

RESEARCH ARTICLE



Indigenous peoples' habitation history drives present-day forest biodiversity in British Columbia's coastal temperate rainforest

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Abstract

1. Long-term human habitation has transformed the earth's surface. The combination of time and complex human–environment interactions in remote regions of North America has likely resulted in modified landscapes, though we often consider these regions free of human influence due to the absence of industrial development.
2. We examined long-term impacts of human resource-use on British Columbia's coastal rainforest communities. We focused on the region's widespread habitation sites with extensive shell middens to test the legacy of ancient human occupation in present-day plant communities.
3. Ten habitation sites and 10 control sites in similar locales were selected for floristic surveys and soil sampling. We tested whether plant communities at habitation sites reflected a 'cultural plant-use legacy', with greater presence of culturally significant plant species, and/or a 'marine nutrient subsidy legacy' from human use, with increases in species that prefer nutrient-rich soils.
4. We found that the habitation sites had different plant assemblages than the control sites and were dominated by plants with both higher nutrient requirements and cultural significance. We demonstrate that long-term occupation has led to strong differences in plant community structure between sites, countering the notion that this is a pristine landscape. We emphasize the value of interdisciplinary approaches and considering past human resource-use when examining current plant communities.

KEYWORDS

community composition, ethnoecology, habitation sites, legacy effects, shell midden

1 | INTRODUCTION

It is widely recognized that humans have played a large role in transforming the earth's surface and that few, if any, ecosystems are without human influence (Shackelford, Standish, Ripple, & Starzomski, 2018; Vitousek, Mooney, Lubchenco, & Melillo, 1997). Up to three-quarters of ice-free land surfaces have been influenced by humans, whether through intentional or unintentional disturbances (Ellis & Ramankutty, 2007). Modern landscapes not only reflect contemporary influences, but also embody the legacies of past human activities: the results are landscapes with characteristics determined by long and complex interactions between human activities and the natural environment. These persistent legacies have been described in tropical (Clement, McCan, & Smith, 2003) and temperate soils (De Smidt, 1977), forest composition (Levi et al., 2018) and landscape modifications that influence resource productivity (Engdawork & Bork, 2014; Groesbeck, Rowell, Lepofsky, & Salomon, 2014). The damaging effects of activities such as habitat destruction, fragmentation and over-harvesting are widespread, and human-dominated landscapes prevail globally (Ellis & Ramankutty, 2007). However, there are alternative models for how humans can interact with their landscapes. Examples of this can be found in the Central Coast of British Columbia (BC), Canada, where there is much evidence of sustained long-term occupancy (Deur & Turner, 2005; Groesbeck, 2013; Pomeroy, 1980; Turner, Lepofsky, & Deur, 2013).

The Central Coast of BC, Canada, is an area known for its remoteness, large tracts of land far from industrial activity, unique landforms and wildlife (e.g. DellaSala et al., 2011). However, a large body of archaeological work and indigenous knowledge shows human presence at some past sites of habitation, or sites with evidence of long-term occupation and land use and hereafter referred to simply as habitation sites, has been continuous at the regional scale for 13,000 years or more (see Cannon, 2000; Carlson, 1979; McLaren & Christensen, 2013). For approximately 400 human generations, people managed and consumed nearby terrestrial and marine resources on these sites.

Many of the habitation sites have extensive shell middens, which are often described as accumulations of cultural refuse, or kitchen mounds, that have built up over time and over generations of use. At habitation sites, the shell midden material may have been used as foundation for housing structure or for other purposes (see Blukas-Onat, 1985). The composition of these shell middens reflects the activities at these sites and often includes materials such as clam and mixed shells, bones of land and sea mammals, fire-cracked rocks, fish bones, stone tools, human remains and other organic artefacts that form stratified berms (Blukas-Onat, 1985; McLaren & Christensen, 2013; Pomeroy, 1980; Sawbridge & Bell, 1972).

Forests in this region have been shaped by an extensive anthropogenic fire history (Hoffman, Gavin, Lertzman, Smith, & Starzomski, 2016; Hoffman, Gavin, & Starzomski, 2016; Hoffman, Lertzman, &

Starzomski, 2017) and despite the habitation sites being abandoned for over 125 years, the productivity of modern forests growing on habitation sites shows the enhanced productivity (Trant et al., 2016). Little is known, however, about how these long-term human modifications have influenced understory vegetation. As the materials of the shell middens break down over time, we can expect changes in available nutrients, a higher pH and possibly different drainage potential than areas without shell midden (Blukas-Onat, 1985). This in turn is likely to influence plant community composition. In other regions, studies have found that shell middens have the potential to alter their local environment in terms of soil qualities (Sawbridge & Bell, 1972; Smith & McGrath, 2011) and vegetation communities. Examples of such changes within plant communities include increased introduced species, increased species richness and unique or shifted species assemblages found on sites with shell middens (Cook-Patton, Weller, Rick, & Parker, 2014; Karalius & Alpert, 2010; Kelly, 2006).

We also expected, along with the effects of the nutrients derived from shell middens, that the long-term historical use of certain plant species on the habitation sites would influence the plant community that we see today. Plants were, and still are, an important part of the diet of the First Nations of the Pacific Northwest, and there are many examples of management practices that enhanced plant production (see Deur & Turner, 2005; Turner et al., 2013). Some examples of managed species include salmonberry, *Rubus spectabilis* (pruned, shoots cut for future regeneration); thimbleberry, *Rubus parviflorus* (shoots cut for future regeneration, burned); and red huckleberry, *Vaccinium parvifolium* (fertilized, pruned, burned and transplanted; Turner, 2014). With the long history of occupation on these habitation sites, we expect that the managed plants would remain abundant within the understory plant community, despite the fact that these sites' period of most intense human use largely ended by the late 19th century.

The goal of this study was to examine how long-term resource-use and land management have influenced understory forest vegetation in the coastal landscapes within this region. Habitation sites with known long-term use and extensive shell middens are common in the region (McLaren & Christensen, 2013; Pomeroy, 1980), and nearby control sites that are similar except for midden accumulations are easily located. We used a paired-site study design, making a comparison with control sites that did not have shell middens, and have no known history of intensive occupation. We tested two hypotheses: (a) the vegetation on habitation sites would reflect a 'cultural plant-use legacy' with a greater presence of plant species with high cultural significance and likely past cultivation and use. This hypothesis was tested using several response variables including cultural plant-use metrics, plant communities and plant species richness; (b) the vegetation on habitation sites would reflect a 'marine nutrient subsidy legacy' from human use and have increased cover of species that have high-nutrient level requirements compared to the control sites. Soils would also demonstrate higher Ca and other limiting nutrients on habitation sites compared to control sites. The legacy of resource subsidy has been observed before (e.g. Cook-Patton et al.,

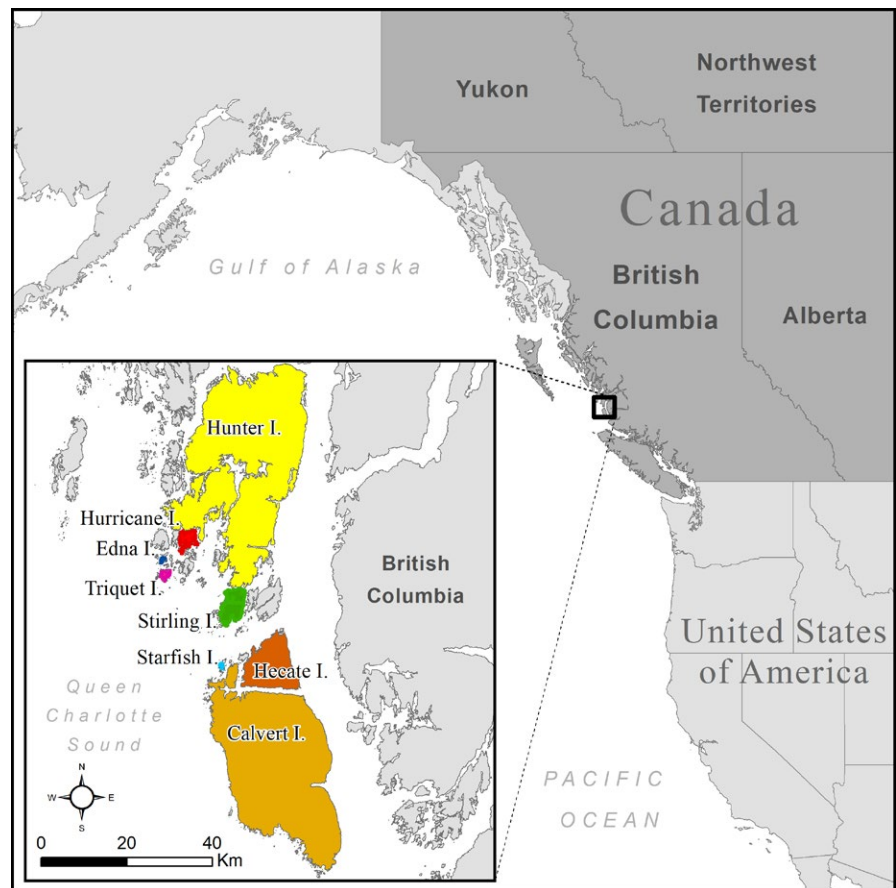


FIGURE 1 Map of the study region. Each highlighted island had at least one pair of habitation-control sites

2014), but looking specifically for a cultural signal in this way has not; the evaluation of both at the same time is also novel.

2 | MATERIALS AND METHODS

2.1 | Site description

The study region is located on the Central Coast of British Columbia, Canada, within the Hakai Lúxvbális Conservancy, the largest protected area on BC's coast. All sites are classified in the CWHvh2—the central variant of Coastal Western Hemlock (CWH) biogeoclimatic zone in the very wet hypermaritime subzone (Klinka, Pojar, & Meidinger, 1991). The CWH occurs along the entire BC coast from sea level to 900 m (Pojar, Klinka, & Demarchi, 1991), with the hypermaritime subzone characterized by cool summers and mild winters with a mean annual precipitation of about 2,230 mm and mean annual temperature of 8.2°C (Klinka et al., 1991). Soil formation in these wetter zones occurs primarily by means of organic matter accumulation. These soils are generally nutrient poor, as the high precipitation allows for nutrients to be easily leached; the mor humus form is dominant. Characteristic species of this zone include western hemlock, *Tsuga heterophylla* (Raf.) Sarg.; western redcedar, *Thuja plicata* (Donn ex D. Don in Lamb); Sitka spruce, *Picea sitchensis* Bong.; salal, *Gaultheria shallon* Pursh; deer fern, *Blechnum spicant* (Linnaeus) Smith; false azalea, *Menziesia ferruginea* Hook., lanky moss, *Rhytidiadelphus loreus* Hedw.; and step moss, *Hylocomium*

splendens Hedw. (Green & Klinka, 1994). Our fieldwork took place from May to August 2014 on eight islands on the Central Coast: Calvert, Hecate, Starfish, Triquet, Edna, Hurricane, Hunter and Stirling islands (Figure 1).

All habitation sites used in this study were chosen because these were places where people lived and harvested marine resources, which is evident in the shell middens present at each of these sites. There is little information about how site usage varied through time, though the majority of these sites are thought to have had continuous seasonal occupation for past millennia, with some sites, such as one on Calvert Island, having evidence of human activity dating back over 13,000 years (McLaren et al., 2018). These sites have not been used with historic intensity for at least 130 years though site-specific dates are not currently available. Research is currently underway to date these sites using forest age structure and insight gleaned from stand dynamics (Trant & McKechnie, unpublished).

2.2 | Study design

A paired comparison study was used to test differences between 10 habitation sites (where people lived and with extensive shell middens) and 10 control sites, those without a history of intensive human occupation. The control sites were selected based on proximity to the habitation sites, similarity of site slope and suspected parent material and a lack of shell midden material (determined by visual inspection, auger testing and archaeological records: see McLaren &

Christensen, 2013), suggesting that they had not been occupied in an intensive manner. All sites were dominated by the Coastal Western Hemlock forest type. Three 72 m transects were placed parallel to one another at each site, starting from the forest-intertidal edge. Transects were placed perpendicular to the shoreline and centrally on the habitation sites; this is made for varied spacing between transects, ranging from 10 to 25 m depending on the site configuration. Transect spacing on the control sites was arranged in the same manner, starting at the forest-intertidal edge. Along each transect a 1 m × 1 m quadrat was sampled for vegetation cover every 9 m, totalling 9 plots per transect and 27 plots per site. Data collected from each plot included distance from shore, Universal Transverse Mercator (UTM) coordinates, slope, canopy cover percentage estimate (done visually, placed in bins of 0%–25%, 25%–50%, 50%–75%, 75%–100%), percentage of the plot that was covered by dead woody materials (coarse woody debris—CWD) and percentage of cover for the shrub, herb and ground layers of each species in each plot.

2.3 | Legacy of cultural plant-use on present-day plant communities

To test whether human cultivation of culturally important plant species has legacy effects to present-day plant communities over 100 years after human habitation, we created a cultural plant-use metric, which quantifies the cultural importance of vegetation present. The cultural plant-use metric was created using only species described as being either 'named and moderately important culturally in one or more ways' or 'named in at least several languages and very important as food/medicine/material; widely recognized' (N. Turner, personal communication, 2014) (see Data S1). The percent cover of species in the latter was multiplied by 4, and the former multiplied by 3, to give increased weight to very important species as opposed to moderately important. Scores were then tallied within each quadrat. *Gaultheria shallon* (salal) was not included in the cultural plant-use metric as its ubiquity could potentially overshadow the presence of the less common species.

To document some sporadically occurring culturally important species on a coarser scale, we established belt transects that extended 5 m on either side of the transect line and recorded further information for 14 plant species, which included berry producing and other culturally significant species (i.e. skunk cabbage *Lysichiton americanus* Hult. & St. John; Pacific yew, *Taxus brevifolia* Nutt.; cascara, *Rhamnus purshiana* DC; Pacific crab apple, *Malus fusca* (Raf.) Schneider; and Labrador tea *Rhododendron groenlandicum* (Oeder) K.A. Kron & W.S. Judd). Given the remoteness of these island sites, comprehensive sampling at the larger belt transect scale was logistically infeasible. Thus, the compositional results from these analyses are complementary to, rather than fully independent of, the full composition surveys at the quadrat-scale. The culturally significant species were selected based on personal communication with N. Turner (2014) who is widely acknowledged as an expert in the field of ethnobotany, particularly in BC: for example, *Food Plants of Coastal First Peoples* (Turner, 1995) and *Plants of Coastal British Columbia*

(Pojar & MacKinnon, 2004). Despite the significant negative impacts of disease, displacement and colonial legislation (Duff, 1969), First Nations' culture in BC remains strong (e.g. Moody-Humchitt & Slett, 2015). There is much research on the oral and material histories of various First Nations around BC (e.g. Boas, 1896; Hayden, 1992; Turner, Ignace, & Ignace, 2000), and developing partnerships between indigenous and western scientific knowledge in research (Adams et al., 2014; e.g. Housty et al., 2014). This research forms a strong basis for developing further hypotheses on the human use of resources, including culturally important species. The number of stems for these species was recorded at both site types along the 72 m length of the belt transects (see Data S2). The stem counts on the three belt transects were combined for each species within each site for both site types. We square-root transformed the counts to reduce the influence of more abundant species.

Finally, to understand more general variations in plant community composition, we ran principal coordinate analysis (PCoA) on the ground, herb and shrub vegetation layers, as well as these layers in combination. The species included in the analysis were those that occurred in over 10% of all quadrats. Although not present in this threshold value, *L. americanus* (skunk cabbage), *R. groenlandicum* (Labrador tea), *Ribes lacustre* (Pers.) Poir (black gooseberry), *R. parviflorus* (thimbleberry) and *R. spectabilis* (salmonberry) were also included in the analyses. This was done because they may be reflective of site qualities that are not easily apparent (e.g. water table levels) and may reflect historical site activities (e.g. berry gardens), making them potentially key species that differentiate these site types. The PCoA was calculated on a Chord-based dissimilarity matrix computed for each layer. A Chord-based dissimilarity matrix has been found to accurately capture ecological data while still providing a semi-metric analysis (Legendre & Gallagher, 2001) that can be used to generate meaningful axis scores. Thus, the four principal coordinate analyses were performed to generate scores for the plot data from the three vegetation layers, considered separately and all together. We also calculated the overall species richness within quadrats.

2.4 | Legacy of cultural nutrient subsidy on present-day plant communities and soils

The use of plant and nutrient scores has a long history in assessing site quality in forests of British Columbia, and an enormous amount of research has gone into linking nutrients and plants for use as site indicators in the British Columbia Biogeoclimatic zones scheme, the provincial ecosystem delineation methodology (e.g. Banner, LePage, Moran, & de Groot, 2005; Klinka, Krajina, Ceska, & Scagel, 1989; Meidinger & Pojar, 1991). We thus adopt a similar approach for our sites. Similar to the cultural importance score, we created a nutrient indication score for each quadrat to explore whether plant communities showed evidence of environmental enrichment that might result from human-mediated nutrient legacies. For the nutrient score, all plant species were assigned a nutrient indicator category of high, medium or low (as in Hocking & Reynolds, 2011) based on

a well-established Nitrogen-indicator classification system (Klinka et al., 1989). The percent cover for each species in the quadrat was then either multiplied by 2 for high-nutrient indicators, 1 for medium, -1 for low and then tallied with the other species of the quadrat to create a nutrient indication score.

Additionally, we conducted soil surveys at both site types. Using an AMS[®] soil auger, we obtained 30 samples from each site type of approximately 250 g, which were taken from within the active rooting zone to a maximum depth of 30 cm. These samples were obtained at approximately 10 m from the forest-intertidal ecotone, where, on the habitation sites, shell midden was present. The samples were double-bagged and stored at approximately 2°C until they could be transported to the British Columbia Provincial Government Analytical Laboratory at 4,300 North Road in Victoria. Each sample was analysed by microwave digestion/ICP Spectrometer and by the combustion elemental analyzer for measurements of aluminium (Al), boron (B), total carbon (C), inorganic C, calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), nitrogen (N), phosphorus (P), sulphur (S) and zinc (Zn). The samples were also tested for soil organic matter content, effective cation exchange capacity (CEC), exchangeable Al, Ca, Fe, K, Mg, Mn and Na, and pH. All results were corrected to oven-dry (105°C) basis.

2.4.1 | Statistical analysis

In total, we had seven primary response variables for each quadrat including the cultural plant-use index, nutrient index, PCoA1 axes scores for ground, herbaceous, shrub and combined layers and total species richness. Each of these was modelled against treatment using linear mixed effects models (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) with random effects for site (20 sites) nested in site pair (10 pairs). We also hypothesized that distance from shore, canopy cover, slope and cover of leaf litter and coarse woody debris would affect plant communities and diversity, and therefore these fixed effects were also included. Canopy cover was converted from factorial bins to an ordinal variable ranging from 1 (0%–25% cover) to 4 (75%–100% cover). Distance from shore, canopy cover, slope, leaf litter and coarse woody debris were all standardized by subtracting the mean and dividing by the standard deviation. Correlation and collinearity between predictor variables were checked prior to modelling (Zuur et al., 2009) and no issues were found.

Models were fit using the lme4 package (Bates, Maechler, Bolker, & Walker, 2014) in R (R Core Team, 2017). The residuals of each full model were plotted against fitted values and both random effects for model checking. In the case of the cultural plant-use index, the response variable was a zero-truncated integer value that was poorly fit by a Gaussian distribution. Thus, we fit a negative binomial generalized linear mixed effects model (Zuur et al., 2009) using the MASS (Venables & Ripley, 2013) and lme4 packages. Models of the PCoA axis scores for shrub and herbaceous layers showed some heterogeneity in residuals. However, both response variables were continuous values with no upper or lower bound. Thus, we kept a Gaussian distribution but interpret results with caution. We

used the multi-model inference (MuMIn) package (Bartoń, 2018) for model selection and we determined the ranking of the models for all model combinations in terms of relative importance using the Akaike Information Criteria (AIC_c—corrected for sample size; [Mazerolle, 2013]). All models within ΔAIC_c of 4 from the top model were averaged for a final, single model for each response variable. Results for full model averages are reported rather than conditional model averages. The weight-of-evidence of individual variables is also reported as relative variable importance (RVI), which describes the prevalence or summed weight of each variable among the top model set ($\Delta AIC_c < 4$) and therefore the relative importance of each predictor variable in explaining the response variable given the data and models tested. The higher the RVI, the stronger the evidence supporting that variable's role in influencing our response variables.

We evaluated the soil samples for nutrient level differences between site types using a nested ANOVA. Finally, we used non-parametric methods to compare the stem count data of culturally significant plant species between the two site types (habitation and control sites). We first qualitatively compared stem count composition using nonmetric multidimensional scaling (nMDS) in the vegan package (Oksanen et al., 2013) on Bray–Curtis dissimilarity calculations between sites. We then used a multivariate analysis of similarity (ANOSIM) to test whether site types were compositionally different at a statistical level, and a similarity percentages (SIMPER) approach to rank species according to their contribution to community dissimilarities.

All analyses were conducted in R (R Core Team, 2017).

3 | RESULTS

Overall, we found the two site types surveyed to be different: habitation sites had plant assemblages with stronger presence of culturally important plant species and higher nutrient requirements. Nutrient differences were detected in the soil sampling, supporting the vegetation survey findings.

3.1 | Legacy of cultural plant-use on present-day plant communities

We assessed the presence of culturally important plant species at two scales—with quadrats for small-scale measures and belt transects for larger scales. At the quadrat level, although the site type (habitation) was not statistically significant, there was moderate evidence that ancient human habitation sites have more culturally important plants than adjacent control sites. Site type had the third highest relative variable importance (RVI) value (0.7), after litter (0.71), and canopy cover and coarse woody debris, which both had an RVI of 1 (Figure 2a). There was also no significant interaction between site type and distance from the shore ($RV1 = 0.05$). However, culturally important plants were most abundant in the open shoreline of habitation sites but not on the shoreline of control sites (Figure 3a).

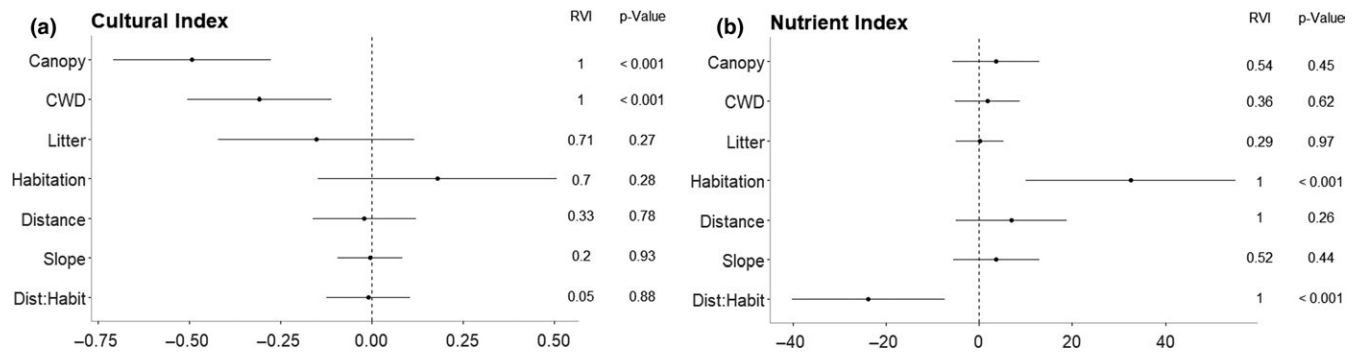


FIGURE 2 Model results for the cultural plant-use index (a) and the nutrient subsidy index (b). All continuous predictors have been standardized (Canopy: canopy cover; CWD: coarse woody debris cover; Litter: leaf litter cover; Habitation: habitation site type; Distance: distance from shoreline; Slope: average site slope; Dist:Habit: interaction between distance and site type). The RVI shows the relative variable importance in the full averaged model with standard deviations. If the standard deviation lines cross 0, there is weak evidence of that variable influencing the response value within the averaged model. The p-value shows statistical significance levels for each variable in the full averaged model

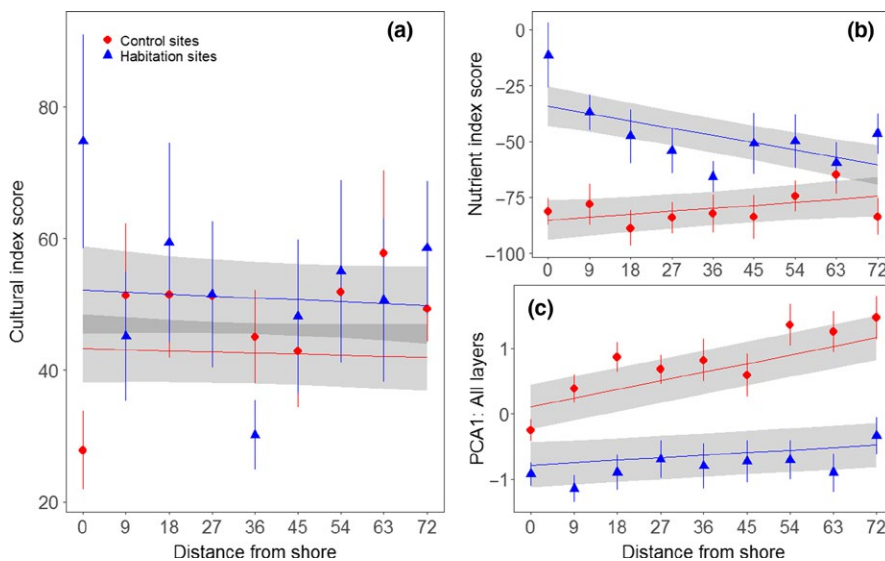


FIGURE 3 Modelled relationships between distance from shore and the cultural plant-use index score (a), nutrient subsidy index score (b) and the PCoA1 score for all layers (c). Lines represent model predictions with grey bands to show standard errors. Red points represent real mean values for control sites at each distance with standard error bars, while blue triangles represent real mean values for habitation sites at each distance with standard error bars. More positive scores of PCoA1 represent species mixes affiliated with drier and more nutrient-poor conditions

When measured at the level of belt transects, the legacy of cultural use was clearer. Seven species were found uniquely on the habitation sites. These include *Amelanchier alnifolia* (Saskatoon berry), *R. lacustre* (black gooseberry), *Cascara sagrada*, *Lonicera involucrata* (Richards.) Banks ex Spreng (black twinberry), *Rubus pedatus* Sm. (five-leaved bramble) *R. Ribes bracteosum* Dougl. Ex Hook (stink currant) and *R. parviflorus* (thimbleberry). The species indicated in bold are regionally rare. *Rhododendron groenlandicum* (labrador tea), *L. americanus* (skunk cabbage) and *Vaccinium ovalifolium* (oval-leaved blueberry) were present on a higher number of control sites than habitation sites. The other four species documented on the belt transects include: *M. fusca* (Pacific crab apple), *R. spectabilis* (salmonberry), *T. brevifolia* (Pacific yew) and *V. parvifolium* (red huckleberry). Overall, the assemblages of these 14 species were found to be significantly different (ANOSIM $R = 0.3$, $p = 0.003$) on the habitation sites compared to the control sites (Figure 4). The species that were most responsible for this difference were *V. parvifolium* (red huckleberry), *R. groenlandicum* and *R. parviflorus*. In combination, these

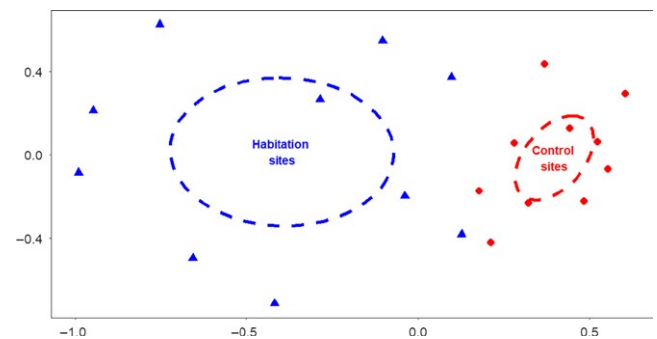


FIGURE 4 NMDS plot of belt transect results. The NMDS was performed on Bray-Curtis dissimilarities calculated using square-root transformed stem count data of culturally important species. Red points represent control sites, while blue triangles represent habitation sites. Dashed circles are centred on the compositional centroid of each type of site (control vs. habitation) and show the 95% confidence interval around the centroid. ANOSIM $R = 0.3$, $p = 0.003$, stress value = 0.19. Given the relatively high stress, these results should be interpreted with caution

three species contribute to approximately 50% of the dissimilarity between site types (Data S3).

Species richness ranged from 18 to 35 within the different layers of the understory vegetation (ground/herbaceous/shrub) on the habitation sites with a total species number of 75, and 12–34 on the control sites with a total species number of 70; overall 90 species were recorded. Table 1 provides an overview of the species richness, as well as the average species richness per quadrat at both habitation and control sites. Species richness was driven predominantly by environmental characteristics of each site, such as leaf litter, distance from shore and CWD (Figure 5a). Site type (habitation) had the fourth highest RVI (0.68) with a nonsignificant negative coefficient estimate.

The first PCoA axis for all layers explained 10% of the variation and was driven primarily by *G. shallon* (salal), *H. splendens* (step moss), *T. heterophylla* (Western hemlock) and *B. spicant* (deer fern). The species assemblage of PCoA1 may be driven by a combination of factors, including the moisture gradient, with some indicator species of moderately dry sites (e.g. false azalea, *Dicranum* sp., twinflower) having an opposite influence to species indicating fresh/very moist/wet sites (e.g. foamflower, clear moss). PCoA1 for ground, herbaceous and shrub layers explained 12%, 14% and 14% (respectively) of the variance in each dataset. The species that had opposing influences in the PCoA1 for all layers had the same signals when modelled as separate layers. Though site characteristics had the strongest relationships with each of the compositional axes, site type had a significant relationship with both the full compositions (all layers together). See Data S4 for more detailed PCoA and model results for each layer.

3.2 | Legacy of cultural nutrient subsidy to present-day plant communities and soils

Present-day plant communities in habitation sites have higher cover of nutrient-rich indicator plant species than control sites (Figure 2b). There were only two statistically significant variables in the averaged model that tested for the effect of nutrient subsidy: site type

($p = 0.005$, RVI = 1), which had a positive relationship with nutrient scores, and the negative interaction between site type and distance from shore ($p = 0.004$, RVI = 1). Both had relatively large effect sizes. At the habitation sites, the presence of plant species with high-nutrient requirements increases; this effect was found to decrease significantly with distance from shore (Figure 3B).

Most soil nutrients were significantly higher in the habitation sites than control sites, including B, Ca, Mn, Na, P, Zn, exchangeable Ca, effective cation exchange capacity (CEC), inorganic C, C:N ratio and pH (Figure 6). On average, the control sites were higher in exchangeable Al and exchangeable Fe. Habitation and control sites were not significantly different with regard to the organic matter content, the content of C, N, Cu, Fe, Na, S and exchangeable values for K, Mn, Mg and Na. The results from the soil samples can be seen in full in the Data S5.

4 | DISCUSSION

Despite these sites having been abandoned for over 125 years, we found persistent differences in the plant communities and soil nutrients on habitation sites. Both small-scale (1×1 m quadrat) and large-scale (belt transect) analyses revealed that plant communities reflected differences in marine subsidies associated with shell middens, cultural associations and overall community and ecological qualities. Other studies have documented elevated species richness related to the physical site alterations resulting from the presence of shell middens (Cook-Patton et al., 2014; Vanderplank, Mata, & Ezcurra, 2014), shifts in woody to more herbaceous plant communities (Cook-Patton et al., 2014) and elevated numbers of edible and culturally important plant species on habitation sites (Levi et al., 2018). Our results provide novel insight into the persistence of marine and cultural legacies shaping plant communities at time-scales infrequently considered.

Overall, we found the nutrient index to indicate a strong relationship with site type, where more species adapted to high-nutrient regimes were positively related to habitation sites. Not surprisingly, the

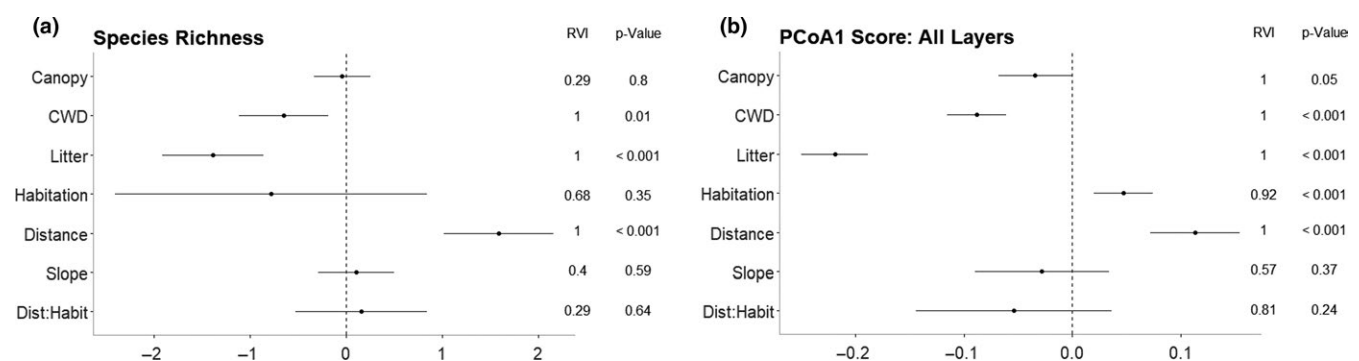


FIGURE 5 Model results for species richness (a) and the PCoA1 score for all layers (b). All continuous predictors have been standardized. The RVI shows the relative variable importance in the full averaged model with standard deviations. If the standard deviation lines cross 0, there is weak evidence of that variable influencing the response value within the averaged model. The p -value shows statistical significance levels for each variable in the full averaged model

TABLE 1 Average plot species richness (\pm SE) and total species richness at habitation and control sites, split by vegetation layer and with all layers in combination

Vegetation layer	Average species richness per m ² : habitation sites	Total species richness: habitation sites	Average species richness per m ² : control sites	Total species richness: control sites	Total species richness: all sites
All layers	9.23 \pm 0.2	75	10.9 \pm 0.2	70	90
Ground layer	4.40 \pm 0.12	22	5.03 \pm 0.11	24	27
Herb layer	2.61 \pm 0.1	35	3.36 \pm 0.11	34	44
Shrub layer	2.21 \pm 0.07	18	2.49 \pm 0.07	12	19

relationship was strongest near the marine–terrestrial interface, which was reflected in the significant interaction between distance from shore and site type. At the shoreline, intensive human activities such as shell midden accumulation would create the most concentrated marine nutrient sources. This suggests that the nutrients from these shoreline activities continue to shape the terrestrial plant community at this smaller scale. Marine nutrient pulses in similar systems have been shown to significantly alter plant communities (e.g. Green & Klinka, 1994), though here the signal was detected over a century after the activity has ceased.

The influence of shell middens was reflected in soil nutrient levels and soil properties at habitation versus control sites, as in another recent study in the same region (Trant et al., 2016). The pH levels may play an important role in influencing the availability of most elements, as well as CEC and soil biotic activity. Soils at habitation sites were much less acidic, and closer to neutral on average. Higher acidity generally results in lower microbial activity, and this can influence the cycling of N (Bardgett, 2005). Both of the site types have high C:N ratios, making N a limiting factor (immobilization of N is occurring more than mineralization). However, the C:N ratio is lower at the habitation sites than the control sites, which suggests the rates of mineralization are different at the two sites and there is less limitation of and likely competition for N on the habitation sites. This difference in potential availability of N may allow for the success of plant species which is otherwise N limited. This pattern of higher pH and lower C:N ratios at habitation is consistent with other studies (Cook-Patton et al., 2014; Sawbridge & Bell, 1972), though likely due to different site histories and contemporary disturbances, such as logging, strong vegetation legacies were not detected.

The cultural plant-use index, measuring the presence of culturally important species at a quadrat-scale, was most strongly related to abiotic conditions. The only two significant variables in the averaged model were coarse woody debris and canopy cover. With a greater canopy cover and increased coarse woody debris, the culturally important species decreased. Berry plants, which are important cultural species, and other cultivated species may in general be more successful with increased light availability and open ground. Many of the culturally important species, like berry plants, are good colonizers of disturbed sites and thus their presence could be the result of ecological rather than cultural drivers, though we do not have a way of disentangling these factors. Counter to our hypotheses, site type was not significantly related to the cultural plant-use index, and there was no significant relationship between the cultural plant-use index and distance to shore or the interaction between site type and distance. At the shoreline, however, there was a dramatic difference in the average cultural plant-use index score between site types (Figure 3a). Given that much of the human activity would have focused at the shoreline, allowing for the accumulation of midden material, cultivation of plant species may have occurred predominantly at that marine–terrestrial interface. Indeed, estuarine root gardens are an important component of human use of these sites (Mathews & Turner, 2017; Mathews, pers. comm.). Thus, the long time since habitation may have reduced the signal of site type in the cultural plant use index over most of the

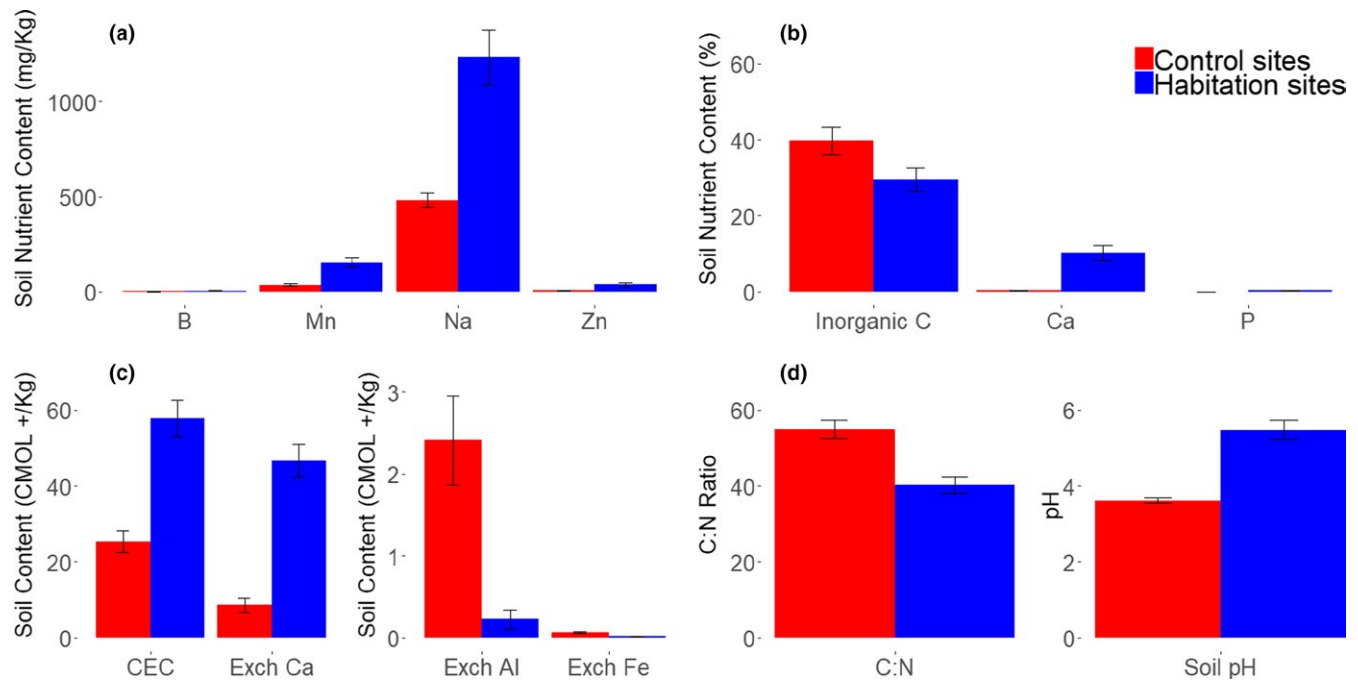


FIGURE 6 Soil sample average values for B, Mn, Zn, Na (a); Inorganic C, Ca, P (b); CEC, exchangeable Ca (c); exchangeable cations Al, and Fe (d); C:N ratio (e); and pH (f) with standard error bars from the means from all samples from both the habitation sites (blue) and control sites (red). B, Mn, Zn, Na, Inorganic C, Ca, P, exchangeable Ca, CEC and pH are all significantly higher on the habitation sites, and exchangeable aluminium (Exch Al), exchangeable iron (Exch Fe) and the C:N ratio are significantly higher on the control sites

transect, making it detectable only at that initial shoreline transect point. Alternatively, the species involved in the cultural index may simply not persist in high abundance at levels detectable within quadrats without continued management. Without human cultivation and management activities, some species may not be competitive and thus decline significantly on the landscape.

Although the site type was not significant with respect to the cultural plant-use index analysed using the 1×1 m quadrats, we found the community composition of the site types to be significantly different. The effects of habitation on community composition could be seen when all layers were analysed together using the PCoA. When analysed more deeply for species that drove full composition patterns at the quadrat-scale, two of the dominant species had high-cultural value (*T. heterophylla* and *G. shallon*; see Data S4 for individual PCoA results and species driving each canopy pattern). Yet, given that the cultural index at the quadrat-scale was not significantly related to habitation history across the full transect lengths, the combination of species and their loadings at the two site types suggest that for small-scale composition patterns, habitation influences could be reflective of nutrient and moisture legacies. Similar to nutrient index results, the PCoA (positive) scores for the control sites increased with greater distance from shore. The effect of distance to shore was not found in habitation sites, however, reinforcing the finding that the species at the habitation sites may be maintaining a unique assemblage beyond the suspected shell midden range.

The habitation signal was much stronger at the scale of the belt transect. As mentioned, belt transects detected seven species unique to the habitation sites: these species are regionally rare and

may represent the effects of historical human movement of culturally important species in the region. Based on archaeological reports and informal observations, we expected and found higher than usual densities of edible fruit-producing plant species. The larger scale of the belt transects was probably more appropriate than quadrat-scales to detect differences in shrub and large herbaceous species communities. From this we suggest that at the small scale, nutrients are driving cultural and compositional trends, but on broader scales (belt transects), human cultivation of key species is likely influencing vegetation patterns (Huston, 1999). Additionally, full composition of belt transects for habitation sites showed much larger variation than for control sites. The different assemblages of plant species on the different habitation sites included in the survey may reflect the different uses of these sites: some may have been primarily resource-gathering sites and may have been occupied seasonally when the fruit-producing species were harvested. The variety of these species occurring within these compact areas surveyed at the habitation sites suggests that they could be landscape legacies, remnants from one-time managed berry gardens. This finding was mirrored in the PCoA scores for individual layers, where variation was consistently higher in habitation sites than in the controls (Data S4). Though logistical constraints of remote island work limited the compositional suite captured by belt transects, the combination of key cultural species presence at the large scale and the significantly different community composition at the small scale strongly support the presence of a human habitation signal in modern plant communities.

Overall, the signal of the habitation site was greatest at the community level, rather than in the individual layers. When the species

were separated into the ground, herbaceous and shrub layers, the abiotic conditions were the primary determinants of composition. We also found that the species richness was lower on the habitation sites, though not significantly, which is similar to patterns documented in Amazonia by Levi et al. (2018) where differences were related to the use of specific plants and not just the species richness. Human preference towards certain species, and the disturbance patterns generated over long time periods could have provided a competitive advantage for some species and may have suppressed diversity (Brewer, 2011). Increased nutrient availability such as those found on habitation sites in this study could also shift competitive relationships and allow dominance of some species at the expense of others. Thus, occupation has likely left a detectable imprint on the landscape through a complex combination of nutrient shifts, altered drainage potential of the shell midden sites and general disturbance from human use over long time periods (e.g. Robertson, Crum, & Ellis, 1993).

Vegetation community differences found here must be interpreted with some caution. Habitation on the BC central coast has a long history, and most shoreline sites with certain physical characteristics (e.g. flat, sheltered, accessible by boat) would have undergone indigenous use at some point (such qualities are generally associated with habitation sites—see Pomeroy, 1980). Though controls were selected to mimic these attributes as closely as possible, we are unable to fully separate the physical site characteristics from the influence of historical habitation. Results from soil nutrient analyses suggest strong abiotic differences between control and habitation sites, but strong similarities within habitation sites. The combination of both abiotic, which may be less influenced by physical characteristics, and biotic differences on habitation sites gives strong support for our inference that human activity has led to persistent environmental patterns on the coast. However, cautious interpretation is needed given the constraints of this study.

Here we demonstrate that indigenous activities over millennia have left a legacy on the plant and soil structure of the landscape, despite the lack of management and occupation in recent history (i.e. in at least the last 125 years). This change of land use is due to colonization, which decimated the First Nation populations to a small percent of their original numbers, largely due to the spread of disease associated with European contact (Duff, 1969; Harkin, 1997). The habitation sites surveyed in this study have unique assemblages of culturally significant species, a vegetative community with higher nitrogen requirements, and a soil composition richer in nutrients than the control sites. The signal of long-term land use is strongest at the community level where it has the biggest impact. Our findings emphasize the important advances that can be made by considering both ecology and archaeology in interpreting forest community structure and landscape patterns (Briggs et al., 2006). Overall, the investigation of habitation sites can provide insight into past cultural practices, and a greater understanding of landscape legacies and how they are reflected in present-day ecology.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

J.A.F. completed all data collection and wrote the manuscript. N.A.S. conducted data analysis and wrote the manuscript. M.D.H. helped with study design, question formation, data analysis and gave essential feedback on all portions of the study. A.J.T. and B.M.S. helped with data collection, question formation, writing and gave essential feedback on all portions of the study. B.M.S. secured funding for all work. All authors gave final approval for publication.

DATA ACCESSIBILITY

The data used in this study are considered sensitive by local First Nations communities. The data will not be made available for public distribution due to concerns around revealing the locations and nature of culturally important sites in these regions. However, access to the data may be granted by request (to the corresponding author and B.M. Starzomski at starzom@uvic.ca), and with permission of engaged parties.

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SUPPORTING INFORMATION

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