Nutrient Subsidies in the Coastal Margin: Implications for Tree Species Richness and Understory Composition

by

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B.Sc., Oregon State University, 2015

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Supervisory Committee

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Abstract

The subsidized island biogeography hypothesis proposes that nutrient subsidies, those translocated from one ecosystem to another, can indirectly influence species richness on islands by directly increasing terrestrial productivity. However, the lack of a formal statistical model makes it difficult to assess the strength of the hypothesis. I created a formal subsidized island biogeography model to determine how nutrient subsidies, in addition to area and distance from mainland, influence tree species richness. My model showed that an increase in terrestrial nitrogen abundance results in a decrease of tree species richness. Soil and plant $\delta\ ^{15}N$ values were higher than expected and it is likely that nutrient subsidies from the marine environment are responsible for ^{15}N enrichment. However, the range of observed nitrogen abundance is similar to inland coastal-zone forests, indicating that islands are similarly nitrogen deprived and may not be receiving enough nutrient subsidies to alter productivity. Tree species decline may therefore be more strongly related to the environmental conditions leading to patterns of nitrogen abundance rather than the abundance of nitrogen itself.

Additionally, I proposed that bald eagles (*Haliaeetus leucocephalus*) are vectors of nutrient subsidies, depositing nutrient-rich guano at nest sites, which could alter soil chemistry and vegetation composition. In an exploratory study of seven nest sites, I found higher soil phosphorous at eagle nest sites relative to control sites (~ 33% higher). Phosphorous is a limiting nutrient in coastal temperate forests, additions help to alleviate chlorosis and slow growth especially when paired with nitrogen. Higher potassium concentration also occurred on eagle-inhabited islands but was not associated specifically with current nest sites, perhaps reflecting differential persistence of macronutrients in the soil. Despite expectations, soil δ^{15}N abundance was not statistically higher at eagle nest sites. Total soil nitrogen was also not statistically higher at eagle nest sites. There were no significant differences between vegetation composition at eagle nest sites and reference sites, but reference sites tended to be dominated by shrub species.

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Acknowledgments

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Chapter 1: General Introduction

The relationship between species richness and area is often referred to as one of ecology’s few general laws (Rosenzweig, 1995). The relationship can be modelled in multiple ways (Tjørve, 2003) but in general, the number of species plotted against sampling area yields a curve that first rises with a steep slope but gradually becomes nearly flat. The resultant species-area curve can be used to estimate species richness, and in this capacity it forms the foundation of the dynamic equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967). The MacArthur-Wilson model, hereafter referred to as the ‘classical island biogeography model’, predicts that island area and distance from mainland determine species richness by controlling the rates of immigration (species arriving on an island per unit time) and local extinction (species lost from an island per unit time). In this model, extinction rates should decrease as island size increases because the island has, for example, increased carrying capacity. Immigration rates should decline on islands farther from the mainland or species pool. Together, the rates of new species arrivals and local species extinctions determine species richness on an island.

The classical island biogeography model has spurred decades of study but it is simplistic and many observed patterns of species richness cannot be fully explained by the model (Case & Cody, 1987; Patiño et al., 2017). For example, small islands can deviate from the general species-area curve, demonstrating both higher and lower diversity than expected under the classical island biogeography model (Case & Cody, 1983; Morrison, 1997; Sfenthourakis & Triantis, 2009; Whitehead & Jones, 1969). Such discrepancies have been documented on the Midriff Islands in the Sea of Cortez, a region that has been used extensively to explore concepts of island biogeography (Case & Cody, 1983, 1987). On these islands, plant diversity is lower than expected on small islands but these small islands also tend to support seabird populations, which contribute large quantities of nutrient-rich guano to the terrestrial environment (Anderson & Polis, 1999; Case & Cody, 1987). In fact, nutrients from nesting seabirds, beach-cast marine algae, and marine carrion provide up to 770 times more nutritional energy and biomass to Sea of Cortez islands than primary productivity does (Polis & Hurd, 1995). Accumulation of these subsidies, which are nutrients translocated from another ecosystem, increased nitrogen and phosphorous concentration in soil and plants (up to 6-fold and 2.4-fold respectively), leading to consumer populations that were up to 13-fold more abundant than unsubsidized sites (Anderson & Polis, 1998, 1999; Polis & Hurd, 1995). These findings prompted questions of whether the addition of nutrient subsidies could be responsible for the observed discrepancies in species richness on small islands. The subsidized island biogeography hypothesis formalizes the above by proposing an amendment to the classic island biogeography model, in which nutrient subsidies indirectly influence species richness by directly influencing productivity through deposition of nutrients (Anderson & Wait, 2001).

The subsidized island biogeography hypothesis is based on the unimodal productivity-diversity relationship which suggests that as productivity (the rate that energy flows through a system, kj/m^2/year) increases so does species richness but as productivity continues to increase, species richness starts to decline (Rosenzweig, 1995).

Following this relationship, the subsidized island biogeography hypothesis predicts that external nutrient subsidies could either increase or decrease species richness by reducing or increasing extinction rates. Nutrient deprived environments are unable to sustain populations of some species, which then go locally extinct but an increase in available nutrient resources allows the would-be extinct populations to survive. However, large quantities of nutrient subsidies could trigger high extinction rates if certain species are better at competing for resources and become dominant in the system (Rosenzweig, 1995; Rosenzweig & Abramsky, 1993).

The subsidized island biogeography hypothesis draws on a significant body of literature, which recognizes that both biotic and abiotic vectors can transport nutrients from one system to another and documents the myriad effects that nutrient subsidies have on ecological processes (Leroux & Loreau, 2008; Polis et al., 2004; Spiller et al., 2010). Subsidy dynamics are especially pronounced at the marine-terrestrial interface because this edge is a highly dynamic ecotone where nutrients, materials, and organisms move across boundaries to form connections between two seemingly disparate ecosystems (Marczak et al., 2007; Moss, 2017; Spiller et al., 2010). For example, the deposition of nutrient-rich marine fog and sea spray can stimulate terrestrial primary productivity (Art et al., 1974; Templer et al., 2015; Weathers et al., 2000). Marine algae and carrion accumulate on beaches, support robust populations of arthropod detritivores, which in turn increases shoreline arthropod predator abundance 85 to 560 times that of inland populations (Polis & Hurd, 1996). Many animals, such as river otter (*Lontra canadensis*), brown bear (*Ursus arctos*), and seabirds, also cross the marine-terrestrial boundary to feed in the productive intertidal or near-shore waters (Ben-David et al., 1998; Hobson et al., 1994; Smith & Partridge, 2004). These species then deposit nutrient-rich excreta or prey remains on land, which increase concentrations of nitrogen, phosphorous, and other macronutrients important for terrestrial primary productivity (Ben-David et al., 1998; Carlton & Hodder, 2003; Hilderbrand et al., 1999; Sekercioglu, 2006).

Despite being rooted in classical island biogeography theory and a deep body of subsidy literature, attempts to test the subsidized island biogeography hypothesis suffer from the lack of a single model demonstrating how island area, distance from mainland and subsidies influence species richness (Barrett et al., 2003). The subsidized island biogeography hypothesis was developed on islands in the Sea of Cortez, a low productivity, arid terrestrial system where ecological impacts of subsidies are stark (Polis & Hurd, 1996), but rarely has the hypothesis been tested outside of the Sea of Cortez system (but see Fitzpatrick, 2018). It is unclear whether predictions will apply to complex, highly productive ecosystems where multiple subsidy vectors, environmental processes, and inherent spatial heterogeneity complicate the connection between subsidies, primary productivity, and species richness (Bedard-Haughn et al., 2003; Marczak et al., 2007; Polis et al., 1997; Robinson, 2001).

The second chapter of this thesis presents a formal statistical subsidized island biogeography model based on the species-area relationship. The species-area relationship assumes that the rate at which new species are found is attributable to the ratio of some function of the number species to the area in which species are sampled. Derivations of this framework yield several mathematical models (He & Legendre, 1996), namely the logistic, power, and exponential models, each of which have proven useful for understanding patterns of species richness (Tjørve, 2003). As the basis of my subsidized island biogeography model, I chose to use the power function, which takes the form:

$$S = CArea^z \tag{1}$$

when species richness is assumed to equal zero when area equals zero (He & Legendre, 1996). In this form, C and z are constants that shape and scale the species-area curve. Additional parameters and interaction between parameters influence shape and position of the species-area curve along y-axis, making it useful for modifying to suit predictions of subsidized island biogeography. My proposed model offers several advantages over previously used methods. Piecewise regression techniques are often used to detect differences in species richness between small and large islands (Barrett et al., 2003; Lomolino & Weiser, 2001) but my model accommodates subsidized island biogeography predictions that nutrient subsidies could increase or decrease species richness across all islands, or could have interactive effects with area or distance from mainland. Rather than categorizing sites according to subsidy presence or absence, my modelling approach allows richness to respond to a gradient of subsidy inputs. Finally, this modelling approach yields estimates of the subsidy effect with confidence intervals whereas previous studies infer effects of subsidies or distance from mainland by interpreting patterns of regression residuals (Barrett et al., 2003; Lomolino, 2000).

I applied my proposed model in a complex ecosystem, using tree species data from coastal islands in the North American temperate rainforest and terrestrial nitrogen abundance as a proxy for a gradient of nutrient subsidies. Temperate forests are nitrogen limited (Elser et al., 2007), so high nitrogen abundance on islands may indicate the presence of subsidies. However, patterns of terrestrial nitrogen should be interpreted with caution because environmental conditions such as terrain slope and carbon-to-nitrogen ratios can significantly alter nitrogen abundance across a landscape (Attiwill & Adams, 1993; Binkley & Fisher, 2012; Michener & Lajtha, 2008). Recognizing these limitations, I explore how patterns of total soil nitrogen, soil and plant nitrogen isotope abundance ($\delta^{15}N$), and foliar enrichment factor are influenced by environmental conditions and use those relationships to inform interpretation of tree species richness patterns.

Nutrient subsidies are transported by a variety of abiotic or biotic vectors, and in Chapter 3 I explore whether bald eagles (*Haliaeetus leucocephalus*) can serve as nutrient links between the ocean and land. Nutrient-rich guano and prey remains can induce significant ecological changes in seabird colonies such as altered soil chemistry, increased primary productivity, and modified consumer dynamics (Barrett et al., 2005; Sánchez-Piñero & Polis, 2000; Wainright et al., 1998; Wait et al., 2005). Bald eagles may have a similar effect as seabirds because their diet is primarily marine-based in coastal areas, they nest and roost on land, and are abundant along the Pacific coast of North America (Anthony et al., 1982; Robards & King, 1966; Stalmaster & Gessaman, 1984). However, unlike seabirds, bald eagles are solitary nesters and therefore guano and prey remains are likely spatially diffuse at the landscape scale and accumulate at a slower rate than in seabird colonies. I proposed that bald eagles are vectors of diffuse, avian-mediated subsidies and examined whether those nutrients from guano and prey remains alter soil chemistry and terrestrial plant communities at the base of nest trees. I predicted that soil sampled at eagle nest trees would differ from reference sites in pH and concentration of phosphorus, potassium, total carbon, total nitrogen, and nitrogen isotope abundance ($\delta^{15}N$). I also expected the plant community under a nest tree to differ from reference sites in species and functional composition, particularly a reduction in woody shrubs and an increase in species tolerant of nutrient enriched soil.

The research presented here was part of a large scientific collaboration called the 100 Islands project, which studied the ecological effects of nutrient exchange at marine-terrestrial interface across several taxa. Multiple principal investigators, graduate students and post-doctoral employees collectively generated data on patterns of species richness for invertebrates, plants, birds, and small mammals on islands along the Central Coast of British Columbia, Canada. My second thesis chapter relied on data collected by Fitzpatrick (2018) as part of the 100 Islands project (Davidson, 2017; Wickham, 2017; Obrist, D., unpublished data; Ernst, C., unpublished data). I collected data for the third chapter but utilized islands that were included in the 100 Islands sampling effort.

Chapter 2: Subsidies in the coastal margin: tree species richness responses to nitrogen and environmental conditions

Abstract

The subsidized island biogeography hypothesis questions whether nutrient subsidies indirectly influence species richness on islands. However, attempts to test the hypothesis suffer from the lack of a formal model demonstrating how area, distance from mainland, and nutrient subsidies influence species richness. The subsidized island biogeography hypothesis was developed in simple ecosystems with low terrestrial productivity and it is unclear whether the predictions apply in complex, relatively productive systems. I created a formal subsidized island biogeography model to determine how terrestrial nitrogen abundance, in addition to area and distance from mainland, influences tree species richness in a complex ecosystem. I found that increased terrestrial nitrogen results in decreased tree species richness but nutrient abundance did not disproportionately affect tree species richness on small islands. Nitrogen isotope values were higher than expected, so subsidies from the marine environment are likely being deposited on land. However, total soil nitrogen on the sampled islands was comparable to nitrogen deficient inland coastal-zone forests, so the quantity of nitrogen subsidies may be minor. Given the limited amount of subsidies and relatively low total nitrogen, tree species richness is probably declining in response to environmental conditions leading to increased nitrogen abundance rather than directly to nitrogen inputs. Unique environmental conditions shaped patterns of different measures of nitrogen, underscoring the importance of carefully considering metrics of nutrient subsidies and interpreting their potential effect on species richness patterns.

Introduction

MacArthur and Wilson’s dynamic equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967) has spurred decades of study but many observed patterns of species richness cannot be fully explained by the model (Case & Cody, 1987; Patiño et al., 2017). For example, small islands can deviate from the predicted species-area curve, demonstrating both higher and lower diversity than expected under the MacArthur-Wilson model (Case & Cody, 1983; Morrison, 1997; Sfenthourakis & Triantis, 2009; Whitehead & Jones, 1969). Islands in the Sea of Cortez display small island discrepancies and the accumulation of nutrient subsidies has been proposed as the mechanism driving observed discrepancies (Anderson & Wait, 2001). Subsidies are resources translocated from one habitat to a second habitat, which increase population productivity in the recipient ecosystem (Polis et al., 1997) and include beach-cast marine algae (Colombini et al., 2003; Wickham, 2017), guano from seabirds (Ellis, 2005), and excrement or prey remains from maritime animals (Carlton & Hodder, 2003). Subsidies from nesting seabirds, beach-cast marine algae, and marine carrion increased soil and plant nitrogen and phosphorous concentrations on Sea of Cortez islands up to 6-fold and 2.4-fold respectively, and increased consumer populations up to 13-fold compared to unsubsidized sites (Anderson & Polis, 1998, 1999; Polis & Hurd, 1995).

The above observations led to the development of the subsidized island biogeography hypothesis, which questions whether externally derived nutrients could explain species richness discrepancies observed on small islands (Anderson & Wait, 2001). The foundation of the subsidized island biogeography hypothesis is the MacArthur-Wilson model (hereafter referred to as the ‘classical island biogeography model'), which predicts that island area and distance from mainland determine species richness by controlling the rates of immigration (species arriving on an island per unit time) and local extinction (species lost from an island per unit time). Under the classical island biogeography model, extinction rates should decrease as island size increases because of increased carrying capacity, and immigration rates should decline on islands farther from the mainland or species pool.

The subsidized island biogeography hypothesis amends the classical model by suggesting that external nutrient subsidies can increase or decrease species richness by altering extinction rates (Anderson & Wait, 2001). This prediction is based on the unimodal productivity-diversity relationship which suggests that as productivity increases (the rate that energy flows through a system; kj/m^2/year) so does species richness but as productivity continues to increase, species richness starts to decline (Rosenzweig, 1995). Nutrient deprived environments are unable to sustain populations of some species, which then go locally extinct, but an increase in available nutrient resources allows the would-be extinct populations to survive. However, large quantities of nutrient subsidies could trigger high extinction rates if certain species are better at competing for resources and become dominant in the system (Rosenzweig, 1995; Rosenzweig & Abramsky, 1993). Few attempts have been made to test the subsidized island biogeography hypothesis and what studies exist suffer from the lack of a cohesive statistical model (Barrett et al., 2003). In this paper, I present a subsidized island biogeography model to understand how island area, distance from mainland and subsidies influence species richness. This model was constructed to accommodate predictions from the hypothesis wherein nutrient subsidies may disproportionately influence richness on small or isolated islands (Anderson & Wait, 2001).

The subsidized island biogeography hypothesis has rarely been tested outside of the Sea of Cortez system (but see Fitzpatrick, 2018). It is unclear whether predictions will apply to complex ecosystems where multiple subsidy vectors, environmental processes, and inherent spatial heterogeneity complicate the connection between subsidies, primary productivity, and species richness (Bedard-Haughn et al., 2003; Marczak et al., 2007; Polis et al., 1997; Robinson, 2001). On Sea of Cortez islands, nutrient subsidies from nesting seabirds, beach-cast marine algae, and marine carrion provide up to 770 times more nutritional energy and biomass to islands than primary productivity does (Polis & Hurd, 1995). On those islands, primary productivity is extremely low and terrestrial food webs are maintained by the constant input of the marine-derived subsidies, making them ‘simple ecosystems’ in the absence of subsidies (Polis et al., 1997). A disparity between subsidy and *in situ* resource abundance increases the magnitude of ecological response to subsidies (Marczak et al., 2007), so a clear connection between subsidy input and terrestrial outcomes is possible in the Sea of Cortez. In contrast, complex ecosystems are those whose complexity exists in spite of subsidies. Quantifying the ecological effects of subsidies becomes difficult in complex ecosystems because increased habitat heterogeneity, high productivity, and edaphic characteristics mediate retention and assimilation of subsidies but also regulate patterns of terrestrial nitrogen abundance whether or not subsidies are present (Attiwill & Adams, 1993; Dawson et al., 2002; Marczak et al., 2007). For example, soil conditions and topography can stimulate both nitrification and denitrification can ultimately reduce total soil nitrogen but enriches remaining nitrogen in stable nitrogen isotopes (Attiwill & Adams, 1993; Högberg, 1997) (Appendix 1). However, nutrient subsidies can also enrich soil in stable nitrogen isotopes and depending on the rate of plant uptake or the physical nature of the subsidy, total soil nitrogen can increase or remain unaffected (Appendix 1). Furthermore, when multiple subsidies operate simultaneously in a recipient ecosystem and differ in physical properties, nitrogen content, and nitrogen stable isotope abundance, the terrestrial nitrogen pool becomes an average of all nitrogen sources weighted by their availabilities (Robinson, 2001). In simple ecosystems, measures of total nitrogen or nitrogen isotope abundance are commonly used to show that a subsidy has been assimilated into a system (Anderson & Polis, 1999; Lindeboom, 1984; Polis et al., 1997). In complex systems, soil and plant nitrogen measures no longer directly match inputs from a single source (Craine et al., 2009). For example, salmon carcasses provide a substantial source of nitrogen to riparian vegetation and terrestrial invertebrate populations in temperate forests (Hocking & Reynolds, 2011; Hocking et al., 2009). Bears forage on salmon in accessible riparian areas, changing the spatial distribution of salmon subsidies but also depositing excrement subsidies that enrich riparian zones in stable isotopes and stimulate soil chemistry processes that further alter nitrogen abundance (Helfield & Naiman, 2006; Levi et al., 2013). The net result is that soil and vegetation are enriched in nitrogen isotopes but do not directly match levels of salmon carcass enrichment (Bartz & Naiman, 2005). These complexities make it difficult to disentangle the effects of terrestrial nitrogen processes from those of subsidies (Bedard-Haughn et al., 2003; Robinson, 2001). Therefore, the common practice of focusing on a single vector of subsidies and assuming that differences in soil or plant nitrogen concentration demonstrates assimilation of that subsidy is not reliable in complex systems (Bedard-Haughn et al., 2003; Polis et al., 1997, 2004).

It is therefore necessary to quantify terrestrial nitrogen abundance using several different measures and understand how environmental conditions influence nitrogen abundance before assuming that nitrogen patterns are solely the result of subsidy input (Bedard-Haughn et al., 2003; Högberg, 1997; Pinay et al., 2003). Using this approach, I questioned how does terrestrial nitrogen abundance, area, and distance from mainland influence tree species richness in a complex ecosystem? I explored how physical conditions alter patterns of total soil nitrogen, soil and plant nitrogen isotope abundance ($\delta\ ^{15}N$), and foliar enrichment factor ($\delta\ ^{15}N_{foliar}$ - $\delta\ ^{15}N_{soil}$) to better understand the mechanisms leading to nitrogen abundance and used those relationships to inform interpretation of species richness patterns.

Methods

Study area

Data used for this analysis come from 91 remote islands in the northeast Pacific Ocean along British Columbia’s Central Coast (Canada) (Appendix 3, Figure 8). The islands are situated in the temperate rainforest ecosystem (Coastal Western Hemlock, Very Wet Hypermaritime subzone, central variant) (Banner, 1993). Heavy fog and rain occur all year, and during the stormy season (October to March) southeasterly winds can reach over 138 kilometres per hour (Hakai Institute, 2017). Moderate annual temperature (8.2 °C ± 0.9) and heavy precipitation (2,951 mm ± 657) results in slow decomposition of organic matter and soils that are nutrient deprived, poorly drained, acidic, and primarily humus (Banner et al., 2005; Kranabetter et al., 2003). Primary productivity is controlled by subtle changes in drainage and nitrogen and phosphorous limitation (Banner et al., 2005; Blevins et al., 2006; Kranabetter et al., 2013; Sajedi et al., 2012). The remote islands included in this study experience very little modern anthropogenic, terrestrial disturbance. Islands sampled in this study were selected as part of a larger program studying subsidy exchange at the marine-terrestrial interface, and details of the selection process can be found in Appendix 2.

Field measurements

Data were collected May to July from 2015 to 2017 as part of another study to determine whether beach-cast marine algae influenced species richness across multiple taxa (Appendix 2). A detailed description of study design can be found in Fitzpatrick (2018) but a brief description of methods is provided below. Sampling was restricted to the coastal margin of an island, the zone beginning at shoreline vegetation and extending 40 m inland. Data were collected along four transects anchored at the cardinal extremes (north, south, east, west) of each island and extended 40 m inland. Tree species identity was determined for a maximum of four trees at 10 m intervals along each transect according to the point-centered quarter method (Cottam & Curtis, 1956; Mitchell, 2010). In this method, the transect and an imaginary line running perpendicular to the transect form quadrants at each sampling point. The species identity of the tree over 10 cm at breast height (1.3 m) closest to the center point in each quadrant was recorded. If no tree was present (e.g. quadrant is at the vegetated edge of an island and extends into the ocean), a zero was recorded. This method biases measurements toward the most common species. In this study, species richness is the total number of species identified in the coastal margin area of each island.

Soils, foliage, and environmental conditions were also measured along the transects (Fitzpatrick, 2018). Data were pooled to yield island-scale average values. Soil samples were used to quantify total carbon, total nitrogen and $\delta\,^{15}$N. Foliar samples from two of the dominant understory species, salal (*Gaultheria shallon*) and false lily-of-the-valley (*Maianthemum dilatatum*), were collected at the beginning and end of each transect. Foliar samples were used to quantify foliar $\delta\,^{15}$N. Trees were assumed to display similar foliar $\delta\,^{15}$N patterns as understory vegetation.

Total soil carbon, total soil nitrogen, soil δ ^{15}N, foliar δ ^{15}N, foliar enrichment factor

Soil and plant stable isotope values, expressed as $\delta\,^{15}$N, are the deviation per mill (‰) from the atmospheric standard (Paul et al., 2007). Foliar $\delta\,^{15}$N values of *G. shallon* and *M. dilatatum* followed a near 1:1 relationship (Appendix 3, Figure 9), so I pooled foliar samples of these two species to derive an average, island-level foliar $\delta\,^{15}$N value. I also derived a foliar enrichment factor ($\delta\,^{15}\mathrm{N}_{\mathrm{foliar}} - \delta\,^{15}\mathrm{N}_{\mathrm{soil}}$) as a proxy for the amount of nitrogen available to plants on each island (Emmett et al., 1998; Michener & Lajtha, 2008) (Appendix 1). Soil and foliar samples were processed at the BC Ministry of Forests, Lands, and Natural Resource Operations' analytical laboratory and the Pacific Forestry Center, both located in Victoria, British Columbia, Canada.

Biogeographical predictors

Biogeographical variables were derived as part of a larger study on subsidy exchange at the marine-terrestrial interface, details can be found in Appendix 2. Table 1 provides a brief description of biogeographical variables used.

Table 1 Biogeographical variables were used to model species richness as well as nitrogen responses to environmental variables. Definitions and details of their derivation can be found in Appendix 2.

Variable	**Unit**	**Description**
Coastal margin area	Hectares	Shoreline vegetation to 40 m inland
Distance to mainland	Kilometres	Shortest linear distance over water
Shore-zone exposure	None	Values 1-6 are very protected to very exposed
Coverage by neighboring landmass	Percent	Amount out of 360 degrees around an island that is occupied by neighboring islands
Shoreline convolution	None	Perimeter to area ratio corrected for island size

Statistical analysis

Subsidized island biogeography model

Numerous mathematical functions have been used to describe the species-area curve (Tjørve, 2003). The subsidized island biogeography hypothesis presents scenarios under which both the shape and/or scaling of the species-area curve could change with added nutrients (Anderson & Wait, 2001). I chose to use the power function as the basis for my subsidized island biogeography model because it has performed well across many studies and is amenable to additional parameters which shape and scale the curve (Dengler, 2009; Tjørve, 2003). I added a distance to mainland parameter and a subsidy parameter to the power function to create a subsidized island biogeography model (Eq. 1) which can be modified to include interactions (Eq. 2):

$$\log Richness \sim \beta_0 + \beta_A \log Area + \beta_D Distance + \beta_S Subsidy \tag{1}$$

$$\log Richness \sim \beta_0 + \beta_A \log Area \left(\beta_A + \beta_{AS} Subsidy\right) + \beta_D Distance + \beta_S Subsidy \tag{2}$$

To determine the strength of the subsidized island biogeography hypothesis, I constructed a suite of models to determine whether area alone, area and distance from mainland, or area, distance from mainland and nitrogen abundance best predicted species richness. This suite of models included all possible combinations of associated predictor variables except models that would include different but related measures of the same variable. For example, both total soil nitrogen and foliar enrichment factor were considered as measures of nitrogen abundance to determine if one exhibited a stronger effect on species richness than the other did. A model only included one nitrogen measure at a time but each nitrogen measure was incorporated into the suite of possible combinations of associated predictor variables.

This modelling approach offers several advantages over previously used methods. Piecewise regression techniques are often used to detect differences in species richness between small and large islands (Barrett et al., 2003; Lomolino & Weiser, 2001) but my model accommodates the subsidized island biogeography prediction that nutrient subsidies could have interactive effects with area or distance from mainland while also allowing nutrients to influence richness independently. It also allows richness to respond according to a gradient of nutrient input rather than relying on categorization of sites by subsidy presence or absence. Finally, my modelling approach yields estimates of the subsidy effect with confidence intervals whereas previous studies infer effects of different variables by interpreting patterns of regression residuals (Barrett et al., 2003; Lomolino, 2000).

Tree species richness was modelled using generalized linear mixed effects with the function glmer() from the R package lme4 (Bates et al., 2015). A Poisson distribution with a log link was selected because variable values were discrete and greater than zero. Due to the sampling method used, tree species richness data did not include zeros. However, given the sample size and mean response, the Poisson distribution is expected to produce very few zeros. Given these conditions, I decided that assuming a Poisson distribution rather than a zero-truncated Poisson was reasonable.

Nitrogen response to environmental variables

Total soil nitrogen and soil δ^{15}N responses were modelled using generalized linear mixed effects with the function glmer() from the R package lme4 (Bates et al., 2015). A gamma error distribution with a log link was selected because predictor variables were continuous and greater than zero. Predictor variables included coastal margin area, terrain slope, shoreline convolution, coverage by neighboring land, and shore-zone exposure. These variables were selected because measures of area are known to affect nutrient concentration on these islands (Fitzpatrick, 2018), terrain slope can stimulate soil and plant nitrogen cycling processes (Appendix 1), and coverage by neighboring land and shore-zone exposure are different metrics of exposure to wind and wave action (Appendix 1 & 2). Foliar δ^{15}N and foliar enrichment factor responses were modelled using linear mixed effects models run with the function lmer() from the R package lme4 (Bates et al., 2015) because variable values were both positive and negative. Predictor variables included coastal margin area, terrain slope, total soil nitrogen, shoreline convolution, coverage by neighboring landmass, and shore-zone exposure. Total soil nitrogen was included because its relationship to foliar δ^{15}N and enrichment factor provides information whether soil nitrogen is readily available to plants (Appendix 1). For each nitrogen response, I constructed a suite of models that included all possible combinations of associated predictor variables. Just as with the subsidized island biogeography modelling approach, an individual model only included one exposure measure at a time.

Previous studies conducted on the same islands demonstrated that island area had a strong effect on soil δ^{15}N (Fitzpatrick, 2018), so area was included in all nitrogen-environmental conditions models. Soil drainage, for which I used slope as a proxy, has a significant effect on nutrient dynamics in this ecosystem (Appendix 1). Consequently, I included slope in all nitrogen-environmental conditions models.

General modelling approach

Island 'node' was used as the random effect in all models to account for regional spatial distribution of islands. Collinearity among predictors was tested by calculating Pearson's correlation values using the R package psych (Revelle, 2017). All model residuals were examined for uniformity and significant outliers. Statistical analyses were conducted using R software, version 3.4.1 (R Core Team, 2017).

For each modelled response, I used the Akaike Information Criterion (AIC) to identify the most parsimonious models. I then selected the 95 % confidence subset of models (0.95 cumulative AIC weight) for model averaging (Burnham & Anderson, 2003). The function aictab() from the R package AICcmodavg (Mazerolle, 2013) was used to generate model Δ AIC$_i$ values for each model and the function modavgpred() from the same package was used with a response link to generate model-averaged parameter predictions and 95 % confidence intervals. Model-averaged predictions were generated from the entire 95 % candidate set and confidence intervals were derived on the scale of the response variable. All models were run using Maximum Likelihood (ML) estimation for model comparison but linear mixed effects models (foliar δ^{15}N and foliar enrichment factor responses) were rerun using Restricted Maximum Likelihood (RML) once the 95 % confidence set of models (0.95 cumulative AIC weight) were selected

(Bolker, 2008). Model order in the 95 % confidence set did not change when RML was used.

Results

General nitrogen patterns

Raw data values for all soil, foliar and biogeographic variables can be found in Table 2. Total soil nitrogen values (0.9 to 2.2 %) were similar to inland coastal-zone forests (0.7 to 3.8 %) but sampled islands had a higher range of soil $\delta\ ^{15}$N values (+0.4 to +12.6 ‰) than inland coastal-zone forests (-2.9 to +6 ‰) (Chang & Preston, 2000; Chang et al., 1996; Prescott et al., 1993; Prescott et al., 2000; Quesnel & Lavkulich, 1980). Inland coastal-zone forests are the same forest site type as this study location (Coastal Western Hemlock, Very Wet Hypermaritime subzone, central variant; Banner, 1993) but are not located at the marine-terrestrial interface. This reduces the likelihood that they are receiving nutrient subsidies from the marine environment. Foliar $\delta\ ^{15}$N values ranged from -5.10 to +11.52 ‰ which is higher than observations for salal foliage (*G. shallon*) from inland coastal-zone forests (-2.5 to +6 ‰) (Chang & Handley, 2000).

The difference between foliar and soil $\delta\ ^{15}$N values decreased as total soil nitrogen increased (Figure 1). Islands with the highest level of total soil nitrogen were also those with net mineralization potential (Figure 1). Carbon-to-nitrogen ratios (C:N), which determine net mineralization potential on regional coastal-zone forests (Prescott et al., 2000), were highly variable on smaller islands but larger islands (coastal margin area > 5 ha) tended to have C:N ratios near 39 (Appendix 3, Figure 10).

Table 2 Observed range, mean and standard deviation of island-level biogeographical and nutrient variables. Nutrient values are averages from multiple samples that were pooled to yield an average value per island. Data were collected on 91 islands. Soil C:N = total carbon-to-total nitrogen ratio.

Variable	**Unit**	**Range**	**Mean (SD)**
Coastal margin area	Hectares	0.01 – 23.56	2.73 (4.37)
Total island area	Hectares	0.01 – 288.04	14.56 (41.72)
Distance to mainland	Kilometres	0.30 – 10.65	3.9 (2.6)
Shoreline convolution		1.0 – 4.27	1.98 (0.65)
Coverage by landmass	Percent (%)	0 – 84.72	28.3 (19.57)
Soil C:N ratio		25.17 – 53.48	38.13 (5.19)
Total soil carbon	Percent (%)	40.24 – 58.67	53.22 (3.79)
Total soil nitrogen	Percent (%)	0.91 – 2.23	1.47 (0.25)
Soil $\delta\ ^{15}$N	Per mill (‰)	0.43 – 12.62	5.95 (3.22)
Foliar $\delta\ ^{15}$N	Per mill (‰)	-5.10 – 11.52	2.58 (4.46)
Foliar enrichment factor		-7.54 – 1.48	-3.37 (1.86)

Subsidized island biogeography model

Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*) were the dominant tree species on study islands (Appendix 3, Table 5). Ten species were observed but the maximum number of species on an island was eight. No single model best described tree species richness trends and foliar enrichment models did not perform better than those including total soil nitrogen (Appendix 3, Table 6). Model averaging across the 95 % confidence set shows that area

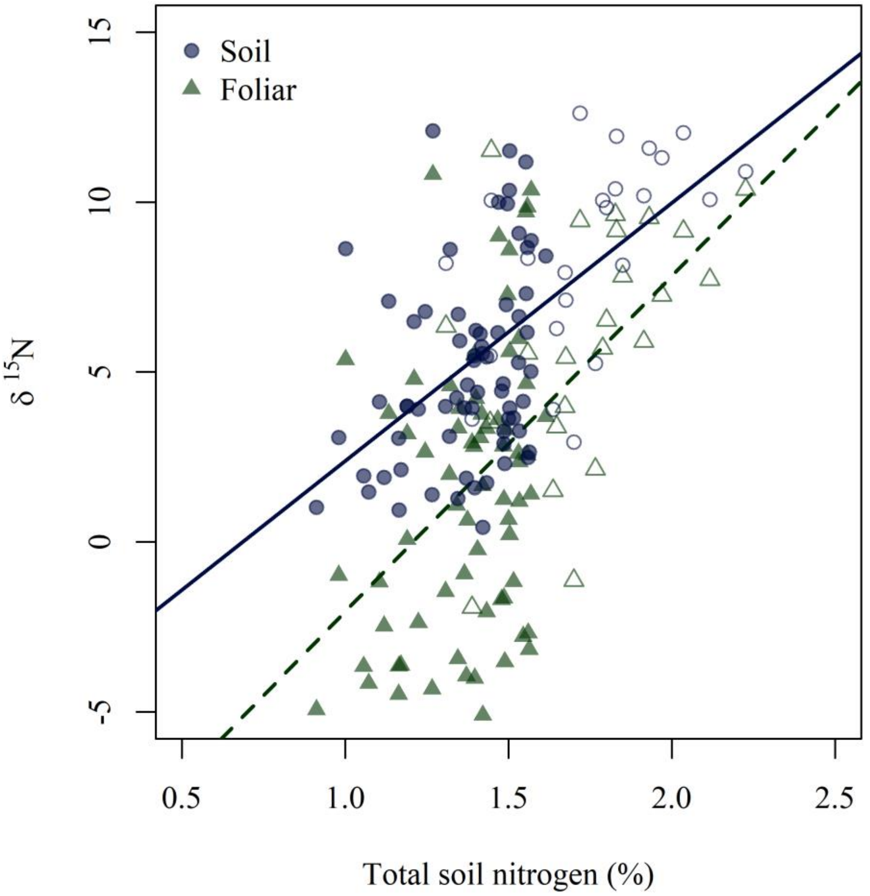

Figure 1 Soil and foliar $\delta\ ^{15}$N values (circles and triangles) increase with total soil nitrogen. As total soil nitrogen increases, the difference between soil and foliar $\delta\ ^{15}$N decreases which suggests that abundance of inorganic nitrogen is increasing. Islands with the highest total soil nitrogen are also those with the potential for net mineralization (open shapes), determined as those with soil C:N ratios less than 35. Mineralization yields inorganic nitrogen (Appendix 1). Elevated $\delta\ ^{15}$N values suggest that at least a portion of nitrogen comes from sources enriched in ^{15}N but the process of mineralization can further enrich soil. Regression lines were used to emphasize relationships between variables.

was a strong predictor of species richness, as is predicted by classical island biogeography (Figure 2). Distance from mainland had a negative relationship with species richness (Figure 2), suggesting that immigration rates decline with distance. Area and distance from mainland were included in every model, therefore parameter weights are equivalent to the cumulative AIC model weight (0.95). My model shows that species richness does not decline with total soil nitrogen (parameter weight 0.21) but shows a minimal decline with foliar enrichment factor (parameter weight 0.50) (Figure 2). The random effect ‘node’ explained very little additional variation for any model (variance ~ 0).

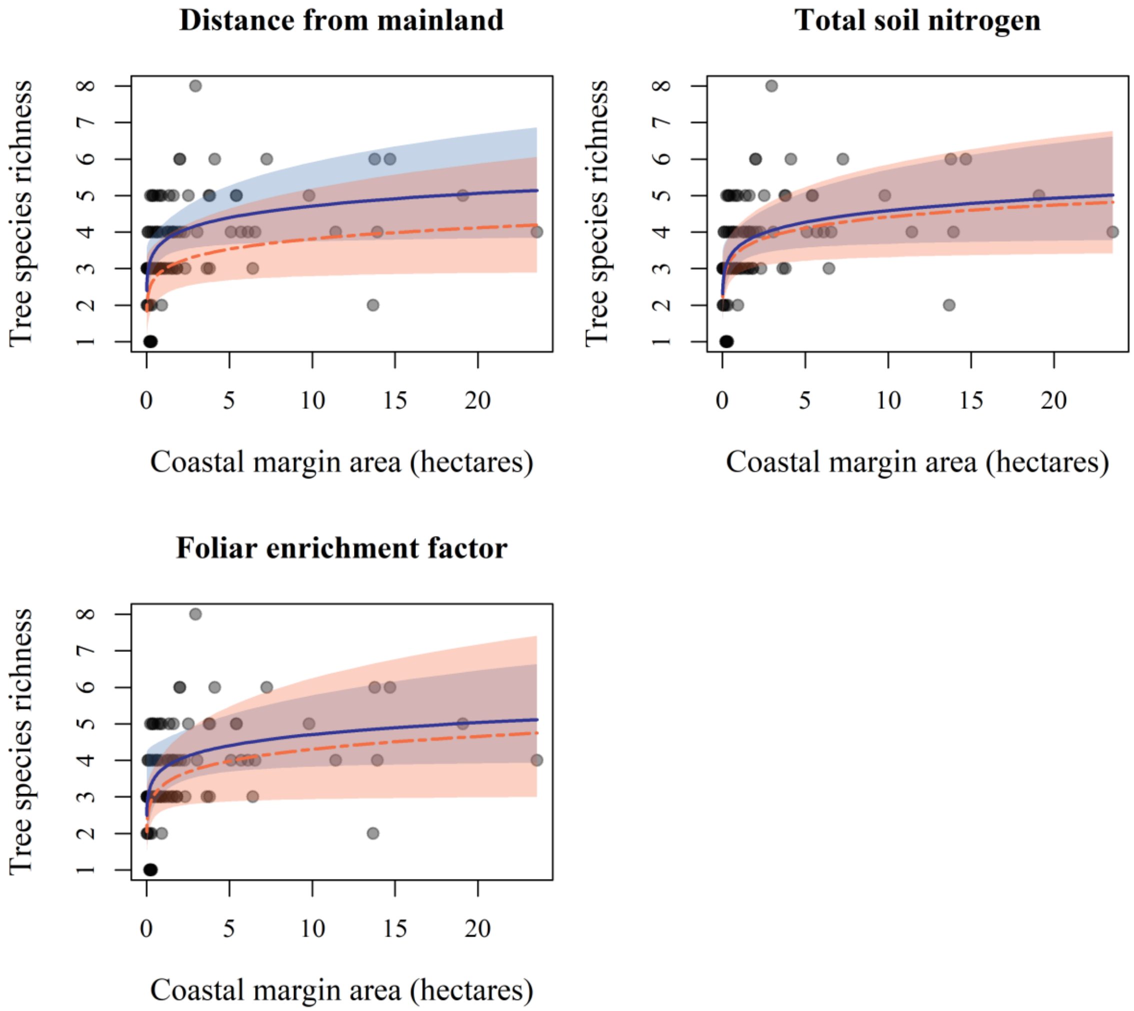

Figure 2 Species richness increased with area, as shown in each of the above plots. Averaged model predictions show that distance from mainland shifts the species-area curve along the y-axis (top left plot). The dashed line in the distance plot represents averaged model predictions for islands 4.5 km from the mainland (third quartile value of observed distances). The solid line is predictions for islands 2.6 km from mainland (first quartile value of observed distances). Total soil nitrogen does not affect species richness (top right plot); the solid line is the prediction for the first quartile value while the dashed line is a prediction for the third quartile value. An increase in foliar enrichment factor results in a slight decline of species richness (bottom left plot). The solid line in the foliar enrichment plot is a prediction for islands with -4.7 ‰ foliar enrichment factor (first quartile value) while the dashed line is a prediction for islands with -2.0 ‰ foliar enrichment factor (third quartile value). The subsidized island biogeography model illustrates how area, distance and nitrogen abundance alter the species-area curve, although the effect for islands in this study is marginal given that confidence intervals overlap. Points are raw data values, confidence intervals represent a 95 % confidence level.

Environmental conditions and nitrogen abundance

Model averaging across the 95 % confidence set shows that as expected, coastal margin area was a strong predictor of total soil nitrogen, soil $\delta\ ^{15}N$, foliar $\delta\ ^{15}N$, and foliar enrichment factor ($\delta\ ^{15}N_{foliar} - \delta\ ^{15}N_{soil}$) responses (Figure 3). Area was included in all models and therefore parameter weight equals cumulative AIC model weight (Appendix 3, Table 7). Coverage by neighboring landmass strongly predicted soil $\delta\ ^{15}N$ and foliar $\delta\ ^{15}N$ (Figure 4) (parameter weight 1 in both cases) but had very little effect on foliar enrichment factor or total soil nitrogen (parameter weight 0.57 and 0.67 respectively). Instead, terrain slope strongly predicted both foliar enrichment factor and total soil nitrogen patterns (Figure 5). Slope was included in all models and therefore parameter weight equals cumulative AIC model weight (Appendix 3, Table 7). As expected, total soil nitrogen was a weak predictor of foliar enrichment factor compared to area and slope (Appendix 3, Figure 11) (parameter weight 0.54). Models for each nutrient response and their respective Δ AIC values can be found in Appendix 3, Table 7.

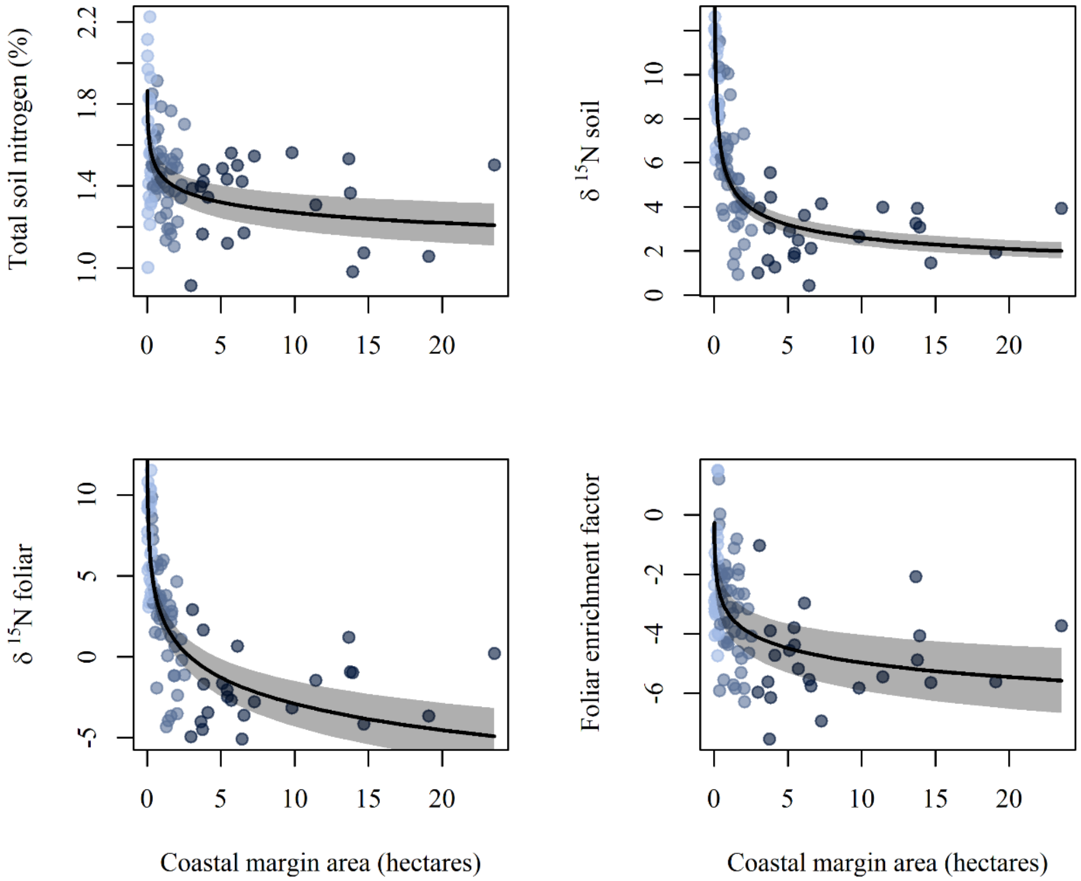

Figure 3 Coastal margin area was the strongest predictor of all nitrogen measures, likely due to the higher proportion of area that interfaces directly with the marine environment (a potential source of nitrogen) on small islands relative to large islands. Points are raw data values and colors grade from light to dark according to according to quantiles of coastal margin area. Confidence intervals represent a 95 % confidence level.

There was low correlation between variables included in the nutrient models except between coastal margin area and shoreline convolution (0.81 Pearson correlation) but both variables were retained in models because each are theorized to play different roles in nutrient subsidization (Anderson & Wait, 2001). Consequently, models including both area and shoreline convolution had high variance inflation factors (> 3.6). Models predicted a stronger influence of coastal margin area than shoreline convolution but collinearity makes it difficult to disentangle the effects of one variable from the other. However, the issues with collinearity are restricted to the interpretation of these two variables and does not preclude drawing inference from the remaining variables. The random effect ‘node’ explained very little additional variation in any model (variance ~ 0).

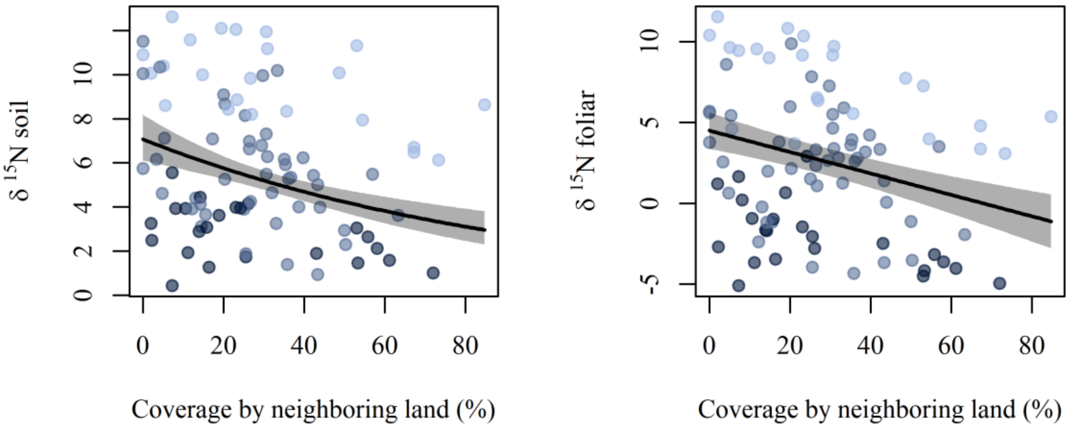

Figure 4 Coverage by neighboring landmass was an important predictor of nitrogen isotope abundance. This suggests that ^{15}N enrichment is directly or indirectly connected to the marine environment. Points are raw data values and colors grade from light to dark according to quantiles of coastal margin area (smallest islands are lightest color). Confidence intervals represent a 95 % confidence level.

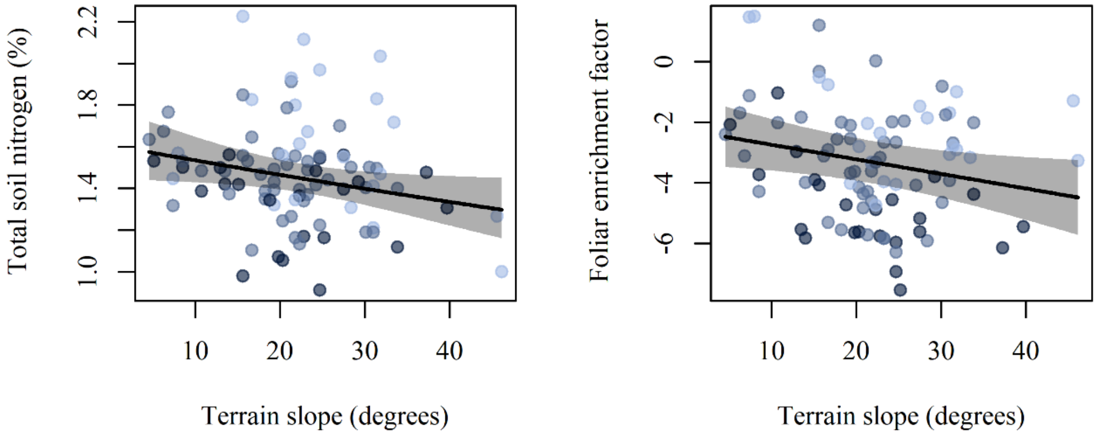

Figure 5 Slope was an important predictor of total soil nitrogen and enrichment factor, suggesting that nitrogen is lost through surface water runoff. Points are raw data values and colors grade from light to dark according to quantiles of coastal margin area (smallest islands are lightest color). Confidence intervals represent a 95 % confidence level.

Discussion

Subsidized island biogeography model

I created a formal subsidized island biogeography model, which incorporated area, distance to mainland, and a parameter for nutrient subsidies. This model was constructed to accommodate predictions from the subsidized island biogeography hypothesis wherein nutrient subsidies may increase or decrease species diversity across all islands, or have an interactive effect with area (Anderson & Wait, 2001). As expected, observed tree species richness increased with area but decreased with distance from the mainland. Tree species richness also declined with increasing foliar enrichment factor (Figure 2), although the effect is small given the limited nitrogen gradient. However, richness did not decline with increasing total soil nitrogen. Contrary to subsidized island biogeography predictions, nutrient abundance did not disproportionately affect species richness on small islands.

Nitrogen abundance in complex systems, terrestrial processes or subsidies?

Some islands had higher soil and foliar $\delta\ ^{15}N$ values than are typically observed in inland coastal-zone forests (Chang & Handley, 2000; Chang & Preston, 2000; Chang et al., 1996; Prescott et al., 1993, 2000; Quesnel & Lavkulich, 1980). The highest soil and foliar $\delta\ ^{15}N$ values were approximately 6 ‰ higher than upper limits observed in coastal zone forests, which suggests that some islands are receiving subsidies although the amount of soil nitrogen (kg/Ha) was not quantified in this study. However, attributing isotopic signatures or ecological effects solely to subsidies becomes difficult in complex ecosystems. Increased habitat heterogeneity, high productivity, and edaphic characteristics mediate retention and assimilation of subsidies but also regulate patterns of terrestrial nitrogen abundance whether or not subsidies are present (Attiwill & Adams, 1993; Dawson et al., 2002; Marczak et al., 2007). In complex systems, careful consideration of how nutrient patterns are influenced by environmental conditions should inform interpretation of subsidy abundance and its connection to ecological responses such as species richness. For example, many potential subsidy vectors are present in this system, including beach-cast marine algae, river otters (*Lontra canadensis*), humans, sea spray or marine fog, and each can increase terrestrial nitrogen abundance and isotope signatures (Ben-David et al., 1998; Colombini et al., 2003; Davidson, 2017; Templer et al., 2015; Trant et al., 2016; Wickham, 2017). However, soil processes such as nitrification and denitrification, and physical processes such as surface water runoff can also mediate total nitrogen abundance and enrich soil and plants in ^{15}N (Attiwill & Adams, 1993; Högberg, 1997). I examined which environmental conditions influence nitrogen abundance and consider whether terrestrial processes or subsidies were most likely to generate observed nitrogen patterns.

Denitrification occurs in anaerobic or water-saturated soils wherein microbes reduce nitrates to nitrous oxide, which is ultimately lost from the soil (Bohn et al., 2002) (Appendix 1). During denitrification, nitrous oxide is ^{15}N depleted, the remaining soil becomes enriched in ^{15}N, and total soil nitrogen declines because of gaseous nitrogen loss (Michener & Lajtha, 2008). If denitrification were a dominant process on these islands, it would most likely occur on flat terrain, due to heavy rain and humic soils which raise the water table (Banner et al., 2005). In denitrifying locations, I would expect foliar enrichment factor and total soil nitrogen to decline in due to microbial use of nitrates and soil δ^{15}N values to increase due to fractionating processes. However, I observe the highest total nitrogen in flat conditions and no relationship between soil $\delta^{15}N$ and slope. Furthermore, I observe high foliar enrichment values on flat terrain, which indicates an abundance of available nitrogen. Given these circumstances, it is not likely that denitrification is the dominant process driving observed nitrogen patterns.

Soil mineralization could also lead to elevated levels of ^{15}N. Low carbon-to-nitrogen ratios (C:N) stimulate net mineralization, which is the microbial decomposition of organic matter into inorganic nitrogen such as ammonium and nitrate (Dawson et al., 2002; Michener & Lajtha, 2008; Nadelhoffer & Fry, 1988) (Appendix 1). Nitrates produced in mineralization are depleted in ^{15}N relative to the soil and remaining soil becomes enriched in ^{15}N (Michener & Lajtha, 2008). Coastal-zone forests with C:N ratios under 35 show appreciable net mineralization and approximately 25% of sampled islands meet these conditions (Appendix 3, Figure 10) (Prescott et al., 2000). Mineralization occurs in aerobic conditions (well-drained soils) and sites with moderate to high terrain slope tend to yield better drained soils than flat sites (Banner et al., 2005). If substantial mineralization were occurring in well-drained sites, I would expect slope to be positively associated with both soil $\delta^{15}N$ and foliar enrichment factor. This is not the pattern I observed. Instead, increasing slope leads to a decrease of total soil nitrogen and enrichment factor but has no effect on soil $\delta^{15}N$. This loss may instead be due to surface-water runoff, which is substantial in these impermeable bedrock systems and exacerbated by increasing slope. The observed decline in foliar enrichment factor suggests a reduction in the abundance of inorganic nitrogen which is water soluble and prone to loss through surface-water runoff (Attiwill & Adams, 1993). In this study region, surface water runoff results in significant losses of dissolved organic carbon (Oliver et al., 2017) and it is likely that our patterns of nitrogen loss are also attributable to this mechanism. Net mineralization may still be occurring, but is likely overwhelmed by nitrogen loss due to runoff.

As explained above, it is unlikely that nitrification or denitrification are the main mechanisms responsible for the observed high $\delta\ ^{15}$N values or foliar enrichment and total soil nitrogen patterns. Subsidy input is a likely alternative. I observe the highest soil and foliar $\delta\ ^{15}$N values on small islands that are not sheltered by neighboring landmasses, which suggests a connection to the marine environment. This is consistent with other studies that suggest small islands have more resources per unit area than large islands due to higher perimeter-to-area ratios (Polis & Hurd, 1996). In effect, small islands have a higher interface with the marine environment so subsidies may accumulate more on small islands and have a larger ecological impact than on large islands (Polis & Hurd, 1995; Wiens, 1992). In a separate study on these islands, Fitzpatrick (2018) found that soil $\delta\ ^{15}$N values on large islands decline much faster than those on small islands with increasing distance from shoreline. This further indicates a connection to the marine environment. My data cannot be used to determine a subsidy source, but I consider several scenarios below.

Ocean water in this region is rich in nitrogenous compounds (Varela & Harrison, 1999; Whitney & Freeland, 1999; Whitney et al., 1998) and has a $\delta\ ^{15}$N value of approximately + 9 ‰ (Liu & Kaplan, 1989). Although sea spray contains salts which can inhibit tree growth, spray can contribute nitrogen to terrestrial systems (Lane et al., 2008; Michener & Lajtha, 2008; Remke & Blindow, 2011). High wind speeds (30 to 138 km per hour) are sustained throughout the year in this area, so it possible that deposition of nutrient-rich sea spray is a continuous input (Hakai Institute, 2017). Marine fog is also a likely source of ammonium and nitrate in our system just as it is in other coastal Pacific ecosystems (Ewing et al., 2009; Templer et al., 2015; Weathers et al., 1988, 2000). In northern California, ammonium from fog water is enriched in ^{15}N by + 11.36 ± 2.68 (Templer et al., 2015) and is an important source of nutrients for redwood forests (Dawson, 1998). No attempts have been made to quantify nitrogen concentration or isotopic signature of sea spray or marine fog on islands in this study region but could be done using salt traps (Barbour, 1978) or fog harps (Fischer & Still, 2007).

Patterns of nitrogen enrichment on small, exposed islands may also be due to animal usage. Nutrients coming from marine sources or those high in the food web will have higher δ ^{15}N values than those at the base of the food web due to fractionating processes (Michener & Lajtha, 2008). This general rule is the basis for determining that high δ ^{15}N values in soil or plants originate from sources other than plant-based atmospheric fixation (Dawson et al., 2002; Robinson, 2001). Islands in this study support few high trophic level animals relative to the mainland but bald eagles (*Haliaeetus leucocephalus*), various seabirds, and river otter (*Lontra canadensis*) occur in high abundance (Blood & Anweiler, 1994; Davidson, 2017). These species feed directly on marine-derived resources such as fish which further enriches their excreta in ^{15}N relative to those with strictly terrestrially based diets (Ben-David et al., 1998; Hobson et al., 1994; Michener & Lajtha, 2008; Vermeer & Morgan, 1989). Continued deposition of animal excreta can enrich soil and plants in ^{15}N and alter a site’s nitrogen dynamics relatively quickly compared to geologic processes (Frank & Evans, 1997; Högberg, 1997; Michener & Lajtha, 2008). However, few field studies have documented the effect of multiple subsidy inputs on soil and plant $\delta^{15}N$. Although biotic vectors of subsidies use islands of all sizes, their impact would accentuated on small islands because minimal area over which nutrient subsidies would be concentrated (Anderson & Wait, 2001; Marczak et al., 2007; Ries et al., 2004).

This study region also has a deep history of human occupation, with continuous Indigenous occupation occurring over 14,000 years into present day (Mackie et al., 2011; McLaren et al., 2018). Evidence of Indigenous activities may not be obvious on the landscape but can influence terrestrial ecology and nutrient dynamics. For example, shellfish middens at habitation sites exhibit higher soil calcium and phosphorous concentrations than control sites but no statistical difference in nitrogen abundance (Trant et al., 2016). This altered soil chemistry influences forest productivity, with western redcedar trees (*Thuja plicata*) growing on midden sites exhibiting greater radial growth, higher wood calcium concentrations, less top die-back, and increased height (Trant et al., 2016). Sampling locations for this study did not overlap with known habitation sites but human use of this landscape is widespread and likely contributes to landscape-scale heterogeneity of soil properties outside of known settlements or seasonally used camps.

Species richness: nitrogen abundance or environmental conditions?

Subsidies are generally expected to increase population productivity in the recipient ecosystem (Polis et al., 1997). In this study system, nitrogen is a limiting nutrient and in order for subsidies to increase primary productivity, nitrogen must be in an accessible form (Attiwill & Adams, 1993; Elser et al., 2007). I did not measure primary productivity but used foliar enrichment factor as an indicator of increasing abundance of inorganic nitrogen, which is readily available to plants (Appendix 1). If subsidies were substantially increasing abundance of available nitrogen, I would expect foliar enrichment factors to approach zero on islands with elevated $\delta\,^{15}N$ values but this is not the pattern I observed. This indicates while soil and plants are both being enriched in ^{15}N, a substantial increase in the abundance of inorganic nitrogen is likely not associated with that enrichment. Additionally, total soil nitrogen only marginally increases on exposed islands (where $\delta\,^{15}N$ is highest), which further supports the conclusion that subsidy input is minimal. However, despite a minimal subsidy input the model predictions still suggest a slight reduction in richness. Quantifying the amount of nitrogen in the soil (kg/Ha) would offer insight into whether differences in total nitrogen are large enough to influence species richness. Additionally, it is possible that the observed ecological response would be strengthened by expanding species richness to include understory vegetation.

Mounting evidence suggests that the ecological effects of subsidies vary according to recipient habitat type and productivity differentials (Marczak et al., 2007). A large interface between a donor and recipient ecosystem, such as high perimeter-to-area ratio, increases the flow of subsidies but if the ratio of incoming subsidies to *in situ* resources is small, the ecological effects of subsidies are minimal (Marczak et al., 2007). My results add to this evidence. I observed islands with high perimeter-to-area ratios (small islands) and direct exposure to the marine environment had highly ^{15}N enriched soil and plants. However, low total nitrogen and foliar enrichment values indicate these small, exposed islands have not received or at least retained substantial amounts of incoming nitrogen. Under low nitrogen conditions, plants tend to have lower $\delta\,^{15}N$ values than their source nitrogen potentially because mycorrhizae mediate nitrogen acquisition and fractionate against ^{15}N (Högberg, 1997; Hogberg et al., 1999). However, when available nitrogen is abundant plant roots can acquire nitrogen without the support of mycorrhizae (Hobbie et al., 1999) so plant tissue more closely reflects the ^{15}N of the nitrogen source (Hobbie et al., 1999). In my study, low total nitrogen and foliar enrichment factors suggest that incoming nitrogen was not disproportionately higher than *in situ* nitrogen resources. Consequently, I did not observe a dramatic richness response to nitrogen subsidies.

Since subsidy input or retention is likely minimal, the decline in species richness may be due to environmental conditions leading to nitrogen patterns rather than nitrogen abundance itself. This study system receives nearly 3 m of rain annually and soils are primarily humus with high water retention (Banner et al., 2005; Hakai Institute, 2017). Under these conditions, flat terrain is often water-saturated (Banner et al., 2005; Kranabetter et al., 2013). I observed the highest nitrogen abundance on small, flat islands but western hemlock (*T. heterophylla*) and Sitka spruce (*P. sitchensis*) are far less tolerant than western redcedar (*T. plicata*) of soil moisture surpluses and this intolerance may outweigh the effect of slightly higher total soil nitrogen (Antos et al., 2016; Sajedi et al., 2012). In this hypermaritime climate, even subtle changes in topography can increase soil moisture and occurrence of anoxic conditions can induce a shift in species composition (Sajedi et al., 2012). Furthermore, small islands have a higher edge-to-interior ratio than large islands which means that a large part of the island interfaces directly with the marine environment. High wind, salt spray, and wave disturbance at the island edge likely creates harsh growing conditions, which could also trigger a decline of species richness on small, flat islands.

Slight increases in nitrogen may not be enough to shift tree species richness but it may give understory species a competitive advantage, further exacerbating effects of water saturation. Fertilization trials in similar inland coastal-zone forests show that western redcedar, western hemlock, and Sitka spruce compete poorly with salal shrubs (*G. shallon*) for soil nitrogen (Chang et al., 1996). Salal is ubiquitous across the study islands (Fitzpatrick, 2018) and thrives in a variety of environmental and nutritional conditions (Bunnell, 1990). Repeated application of 100 to 300 kg N/ha coupled with 50-100 kg P/ha is necessary to stimulate long-term productivity in western redcedar, western hemlock, and Sitka spruce (Blevins et al., 2006) whereas extremely high applications of nitrogen (1,000 kg N/ha) are necessary to reduce salal biomass (Bennett et al., 2004). The islands in this study are likely not receiving enough nitrogen to outcompete salal and below ground interception of nitrogen by salal roots may limit tree richness to those species least affected by this competition, such as western redcedar (Chang & Preston, 2000; Chang et al., 1996). Similarly, the decline of plant richness in salmon subsidized watersheds was attributed to competitive dominance by species best adapted to nutrient acquisition in riparian zones (Hocking & Reynolds, 2011).

Future considerations

To clarify the ecological impact of nutrient subsidies in complex systems, multiple measures of nitrogen abundance should be used to characterize subsidy input. The influence that environmental conditions have on nutrient patterns should inform interpretation of ecosystem responses to nutrient subsidies. In fact, a parameter for relevant environmental conditions may be a necessary part of a generalizable subsidized island biogeography statistical model. Furthermore, quantifying the amount of nitrogen in the soil (kg/Ha) would strengthen comparisons between islands as well as regional forests.

Differentiating between organic and inorganic nitrogen abundance would provide much needed clarification on changes in nitrogen availability due to nutrient subsidies. Nutrient subsidies are differentially processed by soil and plants and a measure of total soil nitrogen, soil $\delta^{15}N$ or foliar $\delta^{15}N$ alone does not make a suitable metric for primary productivity if nitrogen is ultimately inaccessible to plants. As I’ve shown and others emphasize (Helfield & Naiman, 2006; Pinay et al., 2003), some sites may be predisposed to making nutrients available to plants through soil processes or losing them before they are even incorporated into the terrestrial system. Soil processes and surface water runoff occur after subsidies are deposited on land and can alter interpretations of the degree to which a site is receiving or making use of subsidies. The physical conditions and environmental context of a recipient habitat should factor into predictions about the quantity and quality of subsidies needed to catalyze ecological effects, as well as the ultimate fate of those subsidies in the soil-plant system.

Conclusion

Increased nitrogen abundance led to a decrease in tree species richness but small islands were not disproportionately affected by subsidies. Given the high soil and plant $\delta^{15}N$ values, islands in this study are likely being subsidized. However, low total soil nitrogen suggests that the quantity of nitrogen subsidies is not substantial. Consequently, the observed effect of nitrogen abundance on species richness was small. The highest abundance of nitrogen occurred on small, flat islands but tree species may be responding to the environmental conditions leading to high nitrogen abundance rather than exhibiting a direct response to nitrogen quantities. Unique environmental conditions shaped patterns of total nitrogen, foliar enrichment factor and nitrogen isotope abundance, which emphasizes the importance of considering how site characteristics mediate nutrient signatures in complex ecosystems.

Chapter 3: Bald eagles (*Haliaeetus leucocephalus*) function as vectors of diffuse resource subsidies in coastal temperate forests

Abstract

The movement of nutrients from one ecosystem to another (nutrient subsidization), is often mediated by biotic vectors. Along coastal North America, bald eagles are abundant, they consume a largely marine-based diet and use nests for prolonged periods of time within a year and over multiple generations. Owing to these traits, I predicted that bald eagles (*Haliaeetus leucocephalus*) would deposit nutrient subsidies in the form of guano and prey remains at nest sites and thereby alter soil chemistry and vegetation composition. In this exploratory study of seven nest sites, I found higher soil phosphorous at eagle nest sites relative to control sites (~ 33% higher). Phosphorous plays a critical role in the nitrogen cycle, and increased concentrations suggest that bald eagles could contribute to nutrient dynamics in coastal temperate forests. Higher potassium concentration also occurred on eagle-inhabited islands but was not associated specifically with current nest sites, perhaps reflecting differential persistence of macronutrients in the soil. I expected to observe elevated nitrogen isotope signatures (δ^{15}N) given bald eagles' position in the trophic web but soil δ^{15}N was not statistically higher at eagle nest sites. There were no significant differences between vegetation composition at eagle nest sites and reference sites, but reference sites tended to be dominated by shrub species.

Introduction

The movement of nutrients from one ecosystem to another (nutrient subsidization), is often mediated by biotic vectors. For example, seabirds forage in the ocean and deposit marine-derived subsidies on land in the form of guano and prey remains (Anderson & Polis, 1999; Moss, 2017). Guano and prey remains are rich in nutrients (Burger, 1978; Hobson et al., 1994; Hutchinson, 1950) and accumulation of these nutrient subsidies can induce significant ecological changes such as altered soil chemistry, increased primary productivity, and modified consumer dynamics (Barrett et al., 2005; Sánchez-Piñero & Polis, 2000; Wainright et al., 1998; Wait et al., 2005). The ecological impacts of avian-mediated resource subsidies are most studied in the context of seabird colonies, where concentrations of birds (and therefore subsidies) are high, site occupation persists over long time-scales, terrestrial productivity is low, and food webs are relatively simple (Anderson & Polis, 1999; Ellis, 2005; Maron et al., 2006; Vidal et al., 2003; Wait et al., 2005). Due to a marine diet and high trophic position, seabird guano is enriched in the stable nitrogen isotope (^{15}N), making it a convenient chemical marker of nutrient subsidy (Buelow et al., 2018; Hobson et al., 1994; Lindeboom, 1984).

However, many bird species consume large amounts of marine-derived food, occur in dense populations, and nest or roost on land in solitary locations rather than in colonies. These characteristics make such bird species likely vectors of marine-derived resource subsidies, yet little attention has been directed to this potential subsidy pathway. This is likely due to the difficulty of isolating subsidy effects when comparatively diffuse inputs may make it difficult to differentiate multiple subsidy sources, or inputs are masked by high terrestrial productivity, or complex food web dynamics (Anderson et al., 2008; Huxel et al., 2002).

Bald eagles (*Haliaeetus leucocephalus*) display similar dietary and nesting characteristics to the seabird subsidy pathway, making them likely vectors of nutrient subsidies (Anthony et al., 1982; Robards & King, 1966; Stalmaster & Gessaman, 1984). In coastal regions bald eagles feed predominately on fish, marine invertebrates, and seabirds but consume their prey on land (Anthony et al., 2008; Blood & Anweiler, 1994; Vermeer & Morgan, 1989). This behavior results in terrestrial deposition of guano and prey remains that are likely chemically or nutritionally similar to seabird guano (Hutchinson, 1950). Unlike seabirds, bald eagles are solitary nesters and therefore guano and prey remains are likely spatially diffuse at the landscape scale and accumulate at a slower rate than in seabird colonies, some of which historically accumulated guano depths greater than 45 m (Kubler, 1948). However, bald eagles can occupy the same nesting territory for multiple decades, repairing and reusing the same nest over repeated breeding seasons (Beebe, 1974; Blood & Anweiler, 1994). Additionally, the bald eagle reproductive cycle ensures occupancy of the nest site for nearly six months of the year from late winter through early fall (Blood & Anweiler, 1994; Isaacs & Anthony, 2011). For these reasons, I predict that repeatedly used nest sites will have high accumulation of guano and prey remains and that long-term deposition of these subsidies will produce similar but lower magnitude ecological changes to those observed at seabird colonies.

This study explores bald eagles as vectors of diffuse, avian-mediated subsidies and examines whether those subsidies alter soil chemistry and terrestrial plant communities. Increased nitrogen (either total nitrogen or $\delta^{15}N$) and phosphorus is common in seabird colony soil, and variable responses of pH, potassium, calcium, total carbon, and salts have been documented (Ellis, 2005; Ligeza & Smal, 2003; Wait et al., 2005). I expected that soil sampled at the base of eagle nest trees would differ from reference sites in pH and concentration of phosphorus, potassium, total carbon, total nitrogen, and nitrogen isotope abundance ($\delta\ ^{15}$N), hereafter collectively referred to as the soil chemistry profile. Vegetation change associated with seabird colonies is often characterized by an increase in annual plants and graminoids, and a decrease in shrubs, trees, or perennial species (Ellis, 2005; García et al., 2002; Maron et al., 2006; Wait et al., 2005). I expected the plant community under a nest tree to differ from reference sites in species and functional composition, particularly a reduction in woody shrubs and an increase in species tolerant of nutrient enriched soil.

Methods

Study area

I selected 14 remote islands in the northeast Pacific Ocean along British Columbia's Central Coast (Canada) (Appendix 4, Figure 12) to investigate whether bald eagles alter soil chemistry and understory vegetation at nesting sites. The islands are situated in the temperate rainforest ecosystem (Coastal Western Hemlock, Very Wet Hypermaritime subzone, central variant) (Banner, 1993) and are covered by zonal forests, characterized by low forest stature, open canopies, and a well developed shrub layer (Banner et al., 2005). Moderate annual temperature (8.2 ± 0.9°C) and heavy precipitation (2,951 ± 657 mm) result in slow decomposition of organic matter and soils that are nutrient deprived, poorly drained, acidic and primarily humus (Kranabetter et al., 2003). Indigenous occupation of this study region has been continuous for 14,000 years (Mackie et al., 2011; McLaren et al., 2018) and soil chemistry at habitation sites differs from the surrounding landscape, particularly exhibiting higher calcium and phosphorous concentrations (Trant et al., 2016). Islands included in this study did not overlap with known habitation sites or seasonally used camps but given the deep Indigenous history, unidentified human usage sites (such as shell-less middens or berry gardens) are possible across the landscape. Being constrained by the geographic remoteness of sites, I collected soil and measured vegetation composition on 14 very small islands, ranging in size from 351 m^2 to 9,272 m^2. Seabird colony studies are often similarly constrained, with samples restricted to as little as a single island but typically averaging nine islands (García et al., 2002; Wainright et al., 1998; Wait et al., 2005).

Data collection and processing

Seven islands had active eagle nests (coded as CV11, GS01, MM04, MM07, MM09, TB10, TB12; Appendix 4, Table 8 for further details) and seven islands without eagle nests served as references (AD04, CV04, GS02, MM01, MM08, TB06, TB07). Each of the seven surveyed nests were confirmed active by presence of adult eagles or offspring during the study period (May to July 2017). Guano and prey remains were observed at the base of every surveyed eagle nest tree.

Soil

Soil samples were taken at the base of nest trees and an interior site located by random distance and bearing on each eagle-associated island. Soil was similarly collected at reference trees and interior locations on non-eagle islands (n = 28 total soil samples, 2 per island on 14 islands). Reference islands were similar in geographic location, size, and exposure to wind and wave action to eagle occupied islands (Appendix 4, Table 8).

Reference trees located on reference islands were selected based on similarity to nest trees in proximity to shoreline, height, diameter at breast height (1.3 m), physical structure, and species. Moss, leaf litter, and duff were scraped away and one soil sample (450 to 650 g) was collected from the surface to a depth of approximately 15 cm. Each sample was homogenized and consisted primarily of humus. Soil pH was measured in a 1:5 aqueous solution using an Oakton PCTestr 35 multiparameter tester calibrated with standard buffer solutions. Three replicate pH measurements were made per sample. Soil samples were analyzed for total nitrogen, total carbon, calcium, potassium, sodium, phosphorus, and marine-derived nitrogen ($\delta\ ^{15}N$), using the Mehlich III method for extractable elements. Soil samples were processed for stable nitrogen isotope enrichment using a Flash 2000 elemental analyser coupled to a ConFlo IV interface and DELTA Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific, Waltham, MA). Stable isotope values are expressed as $\delta\ ^{15}N$, the deviation per mill (‰) from the atmospheric standard (Paul et al. 2007). All reported values are calculated using Isodat3.0 software (Thermo Fisher Scientific, Waltham, MA) and subject to post-run two point linear normalization (Paul, et al. 2007) to correct for instrument drift and changes in calibration gas. Sample processing was conducted by Ministry of Forests, Lands, and Natural Resource Operations (MFLNRO) analytical laboratory and Pacific Forestry Center both located in Victoria, British Columbia, Canada.

Vegetation

Vegetation composition was measured at eagle nest trees and reference trees (n = 14 total vegetation sites). Species-level abundance was measured along two 10 m transects using a modified step-point method (Elzinga et al., 1998). The step-point method provides a rapid assessment of sites and is best suited for capturing major vegetation characteristics because it tends to be biased toward dominant species (Elzinga et al., 1998). At each site, the first transect bearing was randomly selected and the second transect was established 90° from the first transect. Across all 14 sampled islands, transect bearings that led directly to shoreline from the tree were avoided to reduce confounding nutrient effects of ecosystem boundaries, wave action, and reduced soil depth. Data from both transects at a sampling tree were pooled to create total species abundance per sampling site.

Statistical analyses

Soil

One potential outlier was detected in the soil data: an untransformed Ca value 282 % larger than the next value (19,013 $mgKg^{-1}$ and 6,722 $mgKg^{-1}$). This data point comes from a low-lying, narrow, exposed island (MM07) consisting of several shell and sand beaches that nearly bisect the island. The large calcium value was considered valid and retained in further analysis.

Principal component analysis (PCA) was used as a heuristic tool to visualize soil data because variables were correlated and showed approximate linear relationships (McCune et al., 2002). I used the function prcomp() from base R to perform PCA and the result was not rotated (R Core Team, 2017). The first two principal components were retained according to the Kaiser-Guttman criterion (i.e. both had eigenvalues over 1) (McCune et al., 2002). Soil chemistry variables were log transformed to correct for skewness, except pH which is already on a log scale (McCune et al., 2002). Data were then mean centered around zero and scaled to unit variance because variables were measured on different scales (Legendre & Legendre, 2012).

I followed PCA with a model-based framework to understand multivariate soil chemistry responses at eagle nest sites. A multivariate model-based approach offers the advantage of detecting patterns not necessarily apparent when testing individual responses. The soil chemistry profile response was characterized as amount of total carbon, total nitrogen, phosphorous, potassium, sodium, calcium, and marine-derived nitrogen (δ^{15}N). The predictor variable was an interaction between island type (eagle or reference) and within-island sample location (tree or interior). Log-transformed data were modelled using the function manylm() from the package mvabund (Wang et al., 2014). The function manylm() simultaneously fits a linear regression model to each individual soil chemistry variable, and the same assumptions of linear modelling apply to the manylm approach (Wang et al., 2012). Residual plots were examined for normality, heteroscedasticity, and autocorrelation. Hypothesis testing was carried out using the function anova.manylm(), also from the package mvabund (Wang et al., 2014), where the multivariate test statistic is a sum of univariate tests statistics, adjusted for multiple testing and derived from univariate models of each component of the soil response. Within the function anova.manylm(), I used the PIT-trap residual bootstrap method, which gives reliable Type I error rates and preserves correlation within the multivariate response via row-resampling (Warton et al., 2017). I employed 5,000 resampling iterations using residual (with replacement) resampling and a likelihood ratio test. All data exploration and statistical tests were carried out in R 3.4.1 (R Core Team, 2017).

Vegetation

I used non-metric multidimensional scaling (MDS) as a heuristic tool to visualize vegetation species abundance data, recognizing that distance and dispersion effects are likely confounded given the limitations of distance-based methods. Data were square-root transformed to address the large number of zero cases and moderate extreme values (Bolker, 2008). I used the function metaMDS in the package vegan to perform MDS (Oksanen et al., 2013), which uses a random starting configuration and Procrustes analysis to compare iterative solutions and evaluate convergence. By default, the final solution is rotated via principal component analysis, which ensures that the first axis reflects the principal source of variation. I employed the Bray-Curtis distance metric and restricted analysis to two dimensions because they accounted for the largest reduction in stress. Twenty iterations were used to find a stable solution.

Following MDS, I employed a model-based approach to understand how presence of eagles influences vegetation composition. The model-based approach has advantages over distance-based methods such as PCA or MDS: it implicitly models the mean-variance relationship associated with abundance data, allows for multiple testing and predictive modelling and has better power properties (Wang et al., 2012; Warton et al., 2012). Traditional approaches such as ANOSIM, SIMPER or PERMANOVA following distance-based ordination inadequately account for the mean-variance relationship, which leads to inappropriate sensitivity to species with high variance, making detection of between-group differences unreliable (Warton et al., 2012). I used the function manyglm, from the mvabund package (Wang et al., 2014) to model vegetation community abundance as the response and sample location (nest tree or reference tree) as the categorical predictor. Three models were run in which vegetation composition was characterized by species, functional growth form (e.g. shrub, forb, sedge, graminoid), and soil nitrogen status (e.g. low, medium, high). I used the soil nitrogen indicator values listed in Indicator Plants of Coastal British Columbia (Ceska & Scagel, 2011), in which cluster analysis, site descriptors and soil nutrient concentration were to used to identify species indicative of low, medium and high soil nitrogen regimes. The manyglm approach simultaneously fits a generalized linear model (GLM) to each untransformed response variable (e.g. each vegetation species within the community). The models were fit using the negative binomial link. Residuals were examined for compliance with the heteroscedasticity and linear assumptions. Hypothesis testing was carried out using the function anova.manyglm() also in the mvabund package (Wang et al., 2014), consisting of 5,000 resampling iterations using the default PIT-trap resampling (Warton et al., 2017), and a likelihood ratio test to derive a statistic (LR). The multivariate test statistic is a sum of univariate tests statistics adjusted for multiple testing, used to measure the strength of the between-group effect. All data exploration and statistical tests were carried out in R 3.4.1 (R Core Team, 2017). The small sample size limited the ability to draw conclusions from results, but I did observe patterns in nutrient transfer and associated plant community response at bald eagle nest sites.

Results

Soil

Our model shows that soil phosphorous concentration was elevated at eagle nest sites (LR value = 10.1, P_{adj} = 0.03), and there is a trend toward higher potassium concentration on eagle inhabited islands although statistical differences are not strong (LR value = 7.2, P_{adj} = 0.07). Raw, untransformed soil chemistry values are shown in

Table 3. Principal component analysis confirms patterns revealed by the model but also suggests that elevated levels of marine-derived nitrogen ($\delta\ ^{15}$N), in addition to potassium and phosphorous, occur in soils below nest sites (Figure 6). Combined, the first two principal components account for 56.3 % of variance in the original data (PC1 31.6 % of variance, PC2 24.6 %). Eagle nest sites were differentiated from other sample locations along the second principal component which was formed by phosphorous, potassium and $\delta\ ^{15}$N, as well as total carbon (Ctot) (Table 4). All PC2 variables were positively correlated with each other. The first principal component was comprised of sodium (Na), pH, and total nitrogen (Ntot) which are positively correlated with each other (Table 4). Variation in phosphorous, potassium and $\delta\ ^{15}$N between sampling sites is shown in Appendix 4, Figure13.

Table 3 Mean values and standard deviations of soil chemistry from seven islands with eagle nests and seven islands without eagle nests. Sampling occurred at the base of eagle nest trees, eagle island interior sites, the base of reference trees, and reference island interior sites. Values are raw, untransformed data.

Variable	Symbol	Unit	Eagle tree Mean (sd)	Eagle interior Mean (sd)	Reference tree Mean (sd)	Reference interior Mean (sd)
pH	pH		5.29	5.64	5.09	5.5
			(0.5)	(0.6)	(0.5)	(0.6)
Carbon	Ctot	%	56.26	54.2	56.23	56.41
			(2.2)	(5.6)	(2)	(1.6)
Nitrogen	Ntot	%	1.53	1.34	1.35	1.43
			(0.3)	(0.3)	(0.3)	(0.2)
$\delta\ ^{15}$N	$\delta\ ^{15}$N	‰	11.25	8.88	9.84	9.36
			(1.7)	(1.6)	(3)	(2.4)
Phosphorus	P	mgKg^{-1}	339.29	121.14	104.57	144.43
			(244.7)	(30.4)	(45.1)	(51.8)
Potassium	K	mgKg^{-1}	884	693.29	572.57	628.71
			(168)	(140.8)	(166.2)	(211.5)
Calcium	Ca	mgKg^{-1}	5707.57	3807.57	4677.14	4378.86
			(5960.4)	(1021.8)	(1888.9)	(1774.4)
Sodium	Na	mgKg^{-1}	2145.14	1991.14	2087	2348.43
			(960.5)	(1002.4)	(1424.7)	(2202.8)

Table 4 Loadings of soil chemistry variables on two significant principal components for 28 soil samples. Each principal component's predominate variables are in bold.

Variable	Principal Component 1	Principal Component 2
δ^{15}N	0.234436	**-0.44273**
P	0.132164	**-0.52146**
K	0.190703	**-0.43878**
pH	**0.500251**	0.329844
Ctot	-0.31293	**-0.46588**
Ntot	**0.473205**	-0.10587
Ca	0.044292	0.048542
Na	**0.563153**	-0.01147

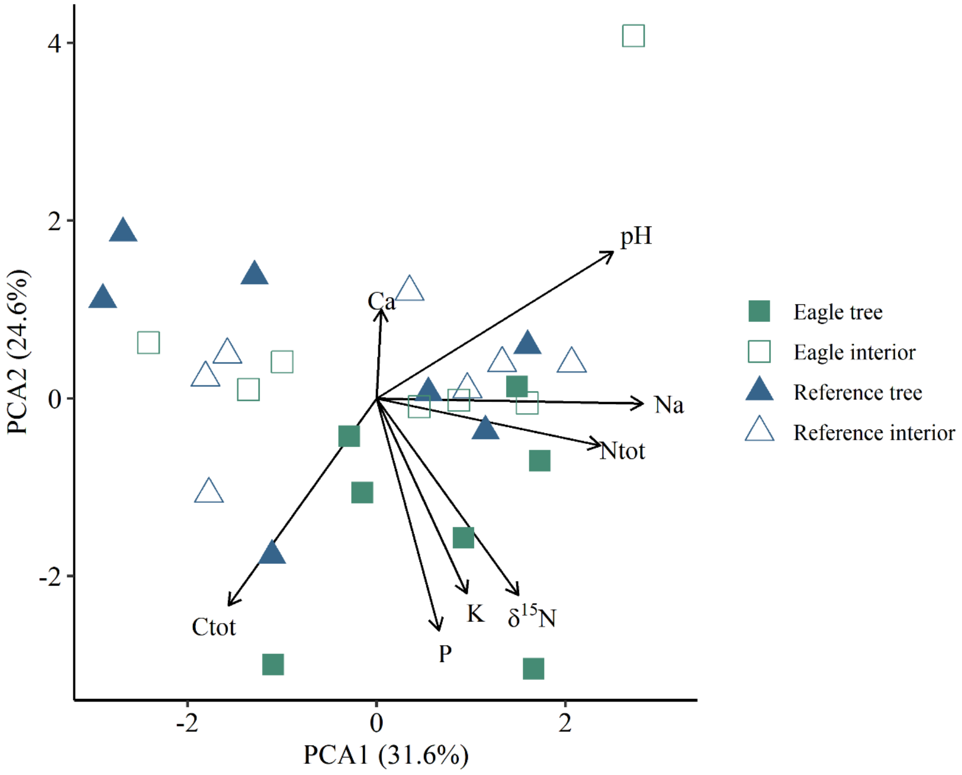

Figure 6 Principal component analysis bivariate plot showing grouping of sample sites by soil chemistry. Ctot = total carbon, P = phosphorus, K = potassium, δ^{15}N = nitrogen isotope, Ntot = total nitrogen, Na = sodium, pH = pH, and Ca = calcium. Soil samples from eagle nest trees (filled square) cluster according to elevated levels of marine-derived nitrogen, phosphorous and potassium. Data were log transformed, mean centered on zero and scaled to unit variance.

Vegetation

There is some evidence that plant species composition differed between nest trees and reference trees (Dev = 38.2, *P* = 0.06), although no single plant species drives differences in composition (all $P_{adj} > 0.1$). I predicted that the vegetation community at eagle nest sites would shift toward species indicative of a high soil nitrogen regime but this was not the case (Dev = 2.5, $P = 0.35$). There is no statistical difference in functional growth form between sampling locations (Dev = 6.5, $P = 0.18$) but see Appendix 4, Figure 14 for general patterns.

The MDS plot shows that all non-eagle islands except for one (MM08) cluster around shrub species *Gaultheria shallon* (GASH), *Rubus spectabilis* (RUSP), *Rubus parviflorus* (RUPA), and *Lonicera involucrata* (LOIN) (Figure 7), reflecting the dominance of these shrubs species in the study region. The single exception to the clustered reference islands is MM08, which clusters with the eagle islands that were characterized by forbs, sedges and graminoids. Although no nest was observed on island MM08, I did observe pronounced eagle activity there. A dead juvenile eagle was found near the center of the island, the island had signs of guano and prey remains, and multiple adult eagles were observed perched in the trees for several consecutive days. I retained MM08 as a “reference island” in analysis because no nest was present and it did not deviate from the soil chemistry patterns of other reference islands. Eagle nest islands do not demonstrate a clear vegetation grouping pattern; some islands are characterized by the same shrubs as reference islands while others are not.

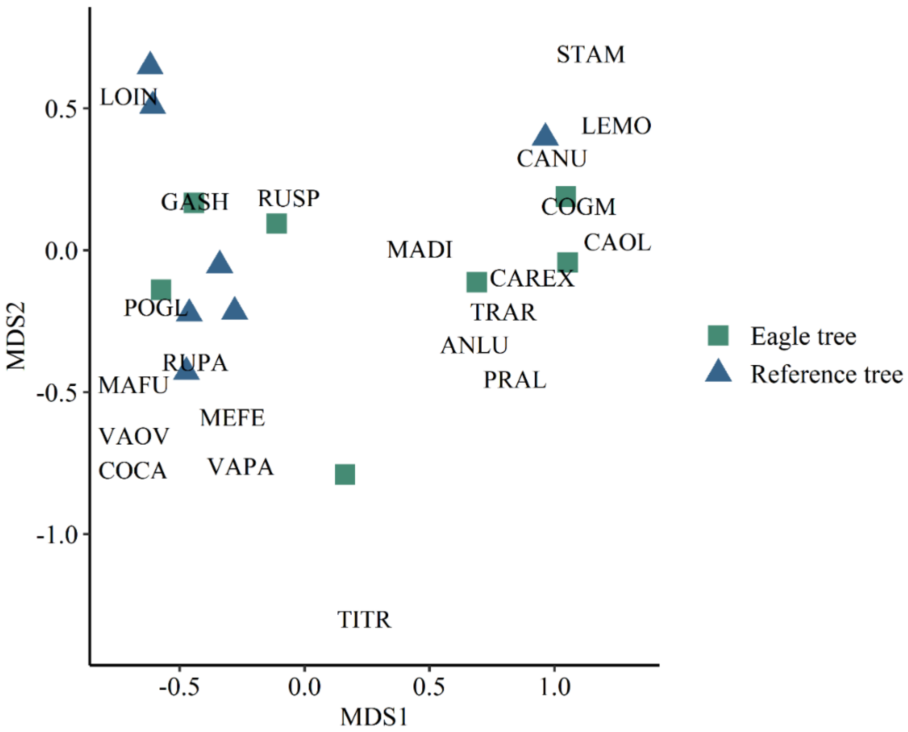

Figure 7 Patterns of observed vegetation communities from eagle nest sites (filled squares) and reference sites (filled triangles) show that reference sites tend to cluster according to shrubs GASH (*Gaultheria shallon*), LOIN (*Lonicera involucrata*), and RUPA (*Rubus parviflorus*). The exception is one reference site which is characterized by the forb COGM (*Conioselinum gmelinii*), and graminoids CANU (*Calamagrostis nutkaensis*) and LEMO (*Leymus mollis*). Eagle nest sites do not appear to have a clear clustering pattern, indicating that no single species or group of species characterize these nest locations. Vegetation species codes (shown) can be referenced in Appendix 4, Table 9. Results are from a Multi-Dimensional Scaling (MDS) ordination analysis of a Bray–Curtis similarity matrix. The final stress of the MDS plot was 0.06, a solution was reached after 20 iterations. Species abundance data were square-root transformed to address the large number of zero cases and moderate extreme values.

Discussion

Bald eagles appear to alter soil chemistry at the base of nest trees, presumably through long-term deposition of guano and prey remains, which were observed at each eagle nest. Specifically, higher concentrations of soil phosphorous were associated with eagle nest sites. Higher potassium concentration may occur on eagle-inhabited islands but is not associated specifically with nest sites, which may reflect differential persistence of nutrients in the soil. Nitrogen isotope enrichment ($\delta\ ^{15}N$) was not significantly higher at eagle nest sites, contrary to my expectations that guano from a high trophic animal with a marine-based diet would lead to elevated $\delta\ ^{15}N$. However, the trend toward higher $\delta\ ^{15}N$ is apparent and would likely be strengthened with increased sample size. Vegetation composition is variable across eagle nest sites, with some being dominated by shrub species while others displayed increased abundance of forbs and graminoids. This may simply reflect natural variation however, because the sample size is small (n = 14).

To my knowledge, this is the first study to quantify the soil chemistry profile and vegetation community associated with bald eagle nest sites. As predicted, observed trends are consistent with soil chemistry changes observed in seabird colonies but occur at a much lower magnitude (Ellis, 2005; Ligeza & Smal, 2003; Wait et al., 2005). Seabird guano is typically high in phosphorous (Ellis, 2005) and my results suggest that eagle guano is likely a significant source of this nutrient. Phosphorus is a limiting resource in North America’s temperate forests (Elser et al., 2007; Filippelli, 2008; Sohrt et al., 2017) so contributions by large, stable populations of bald eagles may therefore be of regional importance. Phosphorous concentrations are also associated with prehistoric human occupation (Schlezinger & Howes, 2000), and although the study area has both a current and deep history of Indigenous habitation (Mackie et al., 2011; McLaren et al., 2018) known human usage sites were not associated with sampled islands.

I did not observe a significant increase in nitrogen (total nitrogen or $\delta\ ^{15}N$), whereas twofold or higher differences in nitrogen are commonly observed in seabird colony studies (García et al., 2002; Ligeza & Smal, 2003; Maron et al., 2006). This could be due to: 1) eagle inputs being obscured by inputs from other vectors of marine-derived nitrogen such as sea spray, river otters, or wolves (Ben-David et al., 1998; Darimont et al., 2009), 2) loss of nitrogen due to leaching or surface water run-off associated with heavy rainfall (Banner et al., 2005), or 3) nitrogen accumulation in vegetation rather than soil. The proximity of soil δ^{15}N, phosphorus and potassium in the PCA plot (Figure 6) suggests that they are correlated and may have a common origin. I think it likely that bird guano is responsible for the observed pattern because it contains substantial amounts of these three nutrients (Ellis, 2005; Hutchinson, 1950).

Vegetation compositional differences were not as pronounced as those observed at seabird colonies, which can experience a total shift from shrub to forb dominated communities (Ellis, 2005). Several factors may be moderating the observed vegetation response. Islands in this study region are dominated by salal (*Gaultheria shallon*), a clonal shrub which performs well in a variety of environmental conditions but is highly competitive in low nutrient regimes (Bunnell, 1990). Even though increases in nitrogen or phosphorous can reduce salal abundance, understory forbs do not necessarily show a positive response (He & Barclay, 2000; Hocking & Reynolds, 2011). Salal’s competitive advantage may explain why no single species drives community-level differences between eagle and reference sites, as well as the observed pattern of shrubs characterizing reference sites but still persisting at some eagle nest sites (Figure 7). A decrease in shrub abundance is often observed at seabird colony sites (Ellis, 2005) but patterns at colonies are hypothesized to be either competitive responses to soil chemistry or successional responses to physical disturbance caused by seabirds (Ellis, 2005; Vidal et al., 2003). Eagles are unlikely to be causing physical disturbance on the ground at nest sites, suggesting observed trends in functional growth form may be a response to soil chemistry. However, prey remains could be attracting other foraging species such as mink or river otter, which could lead to physical disturbance or additional nutrient deposition by these species (Ben-David et al., 1998). Similarly, guano could attract invertebrate foragers (via nitrogen enriched foliage), which in turn could attract predators that cause physical disturbance. In this case, plant functional shifts would be an indirect effect of bald eagle subsidies. I recommend that experimental work such as fertilization trials and detailed sampling target the mechanisms driving soil chemistry and vegetation patterns associated with eagle nest sites. For example, eagle guano and prey remains should be analysed for nutritional content and isotopic signature to clarify the connection between bald eagles and soil chemistry. This region supports a wide range of subsidy vectors such as seabirds, river otter (*Lontra canadensis*), and even humans, making it critical to distinguish the chemical and ecological signature of bald eagles from other vectors (Ben-David et al., 1998; Maron et al., 2006; Trant et al., 2016). Fertilizer trials could distinguish how plant species utilize and respond to guano or prey remains (Szpak et al., 2012) and would be particularly useful for determining uptake and redistribution by clonal plants (e.g. salal). I considered both macro- and micronutrients in this analysis but suggest that future research focus on organic and inorganic forms of nitrogen, potassium, and phosphorous to quantify eagle-derived macronutrients available for incorporation into the terrestrial food web.

Historically, guano-mediated soil chemistry has been treated as a univariate response. Given the synergistic effect of nitrogen and phosphorus enrichment on primary productivity (Blevins et al. 2006; Elser et al., 2007), I recommend that future studies model guano-mediated soil chemistry as a multivariate response. Furthermore, the environmental conditions under which nutrients are mobilized, how interactions between nitrogen, phosphorus, and potassium concentration influence availability, and the temporal dynamics of nutrient accumulation at eagle nest sites should be established. Although seabird subsidy studies typically have small sample sizes, substantial differences in soil chemistry are observed between colony and non-colony sites likely due to the high density of birds at colony sites. I observed soil chemistry patterns similar to those in colony sites but a larger sample size will likely strengthen that signal, given the contrast between high densities of birds at colonies and low densities of birds at eagle nest sites. Future work should explore the spatial and temporal extent of eagle guano deposition because it is unclear how far from nest trees guano is deposited or how deep nutrient accumulation is the soil. The age of an eagle nest or length of occupation of a nest tree could also shed light on variation in nutrient accumulation at nest sites.

Chapter 4: General Conclusion

I used data collected by Fitzpatrick (2018) as part of the 100 Islands project (Davidson, 2017; Fitzpatrick, 2018; Wickham, 2017; Obrist, D., unpublished data; Ernst, C., unpublished data) to determine which environmental conditions led to patterns of nitrogen abundance on temperate rainforest islands and whether nitrogen abundance influenced tree species richness. This research was rooted in the subsidized island biogeography hypothesis, which predicts that nutrient abundance can indirectly influence species richness by directly influencing productivity through addition of nutrients. Attempts to test the subsidized island biogeography hypothesis suffer from the lack of a statistical model demonstrating how island area, distance from mainland and subsidies influence species richness (Barrett et al., 2003). I created a subsidized island biogeography model based on the power function and modified it to include distance from mainland and a parameter for nitrogen abundance which I used as a proxy for nutrient subsidies. I applied this model using tree species data from temperate coastal islands as the dependent variable and showed that as nitrogen abundance increased, species richness decreased.

The subsidized island biogeography hypothesis predicts that nutrient subsidies could either increase or decrease species richness by reducing or increasing local extinction rates. Nutrient deprived environments are unable to sustain populations of some species, which then go locally extinct but an increase in available nutrient resources allows the would-be extinct populations to survive. However, large quantities of nutrient subsidies could trigger high extinction rates if certain species are better at competing for resources and become dominant in the system (Rosenzweig, 1995; Rosenzweig & Abramsky, 1993). Soil and plant δ^{15}N values were higher than expected and it is likely that nutrient subsidies from the marine environment are responsible for ^{15}N enrichment. Modelling shows that small islands exposed to wind and wave action had the highest observed soil and plant δ^{15}N values. As islands become increasingly sheltered by neighboring landmasses, δ^{15}N values decline. The relationship between ^{15}N enrichment and exposure to wind and wave action suggests that there is a nutrient link between the marine and terrestrial environments. Multiple vectors of nitrogen subsidies are possible in this study area so partial contribution from multiple sources makes it difficult to know when naturally occurring δ^{15}N values grade into δ^{15}N values from external sources. However, scenarios of ^{15}N enrichment due to deposition of sea spray and marine fog or islands acting as terrestrial refuges for maritime animals are plausible but remain untested.

Although I did observe a gradient of nitrogen abundance, total soil nitrogen on the sampled islands (0.9 to 2.2 %) is comparable to inland coastal-zone forests, which are considered nitrogen deprived (0.7 to 3.8 %) (Chang et al., 1996; Elser et al., 2007; Collins et al., 2001; Prescott et al., 1993, 2000; Quesnel & Lavkulich, 1980). This suggests that islands are similarly nitrogen deprived systems and are likely not receiving substantial quantities of nitrogen subsidies. The unimodal productivity curve which informs subsidized island predictions suggests that a decline in species richness in response to nutrients happens when nutrient input is substantial (Rosenzweig, 1995). This is likely not the case given the low observed nitrogen values in this study, so richness responses may be due to the environmental conditions leading to increased nitrogen abundance. In fact, validity of the unimodal productivity curve has been challenged as mounting empirical evidence shows a weak relationship between primary productivity and species richness (Adler et al., 2011). Instead, disturbance history, habitat heterogeneity, and assembly history exert simultaneous control over species richness (Grace et al., 2016). Primary productivity in the coastal temperate rainforest is largely driven by changes in topography and accumulation of soil organic matter (Banner et al., 2005; Emili et al., 2006) so I questioned which environmental conditions led to terrestrial nitrogen patterns and used this additional information to aid interpretation of richness patterns.

Total soil nitrogen and foliar enrichment factor ($\delta\ {}^{15}N_{\text{foliar}}$ - $\delta\ {}^{15}N_{\text{soil}}$) both decreased with increasing terrain slope, which may be due to surface water runoff. Nitrate, the end product of mineralization, is more water soluble than ammonium so it is likely lost from the system on steep slopes, resulting in a reduction of total nitrogen (Attiwill & Adams, 1993; Bohn et al., 2002). The highest values of total nitrogen and foliar enrichment factor occur on small, flat islands and these are the conditions where a decline in species richness was observed. Flat terrain is prone to water saturation in this hypermaritime climate but few tree species can tolerate prolonged moisture surpluses. Species richness decline may be due to this intolerance. Finally, small additions of nitrogen may increase the competitive advantage of understory species, reducing tree species richness to those, such as western redcedar, who remain unaffected by increased competition.

Nutrient subsidies such as beach-cast marine algae (Wickham 2017) or marine fog accumulate passively on islands, but some subsidies are mediated by biotic vectors such as seabirds. I conducted an exploratory study to determine whether bald eagles deposit guano and prey subsidies at nest sites, which alter soil chemistry and shift plant community composition. My results show that nest sites have higher phosphorous concentrations than reference sites. Phosphorous is a limiting nutrient in this study area and stimulates primary productivity when applied as a fertilizer in conjunction with nitrogen (Blevins et al., 2006). Higher potassium concentrations are associated with eagle-inhabited islands but not specifically nest sites, which may reflect differential persistence of nutrients in the soil. Contrary to expectations, nitrogen isotope enrichment ($\delta\ ^{15}N$) was not significantly higher at eagle nest sites. Typically, guano from birds with marine-based diets enrich soil in ^{15}N (Ellis, 2005). The lack of elevated ^{15}N abundance may be due to interception of guano by the understory plant canopy or perhaps a small sample size. General trends suggest that $\delta\ ^{15}N$ value are less variable at eagle nest sites. The concentration of other nutrients does not statistically differ between sites but a small sample size limits my ability to detect patterns. Vegetation composition was variable across eagle nest sites, with some being dominated by shrub species while others displayed increased abundance of forbs and graminoids. Despite these trends, composition was not statistically different between sites. Several factors may be moderating the observed vegetation response. Islands in this study region are dominated by salal (*Gaultheria shallon*), a clonal shrub which performs well in a variety of environmental conditions but is highly competitive in low nutrient regimes (Bunnell, 1990). Additions of 1000 kg N/ha are required to substantially reduce salal biomass, at lower fertilization rates understory species may not be able to overcome salal’s competitive advantage (Bennett et al., 2004). This may explain the observed pattern of shrubs dominating reference sites but still persisting at some eagle nest sites. Future studies could quantify differences in inorganic nitrogen abundance between eagle nest trees and reference sites to further characterize the contribution of nutrient subsidies.

This research demonstrates the complex processes that lead to nitrogen abundance and assimilation in temperate forest ecosystems. The ecological effects of subsidies are attributed to their nutritional contribution to a system, but their nutritional contribution is often not explicitly quantified (Anderson & Polis, 1999; Buelow et al., 2018). Instead, proxies such as biomass of beach-cast marine algae and the presence or absence of animals like seabirds are used to represent the nutritional contribution of a subsidy to an ecosystem. Increases in soil or plant nitrogen concentration are often used to demonstrate that an ecosystem has assimilated that subsidy (Anderson & Polis, 1999; Ben-David et al., 1998; Colombini et al., 2003; Vanni et al., 2004). However, correlations between proxies and measures of nitrogen in soil and plants becomes unrealistic in systems where many potential subsidies exist and environmental conditions can shape nitrogen abundance in soil and plants (Bedard-Haughn et al., 2003; Levi et al., 2013; Pinay et al., 2003). I recommend that subsidy studies clarify the physical mechanisms driving nutrient patterns by modelling how relevant environmental conditions influence patterns of nutrient abundance. This approach will provide a more nuanced understanding of subsidy effects than insights made through correlations alone.

Data demonstrating landscape-scale heterogeneity of terrestrial nitrogen is lacking for the Central Coast of British Columbia. Most available soil and foliar nitrogen data originate from localized fertilizer trials conducted on sites actively used for timber harvest (Kranabetter et al., 2013; Prescott & Blevins, 1999). Data generated by the 100

Islands project is the most comprehensive description of nitrogen abundance in this region and the value of dataset is strengthened by including multiple measures of the environmental and physical conditions in which nutrient abundance was measured. These data serve as an invaluable resource for generating hypotheses about the origin and maintenance of nitrogen abundance on understudied coastal forests. My results show that multiple scenarios could lead to observed nutrient and species richness patterns. Future studies could specifically focus on when and where transformative soil processes occur to aid interpretation of nitrogen abundance patterns. Fertilizer experiments that show how different types of subsidies are processed by soil and plants would clarify which measures of nitrogen are best suited to demonstrate that a subsidy has been assimilated by an ecosystem.

Finally, the subsidized island biogeography model I constructed offers a simple, theoretically based framework for testing the effect of nutrients on species richness. The model is not limited to testing the subsidized island biogeography hypothesis and could be used to illustrate the effects of a subsidy (e.g. animal excrement) on various taxa throughout a fragmented landscape or to identify synergistic effects of multiple nutrients (e.g. nitrogen and phosphorous) on species richness.

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Appendix 1: Supplemental considerations

Definitions

Ammonium: An inorganic form of nitrogen (NH_4^+) which plants can absorb through roots using ammonia transporters.

Denitrification: A biological process in which microbes reduce nitrates to gaseous nitrogen (nitrous oxide) which is ultimately lost from the system and returned to the atmosphere.

Foliar enrichment factor: Difference between isotope abundance in foliage and soil, $\delta\ ^{15}N_{foliar} - \delta\ ^{15}N_{soil}$.

Fractionation/fractionating: The ^{15}N enrichment of a material relative to another in a chemical or physical process. Fractionation occurs because more energy is needed to break or form chemical bonds with ^{15}N than ^{14}N so physical or chemical processes tend to discriminate against compounds enriched in ^{15}N. A fractionating process produces ^{15}N depleted products, leaving behind ^{15}N enriched source material. For example, a fractionating process such as metabolism creates ^{15}N depleted waste products but leaves tissue enriched in ^{15}N.

Mineralization: A biological process mediated by soil organisms, wherein organic compounds are decomposed to inorganic compounds.

Nitrate: An inorganic form of nitrogen (NO_3^-) which plants can absorb through roots via several nitrate transport systems.

Nitrification: A biological process in which ammonium is oxidized to nitrite, which are then transformed to nitrates.

Nitrogen isotope abundance (δ ^{15}N): The ratio of ^{15}N to ^{14}N of a sample relative to the ^{15}N:^{14}N ratio of the standard reference material, which is atmospheric nitrogen. Isotopic ratios are generally, small so values are expressed in units of per mil (‰):

$$\delta^{15}\text{N} = 1000\left(\frac{R_{sample} - R_{standard}}{R_{standard}}\right) \tag{2}$$

A positive delta value (δ) indicates that a sample has a higher proportion of ^{15}N than the atmospheric reference material does. In this case, a material is 'enriched' relative to the standard. Negative delta values mean the material has a lower proportion of ^{15}N than the atmospheric reference material does and is 'depleted'.

Total soil nitrogen: The sum of a sample's organic and inorganic nitrogen as proportion of the mass of the total soil sample; N content/mass of sample expressed as a percent.

Volatilization: Enzymatic conversion of ammonium, urea, or uric acid to gaseous ammonia, which is ultimately lost from the system and returned to the atmosphere.

Complexities of Terrestrial Nitrogen Measures

Nitrogenous compounds come in many forms which are differentially incorporated into soils and plants (Attiwill & Adams, 1993). When using terrestrial nutrient concentrations as proxies for subsidization, simultaneously considering multiple measures such as total nitrogen concentration, relative abundances of organic and inorganic forms, and nitrogen isotope abundance may be necessary. Independently, measures of nitrogen may not reflect subsidy inputs but together they provide insight into how nitrogen from a subsidy source is being incorporated into a complex ecosystem (Attiwill & Adams, 1993; Bedard-Haughn et al., 2003; Högberg, 1997).

The physical nature of a subsidy can dictate when and how the terrestrial system will utilize it and consequently, should be considered when determining which nitrogen measures to collect. For example, animal waste products and marine algae are both rich in nitrogen and are recognized as nutrient subsidies in many systems (Frank & Groffman, 1998; Polis & Hurd, 1996b). The total nitrogen content of ungulate urine and beach-cast marine algae differs, approximately 0.36 % and 2.07 % respectively (Hoogendoorn et al., 2010; Villares et al., 2016), but marine algae must undergo multiple stages of decomposition before nitrogenous compounds available to plants and partial decomposition (50 % dry weight loss) can take several months (Colombini et al., 2003; Smith & Foreman, 1984). Urine provides nitrogen in as little as 6 to 10 days by undergoing chemical reactions that convert organic compounds to ammonium, an inorganic compound readily utilized by plants (Frank et al., 2004; Hutchinson, 1950; Michener & Lajtha, 2008). A site receiving urine subsidies can show little to no increase in total soil nitrogen because nitrogen is quickly assimilated by plants and incorporated into plant tissue which is where an increase in total nitrogen is actually observed (Frank et al., 2004). A site accumulating marine algae does show an increase in total soil nitrogen because its organic compounds take time to decompose and are not immediately used by plants (López-Mosquera & Pazos, 1997). Depending on the type of subsidy being introduced to a system, a simple measure of total soil or plant nitrogen may not accurately portray that a subsidy has been incorporation into the system (Craine et al., 2009; Högberg, 1997; Miller & Bowman, 2002).

Soil or plant nitrogen stable isotope values ($\delta\ ^{15}N$) can act as good measures subsidy input and assimilation into an ecosystem because chemical processes such as metabolism or decomposition lead to interpretable patterns of δ^{15}N values (Dawson et al., 2002; Michener & Lajtha, 2008). In general, materials originating from high in the food web will have higher δ^{15}N values than those at the base of the food web because fractionating processes lead to accumulation of ^{15}N enriched compounds through the food web (Michener & Lajtha, 2008). The same fractionating processes lead to higher δ^{15}N values in food webs based on marine primary productivity (Michener & Lajtha, 2008). However, interpretations of values are not necessarily straightforward. Soil δ^{15}N values can significantly change when processes like mineralization (decomposition of organic material), denitrification (conversion of nitrate to gaseous nitrogen), volatilization (conversion of urea or uric acid to gaseous nitrogen), or leaching occur (Bedard-Haughn et al., 2003; Lindeboom, 1984; Mariotti et al., 1981; Mizutani et al., 1985; Nadelhoffer, 1994; Szpak, 2014). These fractionating processes are stimulated by soil moisture, topography, soil substrate, and carbon to nitrogen ratios, leading to ^{15}N enrichment or depletion of soil up to 60 ‰ (Bedard-Haughn et al., 2003; Chang & Handley, 2000; Cheng et al., 2010). This yields extreme heterogeneity of δ^{15}N values across a landscape, where even in the absence of nitrogen subsidies soil δ^{15}N values within a localized area can vary up to 3 ‰ or more and plants can vary up 25 ‰ (Craine et al., 2015; Emmett et al., 1998; Garten & Miegroet, 1994; Templer et al., 2007). For these reasons, it is important to consider how environmental conditions might change the enrichment or depletion of a subsidy's nitrogen once it is incorporated into the soil.

Plant δ^{15}N values can be similar to δ^{15}N values of their nitrogen source (e.g. soil) suggesting that a subsidy has been incorporated into the system (Dawson et al., 2002; Robinson, 2001). However, the extent to which this is true is likely determined by the concentration of soil nitrogen that is available to plants (Cheng et al., 2010; Takebayashi et al., 2010). Under low nitrogen conditions, plants tend to rely on mycorrhizal relationships to acquire nitrogen (Craine et al., 2009; Högberg, 1997). Mycorrhizae acquisition of nitrogen is fractionating so plants tend to have lower $\delta\,^{15}N$ values than their source nitrogen when relying on mycorrhizae for nitrogen (Hogberg et al., 1999). However, when available nitrogen is abundant plant roots can acquire nitrogen without the support of mycorrhizae (Hobbie et al., 1999). Acquisition of nitrogen directly through plant roots is comparatively non-fractionating so under these conditions, plants tend to have $\delta\,^{15}N$ values more similar to those of their nitrogen source (Hobbie et al., 1999). Soil or foliar $\delta\,^{15}N$ values considered independently or in absence of abundance of available nitrogen do not fully describe the nitrogen dynamics of a site, and may lead to false conclusions about the assimilation of a subsidy.

A ‘foliar enrichment factor’ ($\delta\,^{15}N_{\text{foliage}} - \delta\,^{15}N_{\text{soil}}$) may be a reasonable measure to demonstrate that a nitrogen subsidy has been assimilated into a complex ecosystem (Emmett et al., 1998; Fang et al., 2011; Garten, 1993; Mariotti et al., 1981; Michener & Lajtha, 2008). This measure assumes that plant nitrogen content is the end result of a series of decomposition processes that make nitrogen available to plants and that plants are utilizing nitrogen that has accumulated in the soil (Mariotti et al., 1981; Michener & Lajtha, 2008). Several studies have confirmed these assumptions, finding positive correlation among net mineralization, net nitrification and foliar enrichment factor (Cheng et al., 2010; Fang et al., 2011; Garten & Miegroet, 1994; Takebayashi et al., 2010). These soil processes result in an increased abundance of inorganic nitrogen, but a site’s carbon to nitrogen ratio determines of whether net mineralization or nitrification can occur (Prescott et al., 2000). Microbes decompose organic nitrogen into inorganic forms for their own use and generally require a soil C:N ratio of approximately 24 to satisfy their energy and biological maintenance needs. As the soil C:N ratio increases it takes longer for organic material to be decomposed because microbes must find nitrogen for their consumption from other sources like soil nitrate (Attiwill & Adams, 1993). In doing so, they increasingly deplete the soil in the inorganic nitrogenous compounds that plants require. However, when the C:N ratio decreases, microbes have enough nitrogen to meet their own C:N demands and remaining nitrogen is left in the soil for plants to uptake. Under conditions of high inorganic nitrogen abundance, plant $\delta\,^{15}$N values become more similar to soil $\delta\,^{15}$N values and foliar enrichment factor approaches or exceeds zero (Cheng et al., 2010; Fang et al., 2011; Garten & Miegroet, 1994). I assumed that whether inorganic nitrogen is added to the system through net mineralization and nitrification or through a subsidy, foliar enrichment factor would respond similarly. However, foliar enrichment factor does not indicate which subsidy has provided nitrogen to the system, only that the concentration of available nitrogen has increased or decreased.

Recognizing that total soil nitrogen, $\delta\,^{15}$N values, and foliar enrichment factor each have limitations when considered independently, drawing on several measures of nitrogen and environmental conditions can provide a cursory understanding of how a site is processing nitrogen (Högberg, 1997). This approach is likely required to understand the effect of subsidies on species richness in complex systems where multiple nutrient subsidies exist and environmental conditions strongly influence nutrient cycling.

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Appendix 2: Supplementary methods

Data used in this study were generated as part of the 100 Islands project to determine whether beach-cast marine algae influenced species richness across multiple taxa (Davidson, 2017; Fitzpatrick, 2018; Wickham, 2017; Obrist, D., unpublished data; Ernst, C., unpublished data). Fitzpatrick (2018) collected tree species richness, terrain slope, soil samples and vegetation foliage. Bolded words are variables used in the main text of the thesis. !00 Islands project staff selected sampling islands and derived associated biogeographical variables. A general description of the project can be found here: https://www.hakai.org/blog/exploring-100-islands-central-coast/.

Island selection

Islands within the study region were characterized according to biogeographical descriptors relevant to subsidized island biogeography and cross-boundary nutrient transfer which included total area, shoreline convolution, exposure to wind and wave action, and distance from mainland, using the British Columbia ShoreZone dataset (Howes, 2001) and WorldView-2 satellite imagery. A two-step cluster analysis (SPSS v23; I.B.M Corp, 2015) was used to identify and select islands representing a gradient of the desired biogeographical descriptors. Island were defined as a vegetated landmass separated from neighbouring landmasses during high tide. Islands meeting the selection criteria were grouped into geographic “nodes” to facilitate sampling. Considerations such as inaccessibility of islands by small boats and presence of culturally important Indigenous sites made sampling some islands unfeasible. Based on these criteria and constraints, nine nodes were selected with six to 16 islands per node.

Biogeographical variables

Total island area was derived from WorldView-2 satellite images using ArcGIS (ESRI, 2018). Shoreline rocky substrate was excluded from total island area (Cody, 2006). **Coastal margin area** was based on total island area, and was calculated as the zone beginning at shoreline vegetation and extending 40 m inland. **Distance to mainland** was calculated as the shortest linear distance over water to the contiguous North American continent. This variable is expressed in kilometres and was derived from the BC ShoreZone dataset (Howes, 2001).

Following Cody (2006), **coverage by neighboring landmass** is the summation of angles subtended by neighboring islands. Neighboring islands are those within a 250 m shoreline to shoreline radius of the island of interest. The summed angles were then converted to percent coverage, representing the percent of 360 degrees that is occupied by neighboring land. Distances and subtended angles were derived from the aforementioned BC ShoreZone dataset. This study assumed that islands with low coverage by neighboring landmass would be more exposed to wind and wave action. Coverage by neighboring landmass was selected because a nonhomogeneous surface that protrudes from the ocean, like an island, reduces wind speeds experienced by the surrounding environment (Foken & Nappo, 2008). Low wind speeds generate minimal wave action, which reduces the amount of sea spray at the shoreline (Komen, 1994).

The **shore-zone exposure** metric was derived from the BC ShoreZone dataset, which describes the physical character of the island shore-zones using shore units in which the morphology, sediment texture and dynamic physical processes do not vary in the alongshore direction. Exposure categories are assigned based on fetch direction and tidal range and divided into six classes (6 = Very Exposed, 5 = Exposed, 4 = Semi Exposed, 3 = Semi Protected, 2 = Protected, 1 = Very Protected). The “very exposed” category characterizes areas of extreme high wave energy, where shoreline is vertical rock cliff, there is no moderation of open ocean swells in the nearshore, and consequently the splash zone is extremely wide. In contrast, “very protected” shore-zones have very low wave exposure, low diversity of bio-band biota, and have limited intertidal range. A single exposure value was assigned to each island, which reflects most frequently occurring exposure category.

Subsidized island biogeography predicts that a higher shoreline **perimeter-to-area ratio** will increase the flow of nutrients from the ocean to an island because there is a disproportionate amount of land interacting with the marine environment (Anderson & Wait, 2001). The perimeter-to-area ratio was corrected it for island size because the shape of an ecosystem boundary, such island shoreline, moderates the flow of energy between two systems (Ries, et al., 2004). It is hereafter referred to as ‘shoreline convolution’ (Turner et al., 2001):

$$Shoreline\ convolution = \frac{Perimeter}{2\pi} \Big/ 2\sqrt{\frac{Area}{\pi}} \tag{1}$$

In this corrected form, islands deviating from a circular shape lead to shoreline convolution values greater than one regardless of island size. Island perimeter and island area were based on vegetated land only and were derived from WorldView-2 imagery.

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Appendix 3: Supplemental Results Chapter 2

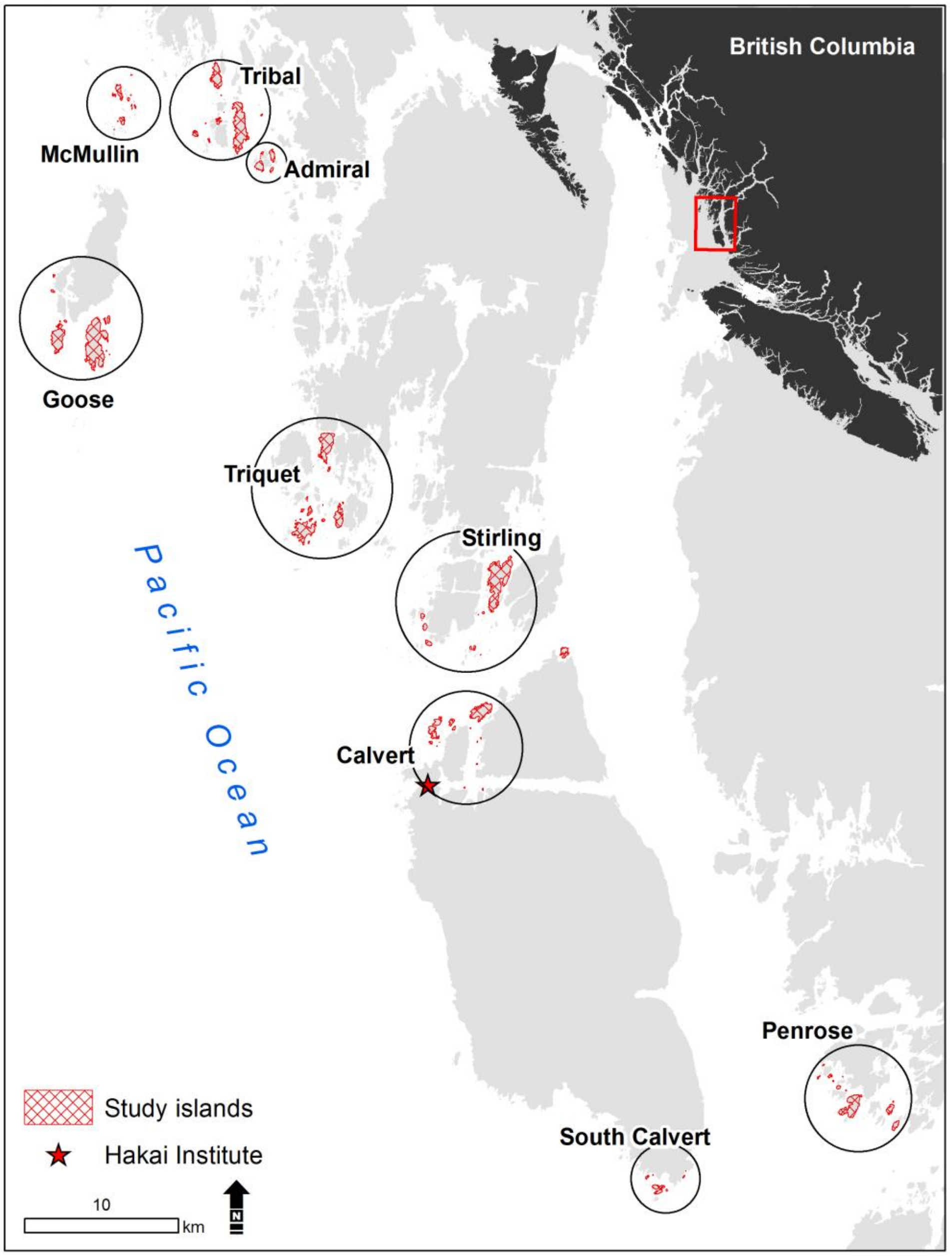

Figure 8 Data were collected on 91 remote islands along British Columbia’s Central Coast (Canada), located in the traditional territories of the Haíłzaqv (Heiltsuk) and Wuikinuxv First Nations people. Although the region has been occupied for millennia by the Haíłzaqv (Heiltsuk) and Wuikinuxv First Nations, their population centers are now concentrated on islands which where not included in this study. Island forests are shaped by wind and waves which leads to low stature, open canopies, a well developed shrub layer, and low productivity relative to other regional forest types. Individual islands are located within island groups or ‘nodes’.

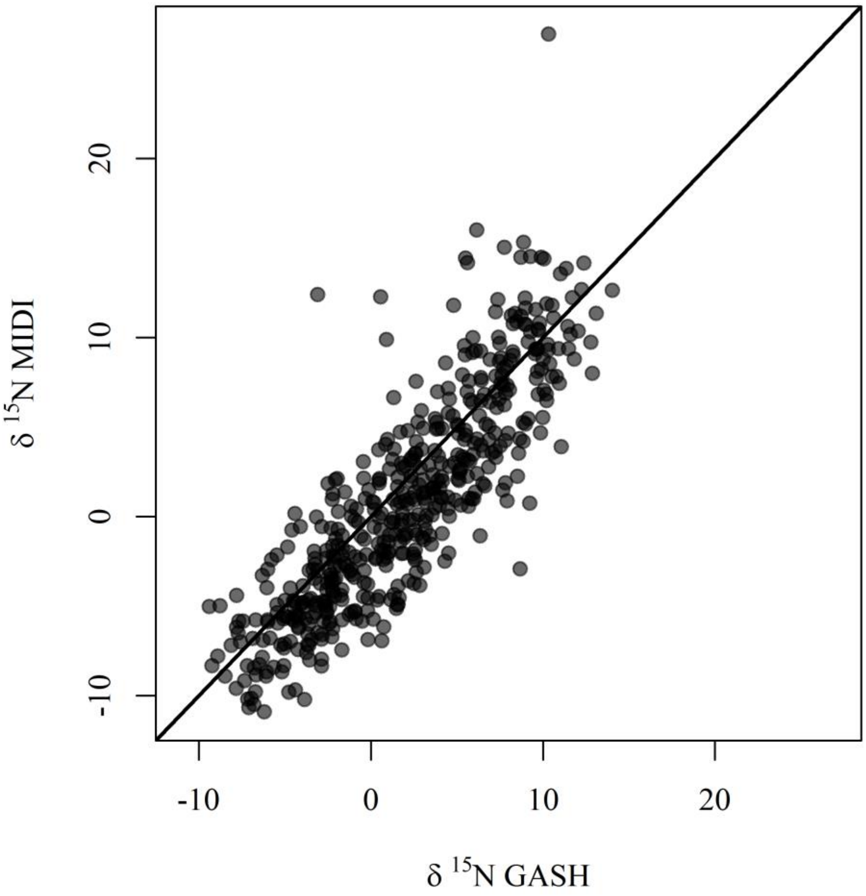

Figure 9 Foliar δ ^{15}N values of the shrub salal (*GASH; Gaultheria shallon*) and forb false lily-of-the-valley (MIDI; *Maianthemum dilatatum*) are very similar, even though ericaceous species (e.g. salal) typically have lower δ ^{15}N values than other species. I pooled foliar samples of these two species to derive an average foliar δ ^{15}N value at the island scale.

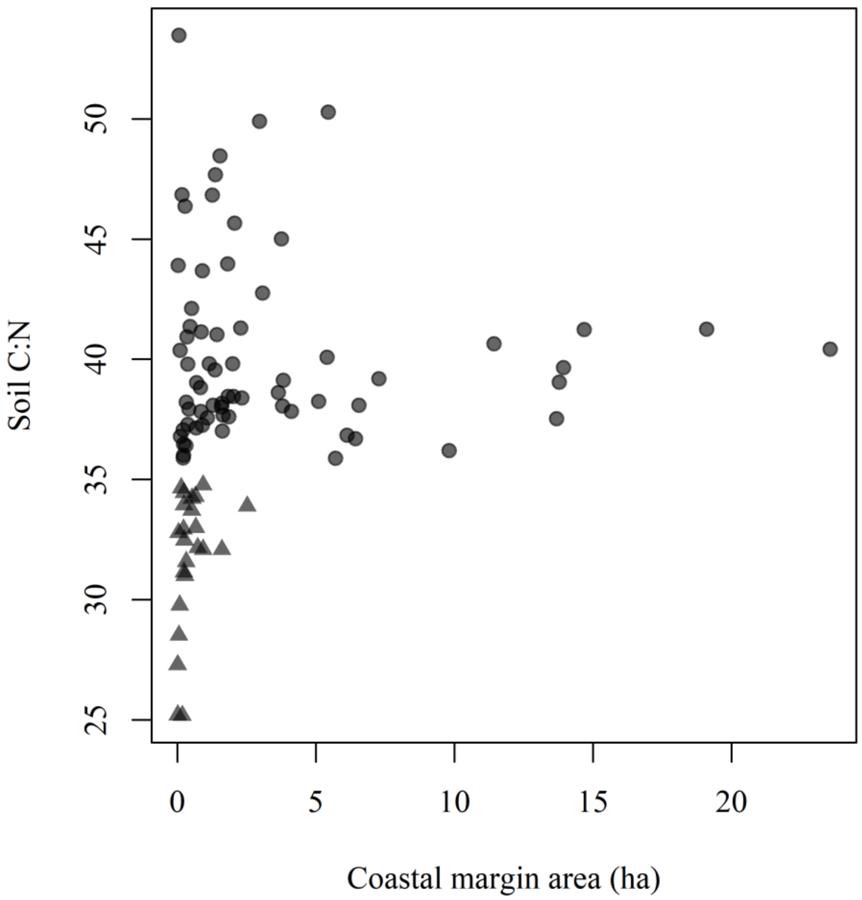

Figure 10 In regional coastal-zone forests, net soil mineralization is strongly predicted by total carbon to total nitrogen ratios (C:N). In similar forest types, soils with C:N ratios less than 35 yield appreciable net mineralization, a process that increases δ ^{15}N values and transforms nitrogenous compounds to readily available forms. If sampled soils behave similarly, approximately 25 % of sampled islands (triangles, n = 23) have the potential for appreciable net mineralization. Larger islands (coastal margin area > 5 ha) tend to have C:N values near 39 while smaller islands have highly variable C:N values.

Table 5 Full list of observed tree species. Sitka spruce, western redcedar and western hemlock were the most abundant species. Relative frequency of a species is the number of individuals divided by the total number of individuals for all species and multiplied by 100.

Scientific name	**Common name**	**Relative frequency (%)**
Alnus rubra	Red alder	0.03
Alnus viridis ssp. sinuata	Green alder	0.17
Callitropsis nootkatensis	Alaska cedar	0.62
Malus fusca	Crabapple	2.21
Pinus contorta var. contorta	Shore pine	0.15
Picea sitchensis	Sitka spruce	30.83
Rhamnus purshiana	Cascara buckthorn	0.87
Taxus brevifolia	Pacific yew	1.10
Thuja plicata	Western redcedar	39.90
Tsuga heterophylla	Western hemlock	24.12

Table 6 Models for species richness were compared using the Akaike Information Criterion (AIC). All models included island node as a random effect. The 95 % confidence set (cumulative weight > 0.95) used for model averaging is bolded. Predictor variables: Area = $\log_{10}$ coastal margin area (hectares), dist mainland = Distance to mainland (km), EF = foliar enrichment factor, totalN = total soil nitrogen (%). K = number of estimated parameters, Δ AIC = difference in the AIC score compared to the top model, w_i = AIC model weight, Cw_i = cumulative AIC model weight.

Model	**K**	**Predictors**	**Δ AIC**	**w_i**	**Cw_i**
Tree species richness					
4	**5**	**EF + area + dist mainland**	**0.00**	**0.17**	**0.17**
2	**4**	**area + dist mainland**	**0.07**	**0.16**	**0.33**
9	**6**	**EF * dist mainland + area**	**0.62**	**0.13**	**0.46**
11	**6**	**EF * area + dist mainland**	**0.73**	**0.12**	**0.58**
3	**5**	**totalN + area + dist mainland**	**1.22**	**0.09**	**0.67**
7	**6**	**EF + area * dist mainland**	**1.57**	**0.08**	**0.75**
5	**5**	**area * dist mainland**	**1.67**	**0.07**	**0.82**
8	**6**	**totalN * dist mainland + area**	**2.36**	**0.05**	**0.88**
6	**6**	**totalN + area * dist mainland**	**2.83**	**0.04**	**0.92**
10	**6**	**totalN * area + dist mainland**	**3.21**	**0.03**	**0.95**
1	3	area	3.61	0.03	0.98
13	9	area * EF * dist mainland	4.59	0.02	1.00
12	9	area * totalN * dist mainland	7.55	0.00	1.00

Table 7 Models for each richness response were compared using the Akaike Information Criterion (AIC). All models included island node as a random effect. The 95 % confidence set (cumulative weight > 0.95) used for model averaging is bolded. Predictor variables: coverage = coverage by neighboring landmass, area = $\log_{10}$ coastal margin area (hectares), slope = terrain slope (%), shzn exp = shore-zone exposure, shore conv = shoreline convolution, totalN = total soil nitrogen (%). K = number of estimated parameters, Δ AIC = difference in the AIC score compared to the top model, w_i = AIC model weight, Cw_i = cumulative AIC model weight.

Model	**K**	**Predictors**	**Δ AIC**	**w_i**	**Cw_i**
Total soil nitrogen					
3	**6**	**coverage + slope + area**	**0.00**	**0.49**	**0.49**
2	**6**	**shzn exp + slope + area**	**1.98**	**0.18**	**0.67**
6	**7**	**coverage + shore conv + slope + area**	**1.99**	**0.18**	**0.85**
5	**7**	**shzn exp + shore conv + slope + area**	**3.96**	**0.07**	**0.92**
1	**5**	**area + slope**	**4.17**	**0.06**	**0.98**
4	6	shore conv + slope + area	6.05	0.02	1.00
Soil δ^{15}N					
3	**6**	**coverage + slope + area**	**0.00**	**0.73**	**0.73**
6	**7**	**coverage + shore conv + slope + area**	**1.99**	**0.27**	**1.00**
1	5	slope + area	17.61	0.00	1.00
4	6	shore conv + slope + area	19.34	0.00	1.00
2	6	shzn exp + area + slope	19.39	0.00	1.00
5	7	shzn exp + shore conv + slope + area	21.17	0.00	1.00
Foliar δ^{15}N					
3	**6**	**coverage + area + slope**	**0.00**	**0.38**	**0.38**
5	**7**	**coverage + totalN + slope + area**	**0.56**	**0.29**	**0.68**
9	**7**	**coverage + shore conv + slope + area**	**1.43**	**0.19**	**0.86**
12	**8**	**coverage + shore conv + totalN + slope + area**	**2.08**	**0.14**	**1.00**
6	6	totalN + area + slope	20.57	0.00	1.00
10	7	totalN + shore conv + slope + area	21.91	0.00	1.00
4	7	shzn exp + totalN + slope + area	22.50	0.00	1.00
1	5	area + slope	23.20	0.00	1.00
11	8	shzn exp + shore conv + totalN + slope + area	23.87	0.00	1.00
7	6	shore conv + slope + area	24.27	0.00	1.00
2	6	shzn exp + area + slope	24.65	0.00	1.00
8	7	shzn exp + shore conv + slope + area	25.87	0.00	1.00
Foliar enrichment factor					
5	**7**	**coverage + totalN + slope + area**	**0.00**	**0.28**	**0.28**
3	**6**	**coverage + area + slope**	**1.30**	**0.14**	**0.42**
1	**5**	**area + slope**	**1.77**	**0.11**	**0.53**
6	**6**	**totalN + area + slope**	**1.82**	**0.11**	**0.64**
12	**8**	**coverage + shore conv + totalN + slope + area**	**2.00**	**0.10**	**0.74**
9	**7**	**coverage + shore conv + slope + area**	**3.27**	**0.05**	**0.80**
4	**7**	**shzn exp + totalN + slope + area**	**3.62**	**0.05**	**0.84**
2	**6**	**shzn exp + area + slope**	**3.76**	**0.04**	**0.89**

7	**6**	**shore conv + slope + area**	**3.76**	**0.04**	**0.93**
10	**7**	**totalN + shore conv + slope + area**	**3.82**	**0.04**	**0.97**
11	8	shzn exp + shore conv + totalN + slope + area	5.62	0.02	0.98
8	7	shzn exp + shore conv + slope + area	5.75	0.02	1.00

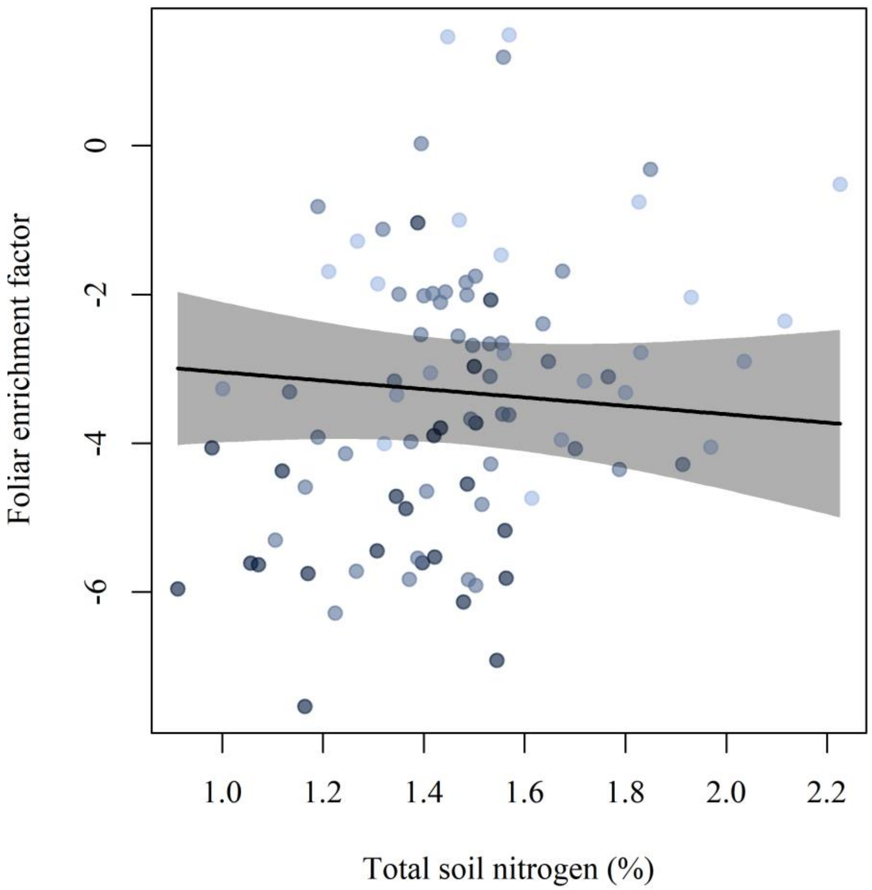

Figure 11 Total soil nitrogen does not differentiate between organic and inorganic forms of nitrogen whereas foliar enrichment factor ($\delta\ ^{15}N_{foliar} - \delta\ ^{15}N_{soil}$) indicates that plants are assimilating inorganic nitrogen in the soil. Foliar enrichment factor is often considered a better indicator of changes in the abundance of inorganic nitrogen than is total soil nitrogen. Our results confirm that total soil nitrogen is a weak predictor of foliar enrichment factor. Points are raw data values and the line represents an averaged model prediction. The averaged model included several other environmental condition parameters, of which coastal margin area and coverage by neighboring landmass were strong predictors of foliar enrichment factor. Colors of raw data points grade from light to dark according to lower, mid, and upper quartiles of coastal margin area. Confidence intervals represent a 95 % confidence level.

Appendix 4: Supplemental Results Chapter 3

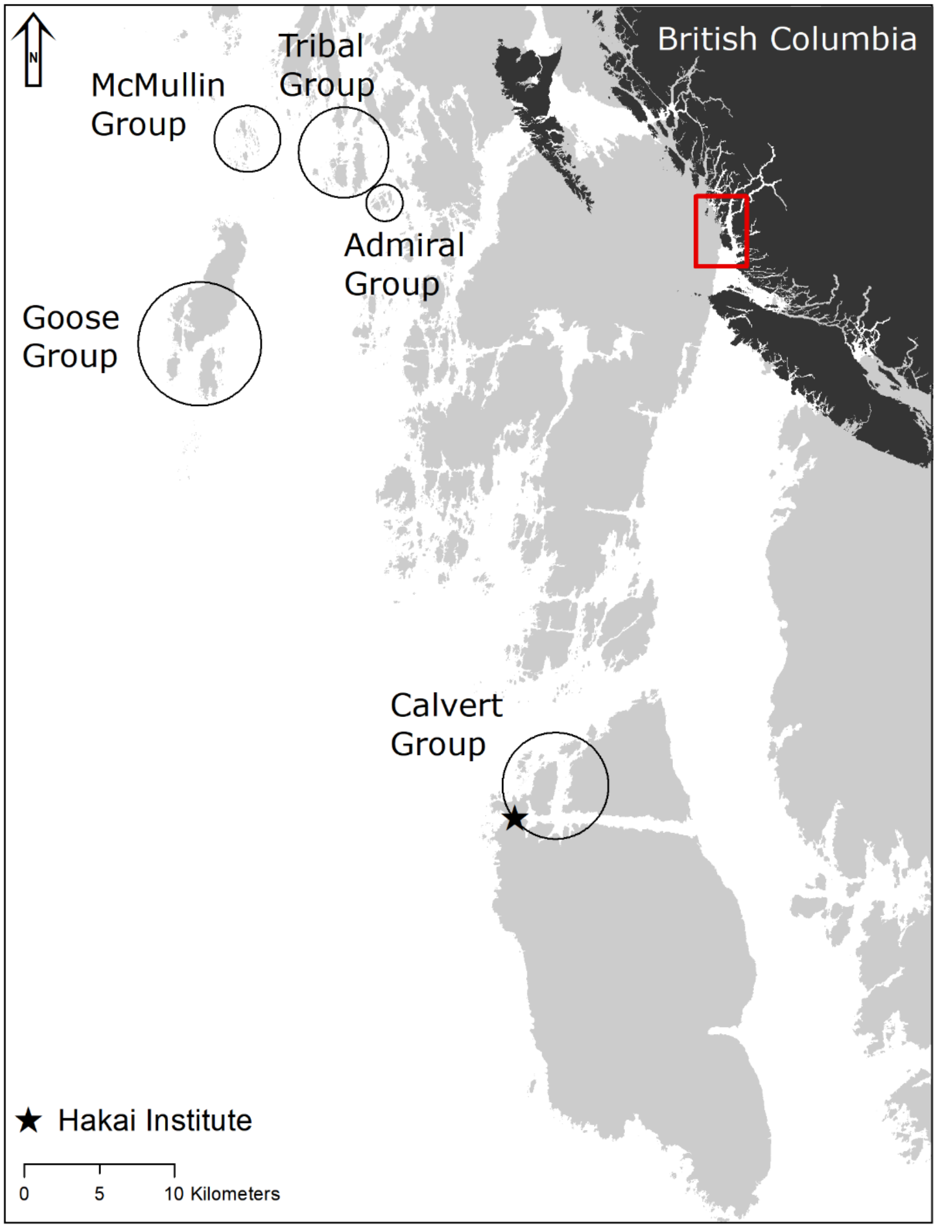

Figure 12 Changes in soil chemistry and vegetation community attributed to bald eagle activity were measured on 14 remote islands of British Columbia’s Central Coast (Canada). Individual islands are located within island groups.

Table 8 Fourteen islands were surveyed. Seven islands had eagle nests and seven islands were selected as references based on similar island area, exposure, and spatial distribution within the study region. Reference trees were selected on reference islands by similarity of species and tree structure to the seven trees hosting eagle nests.

Island	**Type**	**Species**	**Height (m)**	**Diameter (cm)**	**Canopy cover (%)**	**Area (ha)**
CV11	Eagle	*Thuja plicata*	26.8	97.4	93	0.38
GS01	Eagle	*Picea sitchensis*	18.2	56.9	90	0.23
MM04	Eagle	*Picea sitchensis*	19.1	62.5	82	0.22
MM07	Eagle	*Picea sitchensis*	29.5	72.5	90	0.26
MM09	Eagle	*Picea sitchensis*	17.3	61.3	79	0.27
TB10	Eagle	*Tsuga heterophylla*	33.4	75.6	70	0.93
TB12	Eagle	*Picea sitchensis*	17.3	88.4	86	0.32
AD04	Reference	*Thuja plicata*	12.9	57.7	94	0.18
CV04	Reference	*Thuja plicata*	21.5	88.2	90	0.24
GS02	Reference	*Picea sitchensis*	14.1	56	93	0.30
MM01	Reference	*Picea sitchensis*	14.5	50.1	76	0.33
MM08	Reference	*Picea sitchensis*	17.1	59.4	78	0.18
TB06	Reference	*Thuja plicata*	18.7	84.1	92	0.29
TB07	Reference	*Picea sitchensis*	10.9	58.8	93	0.04

Table 9 Species names, codes, functional grouping and nitrogen indicator status of observed vegetation species. The presence of a species at a sampling location (eagle nest tree or reference tree) is indicated by an ‘X’.

Species	**Code**	**Functional group**	**Indicator status**	**Eagle**	**Reference**
Angelica lucida	ANLU	Forb	Rich	x	
Calamagrostis nutkaensis	CANU	Graminoid	Medium	x	x
Cardamine oligosperma	CAOL	Forb	Rich	x	
Carex species	CAREX	Sedge	Rich	x	
Cornus canadensis	COCA	Forb	Poor		x
Conioselinum gmelinii	COGM	Forb	Rich	x	x
Gaultheria shallon	GASH	Shrub	Poor	x	x
Leymus mollis	LEMO	Graminoid	Poor	x	
Lonicera involucrata	LOIN	Shrub	Rich	x	x
Maianthemum dilatatum	MADI	Forb	Rich	x	x
Malus fusca	MAFU	Tree	Rich		x
Menziesia ferruginea	MEFE	Shrub	Poor	x	x
Polypodium glycyrrhiza	POGL	Fern	Medium	x	x
Prenanthes alata	PRAL	Forb	Rich	x	x
Rubus parviflorus	RUPA	Shrub	Rich		x
Rubus spectabilis	RUSP	Shrub	Rich	x	x
Streptopus amplexifolius	STAM	Forb	Rich	x	x
Tiarella trifoliata	TITR	Forb	Rich	x	
Trientalis arctica	TRAR	Forb	Poor	x	
Vaccinium ovalifolium	VAOV	Shrub	Poor		x
Vaccinium parvifolium	VAPA	Shrub	Poor	x	x

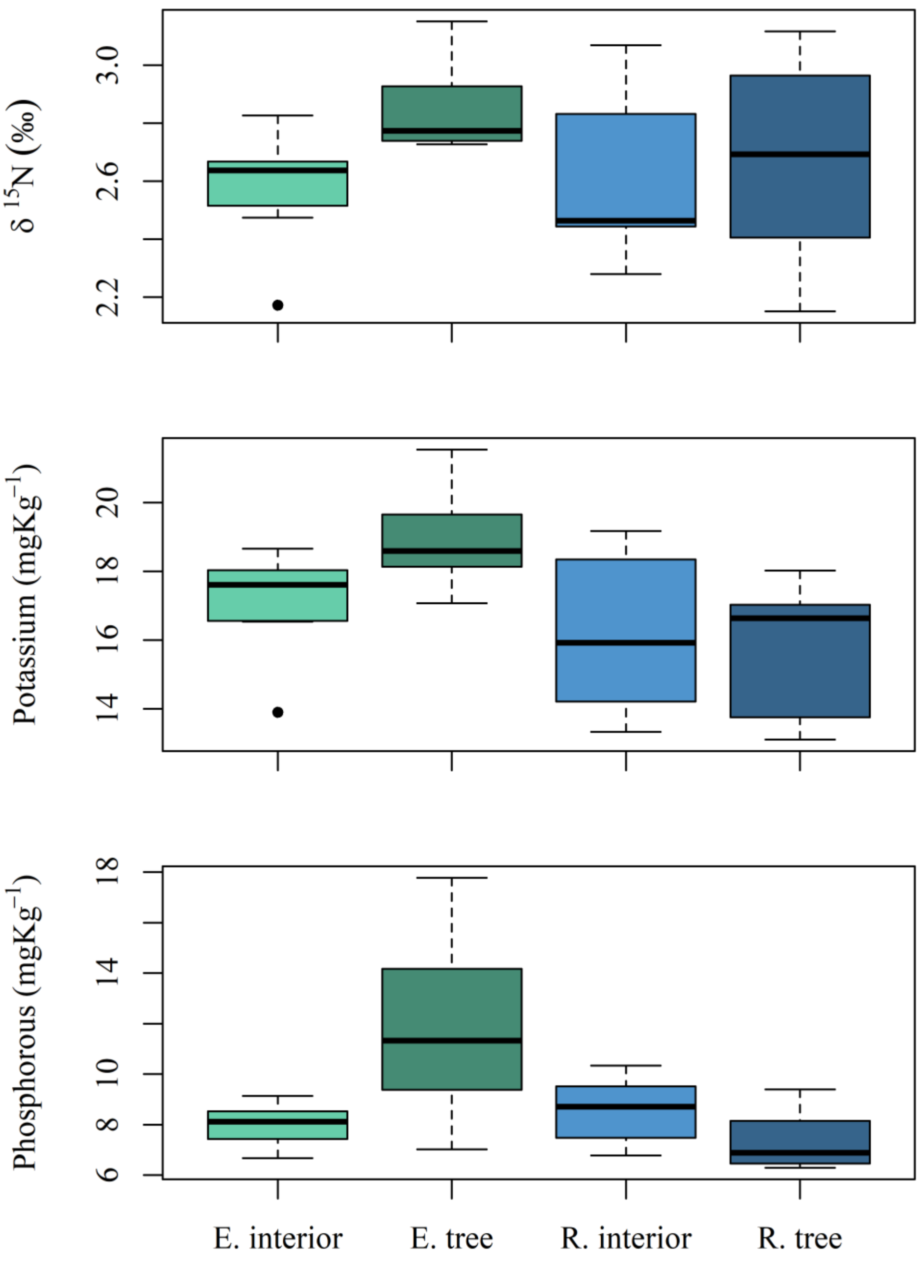

Figure 13 Marine-derived nitrogen ($\delta\ ^{15}N$) in the soil is slightly elevated on eagle-inhabited islands but mean values between sites are not statistically different. Modelling suggests that soil potassium is elevated on eagle-inhabited islands and boxplots demonstrate that pattern. Phosphorous is significantly higher in soil at the base of eagle nest trees.

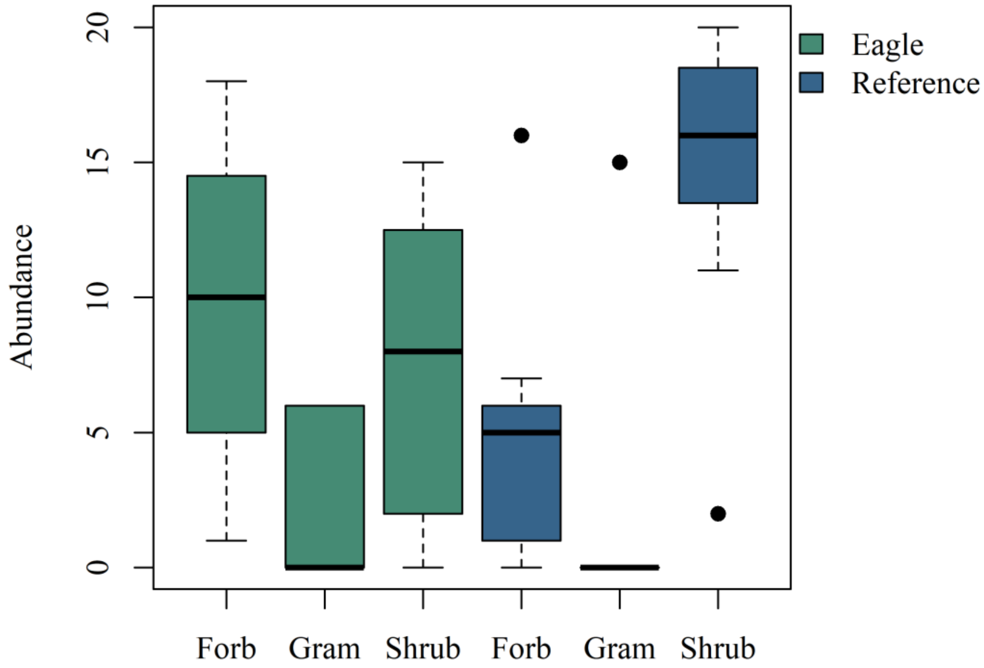

Figure 14 The composition of vegetation at the base of eagle nest trees is highly variable but reference sites tend to be dominated by shrub species. Only one tree species (*Malus fusca*) was observed, data were not included in this figure. Value are raw data and the means are not statistically different.