



# Deer density and plant palatability predict shrub cover, richness, diversity and aboriginal food value in a North American archipelago

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## ABSTRACT

**Aim** Trophic cascades are a common consequence of herbivore outbreak and in the absence of hunting can cause the local extinction of native plant species and communities. We compared plant communities at 66 island and mainland sites to test the hypothesis that deer (Cervidae) determine species cover, richness and diversity and that palatable species become rare at high deer density. We validate a region-wide index of deer density and impact on plant communities in a region where culturally significant food plants maintained by aboriginal people prior to European contact helped to define baseline plant communities.

**Location** Gulf and San Juan Island archipelagos and North American mainland.

**Methods** We conducted surveys of 49 native, 10 exotic and 15 culturally significant plant species and deer sign at 66 sites on 35 islands and mainland to determine deer abundance and plant species cover, richness and diversity. We identified culturally significant food plants facilitated by aboriginal people using ethnobotanical knowledge, quantified plant palatability via cafeteria trials and characterized shrub architecture.

**Results** Native and culturally significant shrub cover, richness and diversity were 52–85% lower at sites with abundant deer ( $0.9\text{--}2.8\text{ ha}^{-1}$ ) versus no deer. However, these values were also 38–82% lower at sites in the lowest deer density class ( $< 0.08\text{ ha}^{-1}$ ) versus sites with no deer present. Palatable cover was 92% lower where deer were abundant versus absent and 28% lower in low-density versus deer-free sites. Shrub architecture provided an easily applied index of native and culturally significant plant cover and deer density.

**Main conclusions** We provide comparative examples of endangered plant communities to demonstrate that, contrary to the intermediate disturbance hypothesis, any positive effect of deer on plant diversity on islands in the Pacific north-west of North America occurs at densities  $< 0.08\text{ ha}^{-1}$ , if at all. This detailed example of trophic downgrading highlights the need and provides the methods to identify herbivore densities compatible with the persistence of all native species in conserved landscapes.

## Keywords

Aboriginal land management, deer, island populations, plant diversity, trophic cascade, ungulate eruption.

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## INTRODUCTION

Herbivores fundamentally affect ecosystem structure and function, particularly where humans directly or indirectly contribute to their population growth and abundance by removing native predators, increasing food supply, curtailing hunting or introducing them to regions they were historically absent from (Caughley, 1970; Hobbs, 1996; Waller & Alverson, 1997; Coté *et al.*, 2004; Martin *et al.*, 2009, 2011; Takatsuki, 2009; Estes *et al.*, 2011). In North America, Europe, Asia and New Zealand, increases in the abundance of native and exotic deer (*Cervidae*) continue to generate concern given observations of rapid ecological change, the extirpation of palatable plants and reduction of understorey habitat that other species rely on for food, nest sites or cover (e.g. McShea *et al.*, 1997; Waller & Alverson, 1997; Horsley *et al.*, 2003; Rooney *et al.*, 2004; Husheer *et al.*, 2006; Gill & Fuller, 2007; Vavra *et al.*, 2007; Martin *et al.*, 2009, 2011). The resulting simplification of plant and animal communities is now recognized globally as a hallmark of marine and terrestrial ecosystems dominated by herbivores and lacking top predators (Estes *et al.*, 2011).

In support of the hypothesis that deer have manifold effects on plant and animal communities at large spatial scales, Chollet & Martin (2013) reported a continent-wide pattern of regional increase in deer abundance and corresponding decline in bird species abundance in North America. Mechanistically, declines occur when browsing reduces territory quality, individual condition and demographic performance by increasing predation rates, eliminating substrates necessary for reproduction and reducing food supply (e.g. deCalesta, 1994; McShea & Rappole, 2000; Martin & Joron, 2003; Martin & Possingham, 2005; Stockton *et al.*, 2005; Cardinal *et al.*, 2012; Holt *et al.*, 2013). Intense browsing can similarly enforce the extirpation of palatable plants without refuge from deer by reducing plant survival, reproduction and patch recolonization rates below those needed to maintain local or regional persistence (e.g. Anderson, 1994; Augustine & Frelich, 1998; Vellend *et al.*, 2003; Chollet *et al.*, 2013). Long-term studies extend these results to show that unregulated herbivore populations can initiate trophic cascades in above- and below-ground biota and sequester ecosystem productivity at the expense of complexity at other trophic levels (Estes *et al.*, 2011; Bressette *et al.*, 2012; Callan *et al.*, 2013).

The above findings imply that the conservation of some native plant and animal communities will require deer populations to be managed at low enough levels that region-specific indicators of plant community composition, persistence and replacement are maintained or enhanced over time. However, the appeal of deer and antipathy towards lethal control by many humans suggest that deer management will remain controversial in the absence of region-specific examples of overabundance and increased public and scientific understanding about the trade-offs involved (Garrott *et al.*, 1993; Waller & Alverson, 1997; McShea & Rappole, 2000;

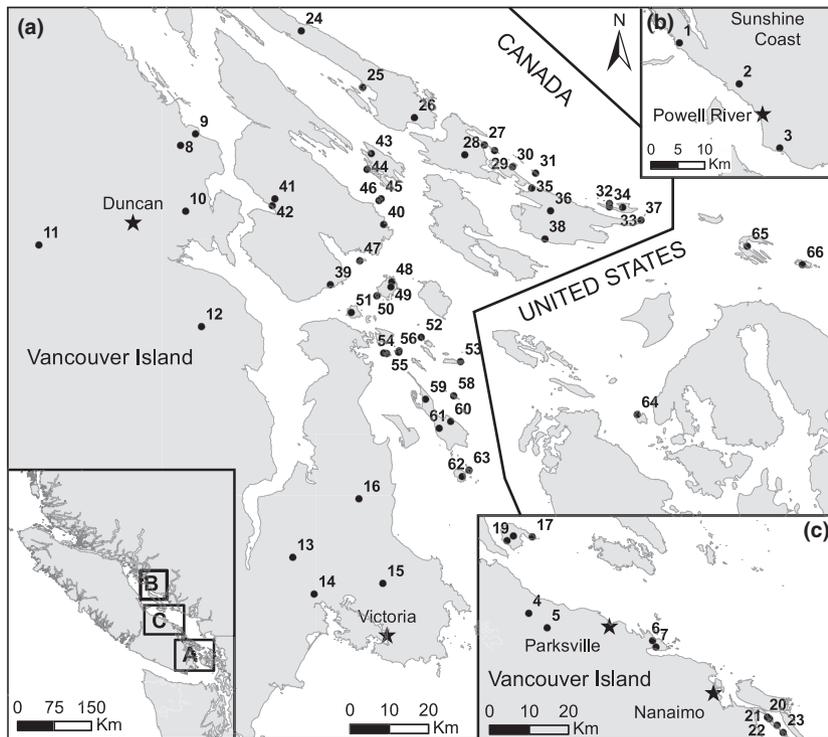
Coté *et al.*, 2004; Martin *et al.*, 2011). Ideally, region-specific examples of deer impacts on native species will include indicators that are accessible without special training and that predict the cover, richness and diversity of valued species.

Indexes of deer impact typically employ focal species inventories or characterizations of species cover, especially species preferred as food and linked to animal health (e.g. McTaggart-Cowan, 1945; Caughley, 1970; Anderson, 1994). However, few indexes are widely applied or validated due to the challenges of characterizing plant communities at multiple deer densities and in their absence, and the potential for variation in plant palatability or abundance to affect herbivore diets (e.g. McTaggart-Cowan, 1945; Kirschbaum & Anacker, 2005; Frerker *et al.*, 2013). Our goal here was to provide a region-wide assessment of deer impacts on plant cover, richness and diversity on 35 islands and the North American mainland of south-west British Columbia (BC) and north-west Washington State (WA, Fig. 1) to test the hypothesis that deer density predicts shrub community state and that palatable species become rare or absent at high deer density. In addition, because the plant communities we studied represent a relict landscape, managed intensively by aboriginal people prior to European contact, but progressively managed by European settlers that sought to reduce fire frequency and promote familiar species, particularly after 1840 (MacDougall *et al.*, 2004), we also characterized deer impacts on the richness and cover of culturally significant food plants to help establish an historical baseline condition (Arcese & Sinclair, 1997). We now develop these ideas and our predictions.

## Historical Background, Hypotheses and Predictions

Outstanding examples of oak savanna habitat, once widespread in western North America but now ~95% reduced in extent (MacDougall *et al.*, 2004; Dunwiddie *et al.*, 2011), still occur in the Gulf and San Juan Island archipelagos of the Georgia Basin (BC, WA), particularly on islands and in isolated forest openings buffered from human disturbance, exotic competitors and abundant herbivores (Best & Arcese, 2009; Bennett *et al.*, 2012; Bennett & Arcese, 2013). Native black-tailed (*Odocoileus hemionus* Rafinesque, 1817) and exotic fallow (*Cervus dama* L., 1758) deer on islands in this region can occur at densities over 20 km<sup>-2</sup> and dramatically reduce shrub cover (McTaggart-Cowan, 1945), bird abundance (Martin *et al.*, 2011, 2013) and the growth, reproduction and cover of native forbs (Gonzales & Arcese, 2008), and facilitate the dominance of exotic grasses (Best & Arcese, 2009; Gonzales & Clements, 2010).

In contrast, prior to the arrival of Europeans in the Georgia Basin (1770s) and into mid-1800s, oak savannas not yet settled by colonists to the region experienced regular fires set by aboriginal residents to enhance fruit and root harvests and hunting opportunities in an intensively modified, culturally maintained landscape (Boyd, 1990; Beckwith, 2004; MacDougall *et al.*, 2004; Turner & Peacock, 2005; Dunwiddie



**Figure 1** Study area in the Georgia Basin, including Gulf Islands of Canada and San Juan Islands of the United States (a), North American mainland (b) and northern Strait of Georgia. The 66 study sites are indicated numerically and correspond to information in Table 1.

*et al.*, 2011; Turner, 2014). Turner (2014) estimated that pre-colonial aboriginal communities harvested one mil *Camassia* bulbs per 1000 humans annually on southern Vancouver Island to secure a principal source of dietary starch. In contrast, a modern transplant experiment found that camas biomass declined in oak meadows subject to high herbivory, but increased  $2\times$  in fenced plots (Gonzales & Arcese, 2008). Many other species relied on historically by aboriginal humans for fruit (e.g. *Rubus*, *Amelanchier*; Turner, 1988, 2014) are also preferred by black-tailed deer as food and fail to fruit where deer exceed  $7\text{ km}^{-2}$  (McTaggart-Cowan, 1945:138). These observations suggest that pre-European deer populations in the Georgia Basin occurred at densities compatible with the persistence of many shrub and forb species aboriginal humans relied on historically as food and that now represent a suite of threatened plant and animal communities (MacDougall *et al.*, 2004; Gonzales & Arcese, 2008; Martin *et al.*, 2011; Bennett & Arcese, 2013; Neame *et al.*, 2013).

However, the range of deer densities commensurate with the persistence of Georgia Basin plant communities is entirely uncertain. Historical accounts by early Europeans make note of plentiful deer (MacDougall *et al.*, 2004), and because they also describe verdant, productive savanna landscapes with few aboriginal residents could be interpreted as evidence that high deer density and plant productivity co-occurred in pre-colonial landscapes. Conversely, other evidence suggests that aboriginal peoples of the Georgia Basin were already markedly reduced in number prior to European contact via the advance of novel diseases introduced elsewhere in North America (Cook, 1976) and that aboriginal populations continued to decline rapidly after 1800 via smallpox,

measles and malaria (Boyd, 1990; Beckwith, 2004). These events can also explain reports of abundant deer by early Europeans because eruptions of ungulate populations afforded abundant food and low mortality are well documented (Caughley, 1970; Estes *et al.*, 2011). Additional evidence is therefore needed to discriminate among possibilities and identify practical steps to conserve native communities.

Given the ideas above, we predicted that shrub species richness and cover would be lowest in sites with high deer density but that diversity would peak in sites with low deer densities under the assumption that limited disturbance will prevent dominance by fast-growing, palatable species (Grime, 1973; Coté *et al.*, 2004; Shea *et al.*, 2004). We also predicted that if deer determine shrub community structure, palatable species should become rare at high deer density, but less palatable species should benefit by deer presence. We also address two applied needs. First, we apply Turner's (1988) concept of cultural significance to ask what deer densities maximize the cover of shrubs relied on by aboriginal residents of the Georgia Basin prior to European contact. Second, we test Martin *et al.*'s (2011) suggestion that the shape of a palatable and widespread shrub (*Holodiscus discolor*) offers a region-wide indicator of deer impact on plant communities.

## METHODS

### Vegetation survey

We estimated shrub species cover, richness and diversity in 239 10-m-radius plots throughout the Gulf (BC) and San Juan (WA) archipelagos and adjacent mainland (Fig. 1,

Table 1). Plots were surveyed from 1 May to 20 June 2011, pooled into 66 sample sites based on proximity (Table 1) and centred on avian point count locations selected to represent landscape-level variation in land use (Schuster & Arcese, 2013). We recorded shrub species richness by identifying all woody species in plots with foliage  $\leq 2$  m above ground and thus available to deer. Cover was estimated by marking plots with flagging tape and recording the areal cover of foliage  $\leq 2$  m above ground for each species and the sum of species, potentially exceeding one via overlap. Species diversity ( $D_H$ ) was estimated as  $e^H$ , where  $H$  equalled the Shannon entropy (cf Jost, 2006). By conducting surveys in a 1 year after all species had leafed-out, we hoped to minimize temporal variation estimated plant cover due to herbivory, phenology or interannual variation in climate.

### Culturally significant species

Turner (1988) introduced an index of cultural significance to quantify the quality, intensity and exclusivity of plant species use by aboriginal people and identified primary food plants as being of high relative value among hundreds of species noted. We therefore summed the richness and cover of fruit-bearing shrubs identified by Turner (1988, 2014; Tables 11.1, 11.2; Turner & Peacock, 2005) as culturally significant food plants to estimate the value of present-day plant communities to pre-European aboriginal residents of the Georgia Basin. Fifteen species in our sample were thus included the following: *Arctostaphylos uva-ursi* L., *Amelanchier alnifolia* Nutt., *Crataegus douglasii* Lindley, *Gaultheria shallon* Pursh., *Malus fusca* Raf., *Oemleria cerasiformis* Landon, *Rubus*

**Table 1** Number of plots and mean (SE) of faecal standing crop (FSC) and shrub species cover, richness and diversity on 35 islands and the North American mainland of the Georgia Basin (see Fig. 1)

Sites	Island	Plots	FSC	Cover	Richness	Diversity
Canada						
1–3	Sunshine Coast	15	0 (0)	80.63 (12.82)	6.53 (0.76)	3.92 (0.73)
4–16	Vancouver	37	2.78 (0.88)	52.42 (6.96)	6.35 (0.54)	3.31 (0.44)
17–19	Hornby	12	4.25 (1.35)	37.5 (7.46)	5.42 (0.69)	2.76 (0.45)
20	Link	5	12.8 (3.09)	7.7 (4)	1.6 (0.24)	1.34 (0.15)
21–22	DeCourcy	5	10.2 (2.73)	4.9 (1.33)	3 (0.32)	1.33 (0.06)
23	Ruxton	5	0 (0)	96 (11.15)	11.2 (0.97)	5.23 (1.17)
24–26	Galiano	15	5.13 (1.69)	34.1 (7.63)	6.93 (0.81)	2.73 (0.31)
27–28	Mayne	10	6.2 (1.89)	18.95 (4.45)	7.6 (0.83)	2.8 (0.48)
29	Georgeson	2	3.5 (2.5)	18.75 (7.75)	8 (1)	2.81 (0.86)
30	Lt. Samuel	3	7 (1.15)	45.33 (10.4)	5.67 (0.33)	2.59 (0.34)
31	Anniversary	2	0 (0)	99.75 (44.25)	12 (0)	12.91 (6.08)
32	Cabbage	2	5.5 (0.5)	64 (8.5)	14 (1)	6.88 (0.46)
33–34	Tumbo	8	6.63 (1.86)	50.44 (12.99)	7.5 (0.5)	2.06 (0.28)
35–38	Saturna	13	17.62 (2.87)	27.08 (8.07)	5 (0.72)	1.93 (0.23)
39–42	Saltspring	15	11.13 (2.51)	43.27 (9.45)	6 (0.76)	2.73 (0.43)
43	Prevost	7	3.57 (1.31)	31.07 (10.58)	5.43 (1.15)	2.26 (0.32)
44	Owl	2	0 (0)	126.25 (0.75)	11.5 (1.5)	10.02 (3.19)
45	E. Channel	2	0 (0)	59.25 (19.25)	8 (2)	4.59 (1.77)
46	W. Channel	2	0 (0)	127.75 (5.25)	9.5 (0.5)	13.22 (1.92)
47	Russell	6	0 (0)	113.5 (20.25)	11.33 (0.99)	10.79 (3.6)
48–49	Portland	9	0 (0)	85.17 (17.19)	11.44 (1.2)	7.24 (1.01)
50	Brackman	5	0 (0)	76 (22.83)	9.6 (1.08)	3.44 (0.66)
51	Piers	6	2.67 (0.95)	40.33 (17.24)	8 (1.34)	2.66 (0.55)
52	Reay	2	0 (0)	42 (5)	5 (2)	3.01 (0.67)
53	Rum	2	4.5 (1.5)	7.75 (5.75)	3 (1)	1.49 (0.34)
54	Lt. Shell	1	0 (0)	179 (0)	11 (0)	9.41 (0)
55	Kerr	3	0 (0)	194 (40.55)	11.33 (0.88)	8.49 (2.35)
56	N. Dock	1	0 (0)	93 (0)	9 (0)	6.05 (0)
57	S. Dock	1	0 (0)	141 (0)	8 (0)	10.33 (0)
58	Mandarte	3	0 (0)	149.33 (9.55)	6.33 (0.88)	4.56 (2.41)
59–61	Sidney	16	14.06 (2.78)	12.63 (3.59)	3.38 (0.51)	1.55 (0.12)
62	D'Arcy	5	9.2 (2.35)	36.5 (12.34)	4.2 (0.37)	2.42 (0.55)
63	Lt. D'Arcy	4	12.75 (4.87)	74.13 (31.94)	8 (0.71)	3.25 (0.54)
United States						
64	Jones	3	20.67 (6.94)	6.33 (3.93)	2.33 (1.33)	1.43 (0.29)
65	Sucia	5	0 (0)	114 (24.92)	9.4 (1.03)	4.64 (0.97)
66	Matia	5	0 (0)	74.6 (18.67)	9 (1)	4.84 (1.49)

*ursinus* Cham. & Schltldl., *R. spectabilis* Prush., *R. parviflorus* Nutt., *R. leucodermis* L., *Rosa nutkana* K. Presl., *Ribes divaricatum* Rydb., *Sambucus racemosa* L., *Shepherdia canadensis* L., *Vaccinium parvifolium* Smith and *V. ovatum* Pursh.

### Deer density

We estimated deer density using faecal standing crop (FSC; Campbell *et al.*, 2004) and known deer density on Piers I, BC (Table 1). FSC was the density of pellet groups ( $\geq 18$  pellets in a 20 cm area) detected in two searches of four,  $2 \times 50$  m strip transects emanating from plot centres in each cardinal direction (survey area = 400 m<sup>2</sup>). Deer density on Piers Island was estimated directly following Martin *et al.* (2011); 18 coordinated observers returned a count of 20 deer (Feb 2012), yielding 0.2 deer ha<sup>-1</sup>. Deer density at each plot *i* was thus estimated as 0.2 deer ha<sup>-1</sup> \* FSC *i*/ha, divided by the mean FSC/ha on Piers Island [mean (SD) = 6.7 (5.9), *n* = 6]. Density estimates were pooled for analysis in five levels to reflect 54 plots with no deer for  $\geq 35$  years (local knowledge and our surveys) and four quartiles for sites estimated at < 0.08, 0.08–0.22, 0.30–0.82, 0.90–2.84 deer ha<sup>-1</sup> ( $n_{plots}$  = 44, 46, 49, 46, respectively).

### Palatability

We measured the palatability of 12 shrubs to black-tailed deer via a cafeteria experiment, by placing branches in random order into capped and buried PVC pipe filled with water and arranged as transects spaced at 2 m in a mowed forest opening (~3000 m<sup>2</sup>). Samples were approximately matched for foliage volume and length (150 cm) and made available from 20:00 h to 08:00 h the next morning, with 8–12 replicates over 2 weeks on Piers I (June 2011). Palatability was estimated as the mean fraction of foliage removed from samples at the end of trials and was supplemented by visual estimates of the fraction removed at 30 min intervals to 22:00 h. Species included common, widely distributed natives (*n* = 11) and exotics (*n* = 1) that, based on experience and local research (McTaggart-Cowan, 1945; Allombert *et al.*, 2005), vary in palatability to deer (*Arbutus menziesii* Pursh., *A. alnifolia*, *Cytisus scoparius* L., *G. shallon*, *Holodiscus discolor* Pursh., *Lonicera ciliosa* Pursh., *L. hispidula* Pall., *Mahonia nervosa* Pursh., *R. ursinus*, *R. nutkana*, *Symphoricarpos albus* L., *V. parvifolium*). Four of these species represent nine of 15 culturally significant food plants listed above at the genus level.

### Ocean spray ratio

Martin *et al.* (2011) suggested the ratio of foliar width at 2 : 1 m above ground on ocean spray shrubs might provide an index of browsing impacts in the Gulf and San Juan Islands because the species becomes umbrella-shaped when browsing limits shoot recruitment. To validate the ocean spray ratio (OSR) as a regional indicator of deer density and

impact, we tested the prediction that native shrub species richness, diversity and cover all decline as OSR and pellet density increased. Focal shrubs were selected as the north-most plant  $\geq 2$  m in height inside plots, or the nearest plant within 100 m of a plot given none inside it (cf Martin *et al.*, 2011; none located in 22 of 239 plots).

### Statistical analysis

We estimated relationships between deer density and shrub species cover, richness and diversity and the OSR using general linear mixed models (GLMMs) that specified deer density and island size as fixed effects and site identity as a random factor. Because the number of plots in sites varied (1–7; Table 1), we weighted models by  $\sqrt{n_{plots}}$  to reduce effects of sampling error. Dependent variables were transformed by log<sub>10</sub> as necessary to normalize residuals, and statistical tests were based on Poisson or normal residual distributions as appropriate. All means appear with a standard error (SE) or back-transformed 95% confidence intervals (Table S1). Vancouver Island and mainland sites were assigned an area 10× the largest Gulf Island surveyed (Salt Spring; Table 1). Palatability was assessed by ANOVA with time, species and foliage remaining as independent and dependent variables, respectively. All analyses were conducted in SYSTAT (2004) or R v.3.0.1; (lme4; Bates *et al.*, 2013).

## RESULTS

### Shrub species richness, cover and diversity

We identified 49 native and 10 exotic shrubs in 239 plots at 66 study sites (Fig. 1). Native richness was 12.6× higher than exotic richness [mean (SE): 6.3 (0.2) vs. 0.5 (0.1)] and similar to total richness [6.8 (0.2)]. A mean of 2.1 (0.1) culturally significant species occurred in plots, but native, exotic, total and culturally significant species richness varied from 0 to 15, 4, 17 and 7, respectively. The mean fraction of plots covered by native, exotic or culturally significant species was 0.51 (0.03), 0.03 (0.01) and 0.26 (0.31), respectively. Species diversity ( $D_H$ ) varied by 34× across plots (range = 0.82–28.13; mean = 3.65 (0.21)). At the site level, shrub cover also varied from very low mean cover (1–2%) on Jones Island and DeCourcy Island, to a high of 187% on Kerr Island (mean = 54.3% (5.4); Table 1). Native richness across sites averaged 6.4 (0.4) species, but ranged from 1.6 (0.2) on Link Island to 14.0 (1.0) on Cabbage Island (Table 1).  $D_H$  varied 11× across sites [range = 1.2–13.2; mean = 3.9 (0.4)].

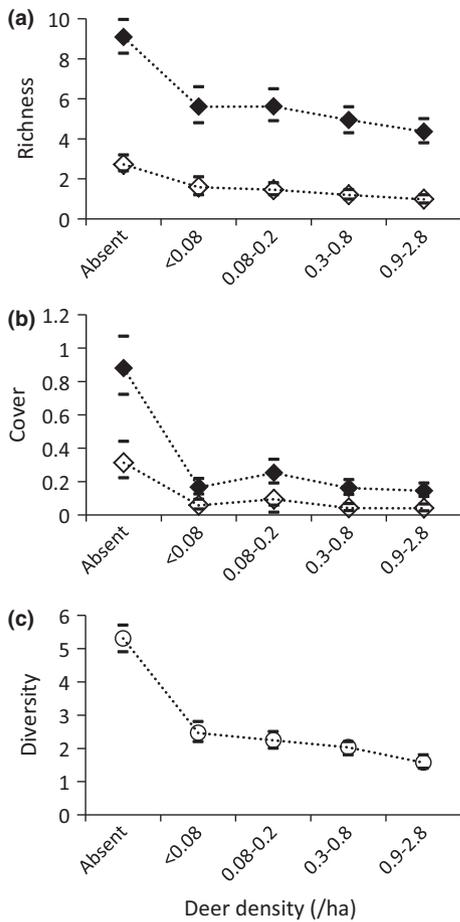
### Deer density

Pellet group density varied from 0 to 95 ha<sup>-1</sup> in plots [mean = 13.9 (1.3)], 0 to 69 ha<sup>-1</sup> across sites [mean = 13.2 (2.1)] and 0 to 52 ha<sup>-1</sup> across 35 islands and the North American mainland [mean = 11.1 (2.4)]. Despite marked variation in pellet density among sites ( $r^2$  = 0.67,

$F_{64,174} = 5.4, P < 0.0001$ ) and islands ( $r^2 = 0.48, F_{35,203} = 5.4, P < 0.0001$ ), island size and pellet density were unrelated at the plot level (Pearson's  $r = 0.02, n = 239$ ).

**Deer density and shrub communities**

Native and culturally significant species richness and cover declined dramatically as deer density increased (Fig. 2a–c, Table S1). The steepest declines occurred between sites with no deer versus those with low-density deer ( $< 0.08 \text{ ha}^{-1}$ ), with native and cultural species richness and cover down by 38 and 42% and 81 and 82%, respectively. Even with deer-free sites excluded, deer density was a negative predictor of native and cultural species richness ( $\beta = -0.03 (0.01)$  and  $-0.014 (0.005)$ , respectively) and cover ( $\beta = -0.31 (0.13)$  and  $-0.20 (0.10)$ , respectively). Because species richness and cover both affect diversity,  $D_H$  also declined rapidly as deer density increased (Fig. 2c, Table S1) and by 54% from sites



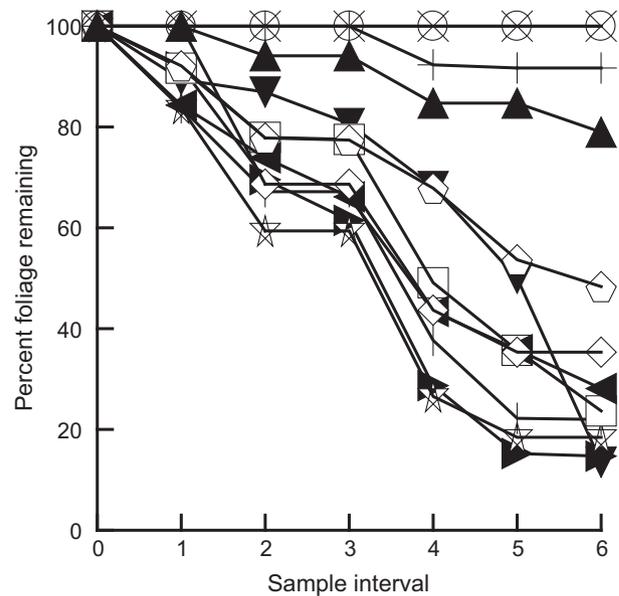
**Figure 2** Mean ( $\pm$  SE) richness and fraction cover of native (solid) and culturally significant (open) shrub species native species diversity ( $D_H$ ; circles) at 65 sample sites on 36 islands and the North American mainland (see Fig. 1). Richness (a), cover (b) and diversity (c) all peaked in sites without resident deer and declined significantly with increasing density (see Methods; Table S1 for estimates).

with no deer to low-density sites. In contrast, exotic richness and cover varied less with deer density, with few significant differences among density classes (Table S1).

**Palatability**

Eight of 12 species in our cafeteria trials had  $\geq 52\%$  of their foliage removed within 12 h of exposure to deer and six lost more than 70% (Fig. 3, Table 2). Four relatively unpalatable species lost 21, 8, 0 and 0% (Table 2). As expected if palatability to deer affects shrub cover and distribution throughout the Georgia Basin, the mean fraction of foliage removed from species in cafeteria trials was a good predictor of change in mean species cover across sites without deer to those with abundant deer ( $R_s = -0.79, n = 12, P < 0.001$ , Spearman Rank test). *Lonicera ciliosa*, the most palatable species in trials (86% browsed; Table 2), had a mean cover of 2.3 (0.3)% in sites with no deer, but just 0.04 (0.3)% in high density sites ( $\geq 0.9 \text{ deer ha}^{-1}$ ). Similarly, *L. ciliosa* was present in 50% of 54 sites with no deer but just 4% of 46 high density sites ( $G = 39.8, \text{d.f.} = 4, P < 0.0001$ ; likelihood ratio test).

Defining ‘palatable cover’ as the sum of eight species with  $\geq 50\%$  of foliage removed and ‘unpalatable cover’ as the sum of the four remaining species (Table 2) revealed a dramatic decline in palatable shrub cover as deer density increased (Table S1). In contrast, unpalatable species peaked in cover



**Figure 3** Percentage foliage remaining in six intervals from 2000 to 08:00 h (see Methods, Table S1). Symbols indicate mean of replicated trials for 12 species listed here from least to most palatable: *Gaultheria shallon* ( $\times$ ), *Mahonia nervosa* ( $\circ$ ), *Vaccinium parvifolium* ( $+$ ), *Cytus scoparius* ( $\blacktriangle$ ), *Rubus ursinus* (pentagon), *Holodiscus discolor* ( $\diamond$ ), *Amelanchier alnifolia* ( $\blacktriangleleft$ ), *Lonicera hispidula* ( $\square$ ), *Arbutus menziesii* ( $|$ ), *Symphoricarpos albus* (star), *Rosa nutkana* ( $\blacktriangleright$ ), *Lonicera ciliosa* ( $\blacktriangledown$ ).

**Table 2** Mean (SE) percentage of foliage remaining after 12 h exposure to deer for 12 species arranged from most to least palatable. Statistical entries refer to fraction of variance accounted for by sample interval in repeated trials (see Methods, Fig. 3 for species names)

Species Name	Lonicera ciliosa	Rosa nutkana	Symphoricarpos albus	Arbutus menziesii	Lonicera hispidula	Amelanchier alnifolia	Holodiscus discolor	Rubus ursinus	Cysts scoparius	Vaccinium parvifolium	Mahonia nervosa	Gaultheria shallon
Mean % Remaining	14 (11)	15 (10)	18 (12)	22 (11)	24 (10)	28 (11)	35 (12)	48 (9)	79 (7)	92 (5)	100 (0)	100 (0)
r <sup>2</sup>	0.5	0.49	0.38	0.36	0.38	0.31	0.31	0.24	0.10	0.09	0.00	0.00
F	7.3	12.3	7.8	7.2	7.8	5.8	5.7	4.1	1.5	0.1	NA	NA
d.f.	6,53	6,77	6,77	6,77	6,77	6,77	6,77	6,77	6,77	6,77	6,53	6,53
P	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.001	0.2	0.6	NA	NA

at intermediate deer density (13–28%) were lowest in the absence of deer (3%), but also low at high deer density (7–10%; Table S1), indicating that even unpalatable species were consumed where alternatives are unavailable (e.g. Fig. 2).

### Ocean spray ratio

Ocean spray ratio varied 1040× [0.1–104; mean = 7.6 (1.0)] across plots but was a good predictor of pellet group density [ $\beta = 0.41$  (0.08)], accounting for ~32% of variance (Fig. S1). OSR also predicted native shrub species cover [ $\beta = -0.19$  (0.08)], richness [ $\beta = -0.13$  (0.04)] and diversity ( $\beta = -1.3$  (0.5; GLMMs, island as random effect)). However, large residual variances imply that robust OSR estimates are needed to reduce sampling error. For example, the variance in native cover, richness and diversity accounted for by mean OSR was highest using sites with  $\geq 5$  shrubs measured (Fig. S2).

### DISCUSSION

Despite many demonstrations that herbivore populations can erupt in the absence of predation to facilitate trophic cascades in plant and animal communities (Caughley, 1970; Coté *et al.*, 2004; Estes *et al.*, 2011), it remains highly uncertain what deer densities can be supported in modern-day plant communities without eliminating other valued native species, particularly culturally significant species known to have been abundant in recent history in the Georgia Basin (e.g. Beckwith, 2004; MacDougall *et al.*, 2004). We found that native and culturally significant shrub species richness, cover and diversity declined by 38–85% as deer density increased at 66 island and mainland sites in the Georgia Basin, complimenting studies of other taxa at smaller spatial scales (e.g. Allombert *et al.*, 2005; Gonzales & Arcese, 2008; Martin *et al.*, 2011, 2013). However, we found no evidence that deer browsing enhanced shrub species diversity (cf Grime, 1973; Shea *et al.*, 2004) even at low deer densities ( $< 0.08 \text{ ha}^{-1}$ ). Instead, palatable plant species cover was 92% lower where deer were common, and 52% lower where deer occurred at low density ( $< 0.08 \text{ ha}^{-1}$ ), than where deer were absent. Compared to sites without deer, shrub diversity also declined by 53% in sites with low-density deer ( $< 0.08 \text{ ha}^{-1}$ ), and by 70% in sites with high deer densities (0.9–2.8  $\text{ha}^{-1}$ ; Table S1). These results indicate that deer reduce shrub species cover, richness and diversity measurably at all densities where they occur in the Georgia Basin and do so severely where they exceed  $0.08 \text{ ha}^{-1}$ . In contrast, Cook-Patton *et al.* (2014) found that white-tailed deer (*Odocoileus virginianus*) preferentially browsed palatable, fast-growing tree seedlings in experimental plots, thereby enhancing survival in slow-growing species and diversity in mixed-species assemblages. We also observed an increase in the mean cover of unpalatable shrubs at intermediate deer densities compared to sites without deer (Table S1), suggesting that these species benefitted at low deer densities. However, unpalatable

shrub cover declined at deer densities  $\geq 0.3 \text{ ha}^{-1}$  (Table S1), and shrub species diversity declined dramatically as deer density increased (Fig. 2c). Taken together, and given the low densities ( $0.03\text{--}0.08 \text{ ha}^{-1}$ ) reported by Cook-Patton *et al.* (2014), these results support the conclusion that any beneficial effect of deer browsing on species diversity may only be observed at deer densities much lower than those reported for the Georgia Basin during the last half century (e.g. Martin *et al.*, 2011; McTaggart-Cowan, 1945; Fig. 2). We now develop these findings in the context of trophic cascades, historical ecosystem states and the deer densities commensurate with the persistence of diverse plant and animal communities.

Our results confirm that relaxing limits on deer population growth can result in eruptions that dramatically affect plant community structure and threaten the persistence of palatable plant species and associated taxa (e.g. Caughley, 1970; Coté *et al.*, 2004; Allombert *et al.*, 2005). These changes are recognized as syndromes of the cascading interactions that follow apex predator removal and have led to the simplification of terrestrial and marine ecosystems worldwide (Estes *et al.*, 2011). In the Georgia Basin, predator removal and modern prohibitions on hunting have resulted in high deer densities on many islands (Gonzales & Arcese, 2008; Martin *et al.*, 2011; Table 1), including islands used historically for aboriginal food harvest (e.g. Elliot, 1983). Our results thus support and extend the hypothesis that unregulated deer populations simplify plant and animal communities of the Georgia Basin by reducing native and culturally significant shrub cover, richness and diversity (Fig. 2a–c), the abundance of birds that rely on shrubs for food, nests or cover (Martin *et al.*, 2011, 2013), and the growth and reproductive rate of meadow plants (Gonzales & Arcese, 2008).

Traditional knowledge of Georgia Basin plant communities, aboriginal land management and our own results also help to define benchmarks for the conservation and restoration of native plant communities. For example, many plant species in our surveys were relied on historically for food and facilitated by aboriginal people throughout western North America and the Georgia Basin prior to European contact (e.g. Elliot, 1983; Turner, 1988, 2014; MacDougall *et al.*, 2004; Dunwiddie *et al.*, 2011; Beschta & Ripple, 2012) and with other species continue to contribute fundamentally to modern aboriginal culture and well-being (Beckwith, 2004; Garibaldi & Turner, 2004; McKechnie *et al.*, 2014; Turner, 2014). Our finding that culturally significant plant species cover and richness declined dramatically in the presence of deer, even at low deer densities (Fig. 2), further suggests that conservation reserves without deer management plans or healthy native predator populations will continue to erode in native species diversity, particularly in the endangered savanna plant communities that prevailed under aboriginal land management (MacDougall *et al.*, 2004; Dunwiddie *et al.*, 2011; Turner, 2014). Indirectly, these results imply that a renewed effort to apply aboriginal stewardship

techniques and knowledge could improve conservation outcomes in these habitats in future.

Martin *et al.* (2011, 2013) suggested that deer densities  $< 0.1 \text{ ha}^{-1}$  are needed to maintain diverse understorey bird communities on islands in the Georgia Basin, given that many species rely on shrubs for nesting, food or cover. Our results suggest densities  $\leq 0.08 \text{ deer ha}^{-1}$  are necessary to maintain native shrub communities at least 50% as rich and diverse as those on islands without resident deer (e.g. Fig 2a–c). These findings match closely the results of McTaggart-Cowan (1945:138) who compared plant cover and deer diets to conclude that preferred shrubs (e.g. *Vaccinium*, *Ribes* and *Rubus*) seldom produced fruit at densities  $\geq 0.08 \text{ deer ha}^{-1}$  on Vancouver Island. Because many preferred foods of deer are species of high cultural significance that thrived under aboriginal stewardship (Boyd, 1990; Beckwith, 2004; Turner & Peacock, 2005; Dunwiddie *et al.*, 2011; Beschta & Ripple, 2012; Turner, 2014), our results also indicate that maintaining culturally and ecologically significant plant communities in the Georgia Basin will require that we maintain deer densities below  $0.08 \text{ ha}^{-1}$ .

Despite these conclusions, it will remain challenging to monitor and manage deer at ecologically sustainable densities due to the costs of estimating density at large spatial scales (Burnham *et al.*, 1980; Bailey & Putnam, 1981; Seber, 1986; Morellet *et al.*, 2001) and concerns about human safety and animal welfare. We addressed the first issue by showing that shrub architecture offers an index of deer density and shrub species cover, richness and diversity in the Georgia Basin (Fig. S1). These results validate Martin *et al.*'s (2011) earlier suggestion and provide an easily applied tool that land stewards can use to assess ecosystem condition and compare management treatments. By comparison, pellet counts suffer bias due to weather, season, habitat and observers and require precise total counts or estimates of defecation and decomposition rate to estimate deer density reliably (e.g. Eberhardt & VanEtten, 1956; Campbell *et al.*, 2004). More sophisticated browse indexes estimate herbivore impacts directly by recording tissue growth or removal or by comparing rumen contents to plant cover (e.g. McTaggart-Cowan, 1945; Anderson, 1994; Morellet *et al.*, 2001; Frerker *et al.*, 2013), but require specialist training and estimates of plant palatability, abundance and distribution to apply regionally (e.g. Frerker *et al.*, 2013). Because ocean spray is conspicuous, widespread and preferred by deer as food in the Georgia Basin (Fig. 3), our results indicate that the ocean spray ratio can be used to simultaneously estimate deer density and native shrub species cover, richness and diversity (Fig. S1 & 2).

## CONCLUSIONS

Our results offer a compelling example of trophic downgrading (cf. Estes *et al.*, 2011) and highlight the need to identify herbivore densities compatible with the persistence of all native species in conserved landscapes. Specifically, we

describe system states in modified and reference sites that illustrate the consequences of deer density on native plant and animal communities (Fig. 2; McTaggart-Cowan, 1945; Gonzales & Arcese, 2008; Martin *et al.*, 2011, 2013; Bennett & Arcese, 2013). Moreover, we show that culturally significant food plants, relied on historically by aboriginal land stewards and currently by modern aboriginal peoples aiming to maintain or reinforce traditional cultural practices, decline dramatically in richness and cover where deer exceed  $0.08 \text{ ha}^{-1}$  (Fig. 2). In contrast, Beschta & Ripple (2012) showed that after a century of suppression by elk (*Cervus elaphus* L.), berry-producing shrubs have recently recovered sufficiently to contribute positively to regional food webs in northern Yellowstone 20 years after the reintroduction of wolves (*Canis lupus* L.). Taken together, these findings are consistent with historical descriptions by European colonists of Georgia Basin landscapes densely populated by aboriginal food plants (MacDougall *et al.*, 2004:459) which are now scarce or extinct where deer are common, but that are also known to rebound given protection from high herbivory (Gonzales & Arcese, 2008; Beschta & Ripple, 2012).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Ocean Spray Ratio as an index of deer pellet density.

**Figure S2** Ocean Spray Ratio as an index of shrub community covers (a), richness (b) and diversity (c).

**Table S1** Mean (*se*) native, exotic and cultural species cover, richness and native and exotic diversity in relation to deer density.

## BIOSKETCH

**Peter Arcese** holds an FBRC Chair in Applied Conservation Biology and focuses research at the interface of theoretical and applied population genetics, demography and conservation of free-living plant and animal populations.

Author contributions: P.A. conceived study, collected and analysed data and led writing; R.S., L.C., A.B. and T.M. contributed essential data, analyses, writing.

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