

Deer Abundance and the Recovery of Woody Plants of the Coastal Douglas-fir Ecosystem



A Collaborative Project of UBC's Forest Renewal Chair in Applied Conservation Biology, the Natural Sciences and Engineering Research Council of Canada, Sallas Forest Ecological Stewardship Committee, and Sidney Island Community

MAY 2019

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Abstract

Over-abundant deer degrade Coastal Douglas-fir (CDF) ecosystems by altering plant architecture and removing most or all palatable vegetation available to them at a site (e.g., vegetation within ~2m of the ground). Deer populations become over-abundant when their numbers are limited only by the amount of food available to them, and it occurs rapidly in the absence of large predators or human interventions (such as hunting), particularly in generalist feeders such as fallow deer (*Dama dama*). In such cases, rapid ‘trophic downgrading’ is common; entailing the loss of native and culturally significant plant species due to ‘over-browsing’, and the subsequent loss of the insect, bird, and mammal species that also rely on these same native plants for food and shelter. Because Sidney Island, BC, represents among the most dramatic examples of trophic downgrading regionally, we hypothesized that more recent efforts to reduce deer density on the island have the potential to reverse the effects of trophic downgrading by initiating an increase in the richness, diversity, and cover of palatable plant species (‘trophic upgrading’). To test this hypothesis, we re-surveyed 35 plots established in 2013 to assess change in plant communities. We observed that native species richness and diversity nearly doubled, and native plant cover increased by 30%, from 2013 to 2019. Although the re-establishment of palatable species not detected in 2013 was limited, with only six highly palatable species having re-colonized one or more plots by 2019, increases in the cover of most native species appeared to result mainly via seedling recruitment. Exotic species also increased 11-fold, but still represented <1% of total cover in plots on average. This indicates the potential for rapid increase in exotic species such as a hawthorn, but is tempered by the fact that native competitors, in the absence of over-browsing, are likely to exclude shade-intolerant and disturbance-dependent invaders from most ‘natural’ habitats. Our findings indicate that a recovery of woody plant species is underway on Sidney Island, but proceeding slowly in comparison to changes observed inside experimental and ad hoc exclosures. A recovery from trophic downgrading to the re-establishment of still rare species with high aesthetic, cultural, and ecosystem service values may require the re-introduction and assisted dispersal of some highly palatable species, and it will be hastened by the further removal of exotic fallow deer, and maintenance of native black-tailed deer at densities known to maximize native shrub and bird species richness and diversity.

Introduction

Over-abundant native and exotic deer degrade Coastal Douglas-fir ecosystems by (1) reducing the richness, diversity, and cover¹ of native, woody plants, (2) reducing plant growth and seedling recruitment, and (3) eliminating habitat for a host of other species (McTaggart-Cowan 1945, Gonzales and Arcese 2008, Martin et al. 2010, Arcese et al. 2014, Duwyn et al. 2015, Arcese et al. 2018).

‘Trophic ¹downgrading’ arises as a consequence of the removal of apex predators from an ecosystem (Estes et al. 2011), leading to increases in prey density and commensurate declines in the structural complexity and diversity of plant and animal communities (Ripple et al. 2016). For example, reductions in shrub cover, diversity, and structural complexity due to over-browsing by deer lead to dramatic reductions in the abundance, richness, and diversity of songbirds in the Southern Gulf and San Juan Islands of British Columbia and Washington State (Martin et al. 2010). Over-browsing can also eliminate meadow plants, shrubs, and trees from island ecosystems (Gonzales & Arcese 2008, Arcese et al. 2014, UBC 2018), a pattern extensively described on Haida Gwaii, where deer are introduced (Allombert et al. 2005). However, although trophic downgrading is widely-described and reversible in some tropical and temperate systems (Estes et al. 2011), little is known about the conditions or tempo of plant species responses to experimental reductions of deer density, or the potential for such reductions to initiate ‘trophic upgrading’ in critically-threatened plant and animal communities in the Pacific Northwest of North America.

Trophic downgrading in Garry oak, maritime meadow, and Coastal Douglas-fir ecosystems has occurred coincident with the cessation of indigenous management practices (e.g., burning, hunting, extensive cultivation of food plants), the removal of apex predators, restrictions on human hunting, and, on Sidney Island, the introduction of fallow deer (*Dama dama*; Turner and Peacock 2005, Gonzales and Arcese 2008, Arcese et al. 2014). Over-abundance can often be recognized as a ‘browse line’ indicating the relative absence of palatable plant tissue below ~2 m vegetation height. On Sidney Island, evident browse lines also indicate the absence of recruitment in desirable trees such as arbutus (*Arbutus menziesii*), Garry oak (*Quercus garryana*), and others highly palatable to deer (UBC 2018). Consequently, we expected that dedicated efforts to reduce deer density on Sidney Island after 2013 might reverse the process of trophic downgrading and advance the restoration of highly diverse and

¹Richness is number of species detected in an area. Diversity measures complexity in communities by combining richness and abundance; *i.e.*, a Douglas-fir forest with a single arbutus tree has a richness of 2, but is less diverse than a comparable forest with more even abundances. Cover is the area of a ground in a sample plot overlain by a focal species in question, as viewed from above.

productive examples of critically-endangered Garry oak, maritime meadow, and Coastal Douglas-fir ecosystems, all of which are recognized as critically-threatened regionally and nationally.

We addressed our expectations above by comparing plant species richness, diversity, and cover for 22 native and 4 exotic woody shrub and tree species. Specifically, we revisited 35 plots (10m radius; 314 m²) established systematically on Sidney Island by Lorraine Campbell in 2013 to obtain baseline estimates of woody plant species cover, richness and diversity. By revisiting those plots in 2019, we were able to assess change given a continuing effort to reduce deer density on the island.

Predictions

We hypothesized that reducing deer density would curtail trophic downgrading and initiate an increase in the richness, diversity, and cover¹ of palatable plant species within plots. Given sharp reductions in deer density after 2013, we expected to observe increases in the richness, diversity, and cover of plant species in accordance with their known or estimated palatability to deer, regardless of their status as native or exotic species. However, we further expected that species of intermediate palatability should recover before highly palatable species, because deer are highly selective of the most palatable plants available to them at a site (Arcese et al. 2014). In addition, because prior surveys indicate that over-browsing by deer had caused the extirpation of many palatable plant species over most of Sidney island by 2011 (Martin et al. 2011, Campbell 2013, Arcese et al. 2014), we expected that a period of recolonization by those species will be necessary before rapid increases cover are possible.

Methods

Study Area

Sidney Island (9 km²; BC, Canada) is situated in the Southern Gulf Island archipelago of British Columbia and supports both native black-tailed (*Odocoileus hemionus columbianus*) and non-native fallow deer (*Dama dama*). Our survey was conducted on the privately-owned portion (80%) of Sidney Island, adjacent to the Gulf Islands National Park Reserve. Deer densities are well-studied in the region and estimated by various methods: the minimum density necessary to sustain the observed number of deer removed from Sidney Island annually and standardized pellet counts suggest that densities approached 150 deer / km² in 2010, but have since reduced by 50-70% since then (unpublished results, Sallas Forest Partners; Martin et al. 2011, Arcese et al. 2014). Given higher-than-average deer densities on Sidney island, and the subsequent degradation of native plant communities, landowners engaged in a cull of exotic fallow deer in 2008 in an attempt to initiate the recovery of native plant, bird, and pollinator communities typical of relatively 'intact' examples of Coastal Douglas-fir forests.

Despite intensive culling, deer densities on Sidney Island in 2014 (62 deer per km²) remained about six times higher than densities known to be compatible with the persistence of native plant communities typical of the region prior to European settlement (<10 deer per km²; Allombert et al. 2005, MacDougall 2008, Martin et al. 2011, Arcese et al. 2014). However, as densities have continued to decline with increased hunting and culling effort, residents have asked for assistance measuring progress on the recovery of native vegetation. Baseline estimates of woody plant species cover, richness, and diversity were first established in 2013 (Campbell 2013) and compared to similar surveys of plant communities on ~40 other islands with high, moderate, or low-density, or no deer populations (Martin et al. 2010, Arcese et al. 2014). In this study, we re-surveyed the plots established in 2013 to test whether reducing deer density initiated a recovery of native woody plants.

Cover of Woody Vegetation

From May 8th to 15th of 2019, we re-visited 35 of 38 existing 10 m radius plots surveyed for woody vegetative cover in 2013 (Campbell 2013; Figure 1). Plot locations were established systematically at about 300 m intervals on ten parallel transects running east to west, spaced 400 m apart (Figure 1). Plot centers were relocated to approximately ± 5 m using a hand-held GPS (Garmin Etrex 20x). Multiple observers surveyed plots to estimate the cover of all woody vines, shrubs, and trees in each plot ≤ 2 m above the ground (i.e., vegetation potentially available to browsing deer) to the nearest 1 percent, averaging values when observers differed in individual estimates. Three sites were not re-surveyed due to inaccessibility.

Statistical Analyses

We compared species richness, diversity, and the percent cover of woody species in 2013 to 2019 using one-tailed paired t-tests ($\alpha = 0.05$). Change in species richness was assessed for native, exotic and total species as three separate groups. Change in diversity was only evaluated for native and total species because there were too few exotic species observed to obtain diversity estimates. Within each plot, the total percent cover of all native, exotic and total species were pooled separately. We then assessed changes in percent cover for native, exotic and total species, and for each of the 22 native and four exotic species observed. Because transformations did not improve the distributions of most raw data (e.g., \log_{10} and $\arcsin(\text{square-root})$), we used the untransformed data for most tests. Exemptions from this protocol were made for analyses of percent cover of native, exotic and total species (\log_{10} transformed). We report sample means with their standard error (SE).

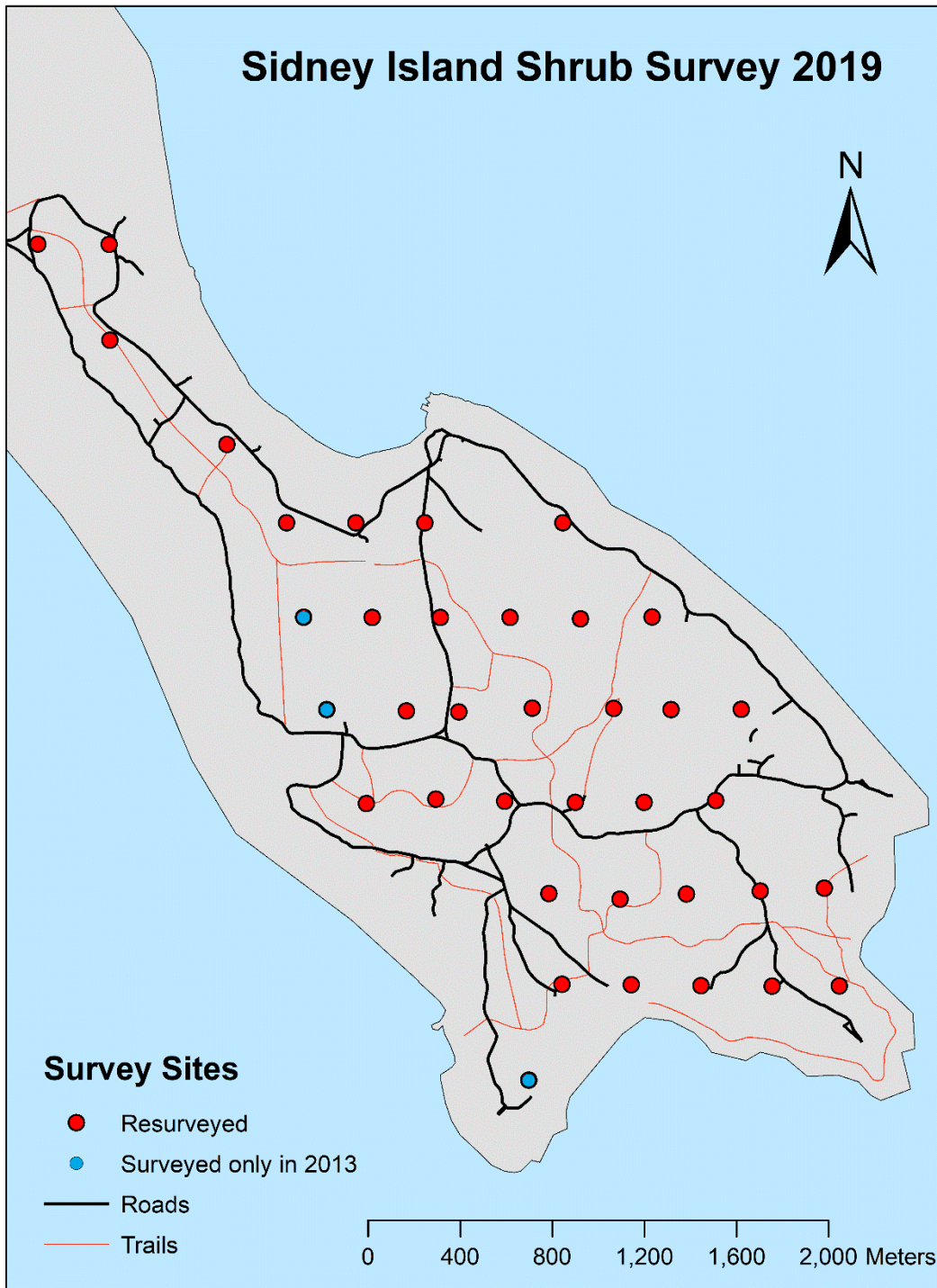


Figure 1. Sidney Island shrub survey locations in 2013 and 2019.

Results

Species Richness and Diversity

Native, exotic, and total species richness all increased from 2013 to 2019 (Table 1, Figure 2). Notably, exotic species richness increased ten-fold (from nearly zero to nearly one exotic species on average per plot), while native species richness increased 1.8 times (Table 1). Total species richness doubled from ~3 to ~6 species per plot between surveys (Table 1). Species diversity also increased by 1.6 times from 2013 to 2019 (Figure 2).

Percent Cover

Native, exotic, and total percent cover all increased from 2013 to 2019 (Table 1, Figure 2). Native cover increased 1.3 times, while exotic cover increased 11 times (Table 1). Despite this sizeable increase, exotic cover comprised < 1% of cover in plots in 2019, whereas natives covered ~30% of plots on average (Table 1, Figure 2). Overall, total cover increased 1.3 times from ~23% in 2013 to 30% in 2019 (Table 1, Figure 2).

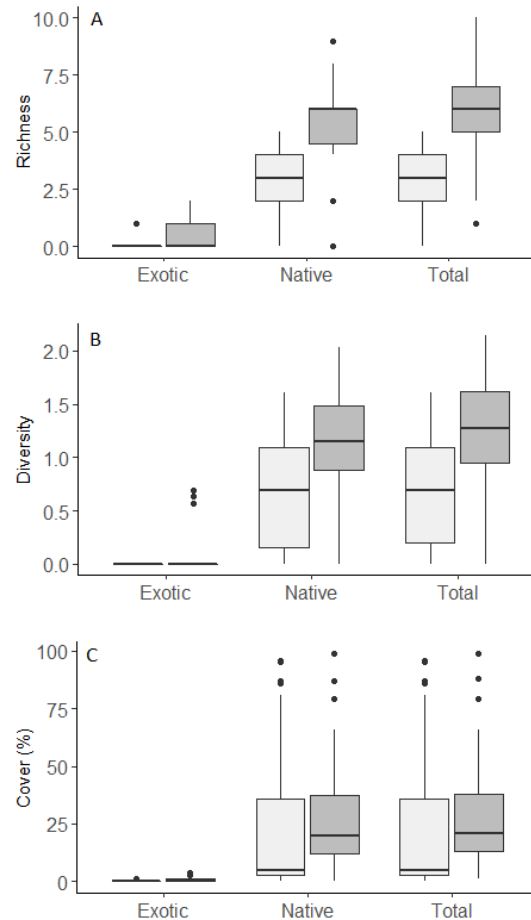


Figure 2. Species richness (A), diversity (B) and percent cover (C) from 2013 (light grey) to 2019 (dark grey).

Table 1. Species richness, diversity and percent cover (%) in 10 m radius plots ($n = 35$) from 2013 to 2019. All differences between years were significant in one-tailed paired t -tests.

	2013 Species Richness	2019 Species Richness	2013 Diversity	2019 Diversity	2013 % Cover	2019 % Cover
Native Species	2.94 (0.24)	5.40 (0.34)	0.72 (0.31)	1.13 (0.23)	23.29 (5.41)	29.74 (4.35)
Exotic Species	0.06 (0.04)	0.57 (0.11)	0 (0)	0.05 (0)	0.06 (0.04)	0.66 (0.15)
Total	3.00 (0.24)	6.10 (0.33)	0.74 (0.30)	1.24 (0.26)	23.34 (5.41)	30.40 (4.29)

Nearly all native species observed in plots increased in cover from 2013 to 2019. Native species with large increases included western redcedar (2.2 times), grand fir (3.4 times), arbutus (2.1 times), ocean spray (6 times), and Garry oak (5 times; Table 2). Other native species showing increases that were not quite ‘statistically significant,’ include hairy honeysuckle (1.75 times higher), red alder (2.21 times), and bigleaf maple (1.85 times higher; Table 2). The only native species not showing an increasing trend in cover was salal, a species that is only utilized extensively by deer as food at moderate to high densities (Table 2). We also detected six native species in plots in 2019 that were not detected in 2013, five of which produce fruits (common snowberry, 0.11%; Pacific willow, 0.06%; trailing blackberry, 0.17%; baldhip rose, 0.06%; saskatoon, 0.03%; and, flowering currant, 0.03%), and three are among the most widely-utilized wood plant species by indigenous people historically.

Exotic English hawthorn also increased from 0.06% to 0.46% cover from 2013 to 2019 (Table 2) and was the only exotic species observed in plots in 2013 (Table 2). By 2019, three other exotic species were detected (Table 2) at very low cover including English holly (0.09%), scotch broom (0.06%), and English ivy (0.06%; Table 2). Although the presence of such species is a concern, the cover little area and are expected to decline under intense competition from natives, as observed in the maritime meadow exclosures (UBC 2018).

Type	Species Name	% Cover 2013	% Cover 2019	Magnitude Change
Native Trees	Arbutus (<i>Arbutus menziesii</i>) ^P	0.57 (0.23)	1.23 (0.32)	2.16
	Western red cedar (<i>Thuja plicata</i>) ^P	2.40 (1.37)	5.34 (1.19)	2.23
	Bigleaf maple (<i>Acer macrophylla</i>) ^P	1.11 (0.96)	2.06 (1.19)	1.86
	Red alder (<i>Alnus rubra</i>) ^P	0.14 (0.07)	0.31 (0.15)	2.21
	Douglas maple (<i>Acer glabrum</i>) ^P	0.09 (0.05)	0.14 (0.06)	1.56
	Black cottonwood (<i>Populus trichocarp</i>) ^P	0.03 (0.03)	0.06 (0.04)	2
	Pacific crabapple (<i>Malus fusca</i>) ^P	0.03 (0.03)	0.03 (0.03)	1
	Pacific willow (<i>Salix lucida</i>) ^P	0 (0)	0.06 (0.04)	New
	Garry oak (<i>Quercus garryana</i>) ^N	0.09 (0.05)	0.43 (0.22)	4.78
	Grand fir (<i>Abies grandis</i>) ^N	0.37 (0.15)	1.26 (0.36)	3.41
	Douglas-fir (<i>Pseudotsuga menziesii</i>) ^N	3.51 (2.06)	4.0 (0.64)	1.14
Native Shrubs	Ocean spray (<i>Holodiscus discolor</i>) ^P	0.09 (0.05)	0.51 (0.07)	5.67
	Hairy honeysuckle (<i>Lonicera hispidula</i>) ^P	0.11 (0.05)	0.20 (0.07)	1.82
	Orange honeysuckle (<i>Lonicera ciliosa</i>) ^P	0.03 (0.03)	0.06 (0.04)	2
	Trailing blackberry (<i>Rubus ursinus</i>) ^P	0 (0)	0.17 (0.06)	New
	Saskatoon (<i>Amelanchier alnifolia</i>) ^P	0 (0)	0.03 (0.03)	New
	Baldhip rose (<i>Rosa gymnocarpa</i>) ^P	0 (0)	0.06 (0.06)	New
	Snowberry (<i>Symphoricarpos albus</i>) ^P	0 (0)	0.11 (0.09)	New
	Flowering currant (<i>Ribes sanguineum</i>) ^P	0 (0)	0.03 (0.03)	New
	Dull Oregon grape (<i>Mahonia nervosa</i>) ^N	0.14 (0.06)	0.71 (0.21)	5.07
	Salal (<i>Gaultheria shallon</i>) ^N	14.54 (4.96)	13.0 (4.17)	0.89
	Tall Oregon grape (<i>Mahonia aquifolium</i>) ^N	0.03 (0.03)	0.17 (0.17)	5.67
Exotic Shrubs	English hawthorn (<i>Crataegus laevigata</i>) ^N	0.06 (0.04)	0.46 (0.12)	7.67
	Scotch broom (<i>Cytisus scoparius</i>) ^N	0 (0)	0.06 (0.04)	New
	English holly (<i>Ilex aquifolium</i>) ^A	0 (0)	0.09 (0.05)	New
	English ivy (<i>Hedera helix</i>) ^A	0 (0)	0.06 (0.04)	New

Table 2. Shrub and tree species in 2013 and 2019 (n=35), expressed as mean (SE) percent cover of plots. Species are arranged in descending order from most to least palatable (Arcese et al. 2014 and

prior knowledge). P, N, and A indicate species that are browsed Preferentially, Not preferentially (i.e., browsed mainly at high deer densities), or Avoided entirely. Significant differences highlighted in bold. The magnitude of change is expressed as a ratio of cover in 2019 to cover in 2013, with values >1 indicative of increased cover in 2019.

Discussion

Recovery of Woody Plants

The cover, richness, and diversity of woody plants on Sidney Island increased as deer density declined from 2013 to 2019 (e.g., 1.28, 1.84 and 1.85 times, respectively; Table 1, Figure 2). These findings are broadly consistent with earlier observations of over-browsing and recovery in maritime meadow plant communities on Sidney Island (UBC 2018). That study compared meadow habitat in and outside of exclosures established in 2013 to find that native plant cover roughly doubled inside exclosures by 2018, but increased only ~20% outside deer exclosures despite declining densities. Together, these results indicate that meadow and woody plant communities are both showing initial signs of recovery from severe over-browsing. However, the striking pace of recovery observed inside versus outside of exclosures, and continuing evidence of severe limits on many palatable species known to be abundant and self-sustaining on islands with fewer deer, also suggests that deer densities on Sidney Island in 2018-19 were still capable of preventing the re-establishment of a productive, diverse, and well-functioning Coastal Douglas-fir ecosystem.

Limits on the re-establishment and/or persistence of palatable meadow and woody plants, particularly those capable of producing large volumes of nectar, fruit, or foraging habitat (foliage), also limit the pace of recovery in native insect, bird, and mammal populations typical of more 'intact' island ecosystems. Such species on Sidney Island include arbutus, which is not producing new recruits due to over-browsing (e.g., arbutus; UBC 2018), and many other which remain rare on Sidney Island but are abundant where deer are few or absent (e.g., dogwood, indian plum, mock orange, thimbleberry, salmonberry, currants). Using such species as 'sentinels' to monitor the performance of extant and/or transplanted examples of such species on Sidney Island may therefore represent a definitive opportunity to estimate the deer densities most likely to promote their growth and spread on Sidney Island. One such sentinel, ocean spray, increased in cover by ~6 times from 2013 to 2019, mainly by producing living tissue within 2m of the ground. When ocean spray grow more rapidly than they are browsed by deer, they become less 'umbrella-shaped'; a trend that also appeared to be underway in 2018 (UBC 2018).

Palatability, recovery and exotic cover

Our 2018 results showed conclusively that inside experimental meadow exclosures where all plants are protected from browsing by deer, natives species demonstrated competitive superiority to exotic species and reduced their cover by half (UBC 2018). In contrast, we found in 2019 that exotic woody species were rare in all plots (<1% cover), despite being detected more often in 2019 than 2013 (Table 2). This finding highlights a potential worry discussed below, but it is also consistent with our expectation that increases in woody species will initially reflect their palatability to deer, their current abundance and ability to produce seed, and their ability to colonize new sites. Secondly, competition among extant individuals and new colonists will influence winners and losers over time, including exotic species.

For example, given further declines in deer density, we expect the cover of less palatable woody species such as salal, dull Oregon grape, and scotch broom to decline as faster-growing but less well-defended species compete for light, water, and nutrients. Such interactions should limit shade-intolerant invaders, such as English Hawthorn, which require disturbed, edge habitat, early-successional habitats to persist (e.g., MacDougall & Turkington 2004, Martin et al. 2010, Arcese et al. 2014, UBC 2018). For example, Waller & Maas (2017) showed experimentally that deer caused the spread and persistence of invasive garlic mustard (*Alliaria petiolata*) in forested habitats by browsing native forest plants that exclude garlic mustard by shading in the absence of deer. The superior competitive ability of native as compared to exotic plants in maritime meadows protected from deer almost certainly explains the patterns of native dominance and exotic declines reported in 2018 (UBC 2018). Despite these gains, however, woody plant species cover, richness, and diversity on Sidney Island still remain similar in 2019 to values recorded on San Juan and Southern Gulf islands with over-abundant deer ($\geq 90/\text{km}^2$; Martin et al. 2010, Arcese et al. 2014). This implies that re-establishing diverse and productive plant and animal communities on Sidney Island is likely to require lower deer densities that occurred on Sidney Island in 2019, and it may require the reintroduction and assisted dispersal of species that are now rare but historically abundant.

Species recruitment patterns

The detection of several species in plots in 2019 that were not detected in 2013 suggests that a period of natural re-colonization will be required before rapid increases in native species cover, richness, and diversity are observed. However, it is encouraging and interesting that five highly palatable fruiting species were first detected in plots in 2019 (e.g., snowberry, trailing blackberry, baldhip rose, saskatoon, and flowering currant; Table 2). This finding suggests that recovery may accelerate if new colonists survive to produce fruits. It also indicates that some species now extinct or relatively rare on

Sidney Island, such as salmonberry, thimbleberry, dogwood, saskatoon, indian plum, orange honeysuckle, and others, may require longer to become re-established.

Many increases in woody plant cover reported here appeared to be due to the recruitment of seedlings in plots, rather than the regrowth of established plants. Increases in the cover of big leaf maple (1.85 times) appeared to be almost entirely due to seedlings. Given that many species common on other islands are rare or absent on Sidney Island, more rapid recoveries by some species may require management actions to facilitate re-establishment by cloning shoots from extant individuals that can be planted in areas prioritized for restoration (trails, balds, roadsides).

The potential spread of exotic species also remains a concern, but the slow pace of change from 2013 to 2019 suggests that time exists to identify and address focal species of concern. For example, although exotic species increased from 2013 to 2019, they still represented <1% of total cover (Figure 2). It is also plausible that Campbell (2013) detected fewer seedlings working alone than the 2-5 observers used in 2019, potentially over-estimating invasion risk. The largest increase among exotic species was recorded in English hawthorn, a shade-intolerant species that is palatable to deer and largely restricted to open areas (Williams and Buxton 1986). Although a high number of seedlings indicates a potential for spread, increased competition with fast-growing natives, assuming that deer density continues to decline, are likely to limit hawthorn distribution to open areas with deeper soils. Actions to reduce spread of English hawthorn might include the removal/ringing of mature trees to reduce colonization. Alternatively, if an exotic species is determined not to be invasive, to offer positive aesthetic and/or ecosystem services (e.g., pollination), or are impractical to control with otherwise benign effects, they are sometimes adopted as examples of novel ecosystems (Hobbs et al. 2009). Open, disturbed sites will continue to provide suitable habitat for recruitment by exotic species such as hawthorn, scotch broom and English ivy. English ivy can also invade shade habitats and climb and kill large trees. However, a more extensive survey would be needed to recommend priority species for removal.

Implications of climate change for recovery

The potential influence of climate on native species recovery on Sidney Island is uncertain, but some evidence suggests southwestern BC's climate is trending towards historic conditions, with potentially positive implications for native plant species well-adapted to summer drought (Hebda 1995, Hellmann et al. 2012). If true, drought-adapted species such as harvest brodiaea, which increased ~10 times from 2013 to 2018 inside exclosures, should thrive in Garry oak and maritime meadow habitats given that deer continue to decline (UBC 2018). Because many iconic species of these critically endangered

ecosystems are well-represented on Sidney Island, and now experiencing an initial recovery from severe over-browsing, the island contributes importantly to the conservation of these ecosystems globally (Pellatt and Gedaloff 2014, Nuszdorfer et al. 1991).

In summary, we observed increases in the cover, richness, and diversity of palatable and culturally significant woody shrub and tree species from 2013 to 2019 as fallow deer density was reduced. Our findings also suggest that deer populations must decline further to facilitate the rapid recovery of native meadow and woody plant species and insure the re-establishment of many still rare or extinct species on Sidney Island, including many species with substantial aesthetic, food, cultural, and/or habitat values. Actions could also be taken to facilitate re-establishing or augmenting a few highly desirable species as ‘sentinels’ which could be monitored annually by community members to provide direct feedback on the deer densities commensurate with desired state of forest and meadow habitats on Sidney Island.

Acknowledgements

We thank the residents of Sidney Island for welcoming us onto their island and for hospitality, friendship and support over the years. The Sallas Forest Ecological Stewardship Committee, Natural Sciences and Engineering Research Council (NSERC), Forest Renewal Chair in Conservation Biology (UBC), and several individual donors made this work possible.

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