded (Rodway & Lemon 2011) and we observed many old, dead salmonberry roots in areas where birds had worn the ground bare. The activities of seabirds at low or declining burrow densities appear to be inadequate to halt natural succession to mainly salmonberry cover on these non-forested islands. We know that salmonberry has been the dominant cover on Triangle Island, forming dense continuous thickets over the interior of the island, since at least 1949 (Carl *et al.* 1951). Burrowing seabirds may thus affect an uneasy balance between natural succession and engineering their preferred grassy nesting habitat. An interesting question is whether different equilibria in the amount of grassy habitat maintained may be reached at different population levels.

Although salmonberry cover decreased when burrow numbers in Cassin's Auklet plots increased between 2009 and 2014, there was no corresponding increase in grass cover. Percent bare ground did increase over that period, likely as an immediate effect of increased traffic and erosion by greater numbers of nesting birds in 2014. As there is likely a time lag in the spread of salmonberry following declines in seabird burrowing activity, there is also likely a time lag in the spread of grass following reductions in salmonberry cover. This would explain the lack of correlation between changes in burrow numbers and changes in percent grass cover, and the negative correlation between changes in burrow numbers and changes in percent salmonberry cover only when burrow numbers were increasing. Vegetation damage and reduction is likely an immediate impact of increased seabird burrowing activities and more immediately apparent than establishment, spread, or recovery of vegetation following seabird impacts. Reduction in forb cover with increasing numbers of burrows in Rhinoceros Auklet plots may be another example of this.

Vegetation trends in relation to changes in burrow numbers within Cassin's and Rhinoceros auklet permanent plots suggested similar impacts of both species, as expected. However, the mix of species in the permanent plots made the results more difficult to interpret. Trends in salmonberry cover were the same between species, and differences in the trends for fern and sedge were due to differences in their percent cover in the plots rather than to differences between

TABLE 2
Changes in mean number of burrows (both Cassin's and Rhinoceros auklets) under different vegetation cover types per plot subsection within Cassin's Auklet and Rhinoceros Auklet permanent plots between 2009 and 2014 on Triangle Island, British Columbia

Plot type	Cover type	Year						ANOVA results[b]	
		2009			2014				
		Mean	SE	N[a]	Mean	SE	N[a]	F	P
	Grass	10.9	0.9	95	16.3	1.2	92	25.16	<0.001
	Salmonberry	5.4	0.6	89	4.3	0.5	91	2.52	0.11
	Fern	5.6	0.8	40	5.4	0.8	42	0.01	0.94
	Forb	2.4	0.4	60	2.7	0.3	75	1.19	0.28
Cassin's Auklet	Bare ground	0.4	0.1	40	1.3	0.2	83	25.23	<0.001
	Salal	0.3	0.2	6	1.0	0.5	6	1.43	0.26
	Sedge	0.0	0.0	5	0.0	0.0	6	NA	
	All	15.9	0.8	120	20.3	1.0	120	25.03	<0.001
	Grass	8.2	0.9	55	8.6	0.8	55	0.13	0.72
	Salmonberry	7.0	0.7	46	5.0	0.5	47	7.55	0.007
	Fern	0.6	0.2	9	1.5	0.6	11	5.35	0.034
	Forb	0.0	n/a	1	0.6	0.2	8	NA	
Rhinoceros Auklet	Bare ground	0.2	0.1	32	0.4	0.1	35	0.93	0.34
	Salal	0.0	0.0	2	0.0	0.0	2	NA	
	Sedge	5.3	1.2	10	2.4	0.6	12	8.31	0.010
	All	14.9	0.7	56	13.9	0.8	56	2.05	0.16

NA = not applicable.
[a] Number of plot subsections containing a particular cover type.
[b] ANOVA results for the effect of year are given from a GLM including plot as a random factor.

species. The positive relationship between burrow numbers and percent bare ground was specific to Cassin's Auklet plots, and the negative relationship between burrow numbers and forb cover was specific to Rhinoceros Auklet plots, but both these effects are consistent with predictions and likely reflect immediate impacts of increased activity when burrow numbers increase. Interestingly, there was a decrease in bare ground and an increase in fern cover in Rhinoceros Auklet plots over the 2009 to 2014 period, which would have been expected if burrow numbers declined. Numbers of Rhinoceros Auklet burrows did decline, but numbers of Cassin's Auklet burrows increased in those plots, and there was no net change in total burrow numbers. Thus, these results were unexpected. Perhaps there is a difference in behavior, such as less socialization and thus less traffic on the surface, of the relatively isolated numbers of Cassin's Auklets nesting in predominantly Rhinoceros Auklet colony areas compared with those nesting in main Cassin's Auklet colony areas that diminishes their habitat impacts. Vegetation changes would then be driven largely by the decreased activity of Rhinoceros Auklets.

Trends in numbers of burrows in different vegetation types reinforced previous conclusions about habitat preferences (Vermeer *et al.* 1979, Rodway *et al.* 1992). Virtually all of the increase in the number of Cassin's Auklet burrows in 2014 occurred in grass and bare ground. This was partially due to an increase in percent cover of those vegetation types but also to an increase in burrow density within those cover types. We expected that numbers of burrows under salmonberry would also increase, but they did not. Thus, the

reduction in salmonberry cover observed in Cassin's Auklet plots was due to increased activity generally on the plot rather than to increased burrowing within salmonberry habitat. This suggests that increased traffic and burrowing affected mainly the perimeter of woody vegetation. Birds preferentially selected grassy or bare ground cover to start their burrows, but their burrows probably extended into and affected the root systems of salmonberry. Perhaps this establishes a front where the battle between natural succession and ecosystem engineering by burrowing seabirds plays out.

Trends in Rhinoceros Auklet plots between 2009 and 2014 were also consistent with the conclusion that burrowing affects the extent of woody vegetation at the perimeter of that vegetation and that these effects depend less on burrow density within the vegetation. The percent salmonberry cover did not increase when burrow density under salmonberry decreased. Burrow densities did increase, although not significantly (see Table 3), in other cover types, which would make sense if burrow density declined under salmonberry but total numbers of burrows in Rhinoceros Auklet plots did not change. Stable or increasing burrow densities and associated biopedturbation in those other vegetation types may have been sufficient to maintain the salmonberry perimeter and keep salmonberry from spreading. The decrease in burrow density under salmonberry in Rhinoceros Auklet plots was likely due to changes in numbers of Rhinoceros Auklet burrows, as numbers of Cassin's Auklet burrows in those plots increased over the 2009 to 2014 interval. Withdrawal of nesting Rhinoceros Auklets from salmonberry cover likely reflects habitat preferences by that species.

TABLE 3
Changes in mean density (per m^2) of burrows (Cassin's and Rhinoceros auklets) within different vegetation cover types in Cassin's Auklet and Rhinoceros Auklet permanent plots between 2009 and 2014 on Triangle Island, British Columbia

| Plot type | Cover type | Year | | | | | | ANOVA results[b] | |
| | | 2009 | | | 2014 | | | | |
		Mean	SE	N[a]	Mean	SE	N[a]	F	P
Cassin's Auklet	Grass	2.87	0.24	95	3.47	0.22	92	3.95	0.048
	Salmonberry	1.11	0.12	89	1.01	0.12	91	0.35	0.55
	Fern	1.34	0.24	40	0.97	0.12	42	2.01	0.16
	Forb	2.15	0.55	60	2.19	0.42	75	0.18	0.67
	Bare ground	0.50	0.23	40	1.11	0.22	83	4.14	0.044
	Salal	0.08	0.05	6	0.23	0.13	6	1.24	0.29
	Sedge	0.00	0.00	5	0.00	0.00	6	NA	
	All	1.27	0.06	120	1.62	0.08	120	25.03	<0.001
Rhinoceros Auklet	Grass	2.36	0.33	55	3.16	0.47	55	2.37	0.13
	Salmonberry	1.07	0.11	46	0.76	0.08	47	5.82	0.018
	Fern	0.83	0.44	9	1.09	0.30	11	1.38	0.26
	Forb	0.00		1	3.12	1.43	8	NA	
	Bare ground	0.30	0.25	32	0.74	0.30	35	0.13	0.91
	Salal	0.00	0.00	2	0.00	0.00	2	NA	
	Sedge	0.83	0.23	10	0.57	0.15	12	1.78	0.20
	All	1.20	0.06	56	1.11	0.06	56	2.05	0.16

NA = not applicable.
[a] Number of plot subsections containing a particular cover type.
[b] ANOVA results for the effect of year are given from a GLM including plot as a random factor.

Surveys at five-year intervals provide snapshots of a dynamic system. This may explain why changes in vegetation do not always match those expected on the basis of differences in burrow numbers. There were significant correlations between decreases in salmonberry cover and increasing burrow numbers for both Cassin's and Rhinoceros auklet colony areas. In spite of that, salmonberry cover increased when burrow numbers increased over some five-year intervals. Vegetation changes reflect interactions throughout the five-year intervals, and if overall seabird activity on the colony during those years was reduced, then salmonberry cover may have expanded more than it contracted.

Other factors undoubtedly affect vegetation communities within seabird colony areas on Triangle Island. Dominant plant species within those areas share many ecological characteristics, occurring on very moist to wet, fluctuating, and water-receiving sites (Klinkenberg 2014). Thus, they may not be differentially affected by changes in precipitation. However, a distinguishing factor that we did not consider in this study is that tufted hairgrass, and some other species such as *Maianthemum dilatatum,* are tolerant of ocean spray (Klinka *et al.* 1989). We have witnessed large patches of salmonberry with dead or dying tops that we speculated had been damaged by wind or salt spray. Greater tolerance for salt spray may contribute to the prevalence of tufted hairgrass on steep perimeter slopes. Seabird burrow-nesting habitat is predominantly on steep perimeter slopes, and the intensity and frequency of storm-force winds that lash these oceanic areas may influence the successional success of salmonberry within colony areas. Lady fern may also be less tolerant of ocean spray, and its main occurrence on the northern side of Triangle Island (Rodway *et al*. 1990) may be a result of prevailing southerly storm winds (Thomson 1981). Frequency and intensity of high winds that generate salt spray (probably affected by climate changes; Young *et al*. 2011) may interact with ecosystem engineering by burrowing seabirds to create dynamic vegetation communities on these seabird islands.

Conservation concern for the recovery of Cassin's Auklets on Triangle Island (Hipfner *et al*. 2010) may be partially ameliorated by the decrease in salmonberry cover associated with increasing numbers of burrowing birds found in this study. These results suggest that, if oceanographic conditions as well as breeding success and survival improve, ecosystem engineering by increased numbers of burrowing birds could gradually push back encroaching salmonberry. This may facilitate the restoration of preferred, grassy nesting habitat, although concomitant increases in grass cover were not observed in this study. Longer-term study during periods of increasing population are required to determine whether the trend of decreasing salmonberry cover continues and whether there is a corresponding increase in grassy habitat. On the other hand, burrow numbers under salmonberry did not increase when overall burrow numbers increased; that is, increases were confined to available grassy habitat. Expanded salmonberry cover may thus limit population increase in the short term. Seabirds may need repeated years of successful breeding, increased recruitment, and adult survival to re-engineer habitat on Triangle Island to support historical population levels. The effectiveness of burrowing seabirds as ecosystem engineers and the important role they play in shaping island ecosystems means that the recovery of breeding populations is a vital step in restoring affected island ecosystems worldwide (Jones *et al*. 2011).

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