Islands in a sea of nutrients:
testing subsidized island biogeography

by

Owen T. Fitzpatrick
B.Sc., University of Victoria, 2013

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Abstract

Islands have typically been considered isolated entities, patches of habitat surrounded by an entirely inhospitable marine or aquatic environment. However, there is increasing evidence that islands can be linked to the surrounding environment through the influx of subsidies, which may alter the relationship between species richness and island area. Little empirical work has been done to test these hypotheses in productive ecosystems, however. To better understand the effects of the influx of marine subsidies on island ecosystems, I assessed plant community responses to wrack biomass in an observational study on 74 small islands on the Central Coast of British Columbia. In Chapter 2, I focused on 1) how seaweed wrack subsidies affect the diversity of understory plant communities, 2) whether wrack subsidies affect the species-area relationship, and 3) whether the effect of wrack subsidies is mediated by landscape-scale habitat characteristics such as island area and shoreline slope. To assess the support for these hypotheses, I used selected from models that combined plant community data, remotely-sensed habitat characteristics, and shoreline wrack biomass. I used hierarchical models to provide further insight into the cross-scale influence of these factors on plot-scale responses. I found that wrack subsidies were associated with increased island-scale plant species richness. Although wrack subsidies did not alter the relationship between species richness and area on these islands, I found that smaller islands had higher levels of marine-derived nitrogen, indicating a greater influence of marine subsidies on the nitrogen pool of smaller islands. My results add to the weight of evidence that marine subsidies are drivers of large-scale patterns of species richness, and that the linkage between islands and the surrounding environment has implications for island communities.

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Acknowledgements

First, I would like to acknowledge that my research took place on the Central Coast of B.C. within the unceded territories of the Heiltsuk and Wuikinuxv Nations.

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Dedication

“Wide enough to keep you looking

Open enough to keep you moving

Dry enough to keep you honest

Prickly enough to make you tough

Green enough to go on living

Old enough to give you dreams”

-Gary Snyder, *Mountains and Rivers Without End*

Chapter 1: A general introduction to islands in a sea of nutrients

Islands have played an important role in ecology, biogeography, and evolutionary theory from the very beginnings of those fields (Lomolino et al. 2010, Santos et al. 2016). The theory of island biogeography (TIB) (MacArthur and Wilson 1967) developed out of island research, and sought to explain patterns of diversity on islands. The theory proposes that there is a dynamic equilibrium of species richness on islands, the result of the balance between rates of extinction and immigration. Island area and isolation are assumed to be the primary island characteristics driving those processes. However, just as the broader field of island research has continued to generate questions and extensions, so too has the TIB (Patiño et al. 2017). One extension to the TIB has been the recognition that island communities are connected to the marine environment.

Islands are, by definition, distinct from and isolated by the water that surrounds them. At most, the surrounding matrix of water is often thought to facilitate the dispersal of certain species (e.g., dispersal by oceanic currents: Vargas et al. 2014, Heleno and Vargas 2015). The discrete and isolated nature of islands is a strength for ecological studies, including the TIB (Wardle 2002, Warren et al. 2015). However, when the TIB was applied to terrestrial habitat fragments, it became clear that the analogy between islands and habitat fragments broke down in at least one aspect: in terrestrial environments the matrix is not entirely inhospitable, and has effects on habitat fragments beyond being a simple measure of isolation (Godron and Forman 1981). Instead, the surrounding matrix can influence the connectivity, edge effects, species richness and composition of habitat fragments (Ricketts 2001, Cook et al. 2002, Laurance 2008, Öckinger et al. 2012). In recent decades, the idea that habitat fragments can be influenced by the surrounding matrix has been reframed to apply to islands surrounded by water as well (Polis and Hurd 1996, Polis et al. 1997, Rose and Polis 2000). In my thesis, I explore the implications of the connection between islands and the marine environment, with a focus on marine subsidies.

When ecosystems are connected, materials, energy, information and organisms can flow between adjacent ecosystems (Cadenasso et al. 2003). These four categories of allochthonous inputs can act as ***spatial subsidies***, by literally subsidizing the productivity of recipient ecosystems (Polis et al. 1997). Subsidies are moved between ecosystems by ***vectors***: biotic (e.g. birds, mammals) or abiotic (e.g. wind, water) forces that are capable of transporting subsidies across boundaries (Wiens et al. 1985).

This flow of subsidies between ecosystems is mediated by the boundary that separates ecosystems. Topographical and biotic characteristics of the boundary determine its ***permeability*** to the flow of subsidies: that is, how far and in what quantities subsidies are able to penetrate the recipient ecosystem (Wiens et al. 1985). Another important characteristic of the boundary between ecosystems is its length relative to the area of the recipient ecosystem. Ecosystems with longer perimeters relative to their overall area (perimeter-to-area ratio, PA) are more exposed to inputs of subsidies from the donor ecosystem, and receive a greater magnitude of subsidies for a given area (Polis et al. 1997, Witman et al. 2004). Therefore, marine inputs are expected to be increasingly important relative to *in situ* terrestrial primary productivity on islands with higher PA ratios (Polis and Hurd 1996).

The flow of subsidies from terrestrial to marine and aquatic ecosystems is ubiquitous, and the consequences of those subsidies on recipient ecosystems worldwide are well recognized (Polis et al. 1997, Smith et al. 1999, Oliver et al. 2017). For example, freshwater discharge from terrestrial watersheds is a major source of dissolved organic carbon to the marine environment on the Central Coast of British Columbia (Oliver et al. 2017).

In contrast, the flow of subsidies in the reverse direction—from water to land—has been less well documented (Schulz et al. 2015). Without gravity driving abiotic transport, upland ecosystems are expected to receive lower subsidy inputs overall (Leroux and Loreau 2008), and biotic vectors of subsidies may be important. In recent decades researchers have demonstrated the transfer and the impact of biotically-transported subsidies such as salmon carcasses (Ben-David et al. 1998, Helfield and Naiman 2001, Hocking and Reynolds 2011), otter feces (Crait and Ben-David 2007, Roe et al. 2010), and seabird guano (Ellis 2005). However, abiotically-transported subsidies may still be important at the marine-terrestrial interface, due to the forces of storms, tides and wind (Talley et al. 2006). These subsidies include marine fog (Weathers and Likens 1997, Weathers et al. 2000, Ewing et al. 2009), sea spray (Art et al. 1974), detritus (Polis and Hurd 1996, Paetzold et al. 2008), and seaweed wrack (Orr et al. 2005, Dugan et al. 2011, Liebowitz et al. 2016).

Just as terrestrial subsidies have impacts on marine ecosystems, marine subsidies have impacts on terrestrial communities and food webs. Subsidized primary producers (e.g., plants) have increased growth rates, higher productivity and cover, and altered composition and diversity (Bilby et al. 2003, Williams and Feagin 2010, Spiller et al. 2010, Roe et al. 2010, Hocking and Reynolds 2011). Subsidized primary and secondary consumers (e.g., invertebrates) show similar trends, with increased density and abundance (Anderson and Polis 1998, Polis and Sanchez-Pinero 2000, Ince et al. 2007, Piovia-Scott et al. 2012). Subsidies are thought to be particularly important where the productivity of the donor ecosystem is high relative to the productivity of the recipient ecosystem (Polis and Hurd 1996). However, some empirical evidence suggests that the importance of marine subsidies may decrease as the productivity of the recipient ecosystem increases relative to the productivity of the donor ecosystem (Paetzold et al. 2008). Alternatively, shoreline permeability or the type of vector may be a more important predictor of the effect size of marine subsidies on terrestrial productivity (Marczak et al. 2007, Mellbrand et al. 2011).

What are the effects of subsidies on island communities in particular, and on the relationship between diversity and island area? To understand this, one must understand the mechanism underlying the species-area relationship in the TIB. The TIB assumes that the relationship between species richness and area is driven by the effect of area on extinction rates (Gotelli 2008). Three assumptions link area, extinction rates and species richness: First, the population density of each species is assumed to be constant across the study area, so that population sizes increase with increasing island area (Gotelli 2008). Second, extinction rates decrease as population sizes grow. Finally, lower extinction rates result in higher species numbers at equilibrium. These assumptions suggest that—in addition to area—any factor that increases population densities (and therefore population sizes) should decrease the extinction rate and increase species richness at the equilibrium point (Gravel et al. 2011).

Subsidies can increase the density and productivity of recipient terrestrial communities, altering a fundamental assumption of the TIB (Anderson and Wait 2001). If subsidies increase population densities on islands that are otherwise low in productivity, the diversity of those islands could increase relative to what would be expected for their size. Conversely, if increases in productivity lead to competitive exclusion by dominant species, the diversity of subsidized islands could decrease relative to what would be expected for their size. Thus, understanding the way marine subsidies to land are modified by island size, shape and other characteristics, is fundamental to refining the theory of island biogeography (TIB).

The connection between subsidies and the dynamics of island populations is the conceptual foundation of the subsidized island biogeography (SIB) hypothesis (Anderson and Wait 2001). The SIB hypothesis extends the TIB by linking marine subsidies, boundary characteristics, and the assumptions of TIB. A key prediction is an interaction between island size and subsidy inputs. Small islands, with larger perimeter-to-area ratios, may experience greater inputs of subsidies than would be expected for their size. In turn, these subsidies may increase or decrease the density of populations, leading to increases or decreases of diversity. Ultimately, the relationship between species richness and area could be altered by subsidy inputs affecting smaller islands disproportionately.

It is in this context that the 100 Islands Project attempts to understand the dynamics of species diversity and marine nutrient subsidies on islands of the Central Coast of British Columbia. The 100 Islands Project is an ongoing, interdisciplinary collaboration between researchers at the University of Victoria, Simon Fraser University, and the Hakai Institute. We combined remote sensing and ecological field data to measure species richness, forest-structure, landscape-scale variables, and subsidies on 74 small islands across 2000 km^2 on the Central Coast of British Columbia. Researchers are studying the diversity of different taxonomic groups, including birds, plants, invertebrates and mammals. The composition and abundance of seaweed wrack deposited on island shorelines (a putative source of subsidies) was surveyed as well. A key component of this project is to understand patterns of diversity of vascular plants.

The outer islands of the Central Coast of British Columbia lend themselves to studying the influence of marine subsidies on plant communities in several ways. They are continental islands, ranging from just under 11 km to only 300 m away from mainland British Columbia. The biogeography of continental islands is less dominated by long-term processes such as speciation, but is instead driven by processes on shorter time-scales, including stochastic events, disturbances, and ecological interactions (Lomolino et al. 2010). Furthermore, the islands we selected are relatively small, ranging from just over 100 m^2 to 3 km^2. Both area (Lomolino and Weiser 2001) and isolation (Weigelt and Kreft 2013) may be less important than other factors—such as subsidies—on small, close islands (Lomolino et al. 2010).

Soils of the outer islands of the Central Coast are nutrient-limited, a result of nutrient poor granodiorite bedrock, intense rainfall, and infrequent disturbance events that serve to uplift and aerate mineral soils (Banner et al. 2005). As a result, forests are nitrogen and phosphorous-limited (Kranabetter et al. 2003, 2005), and shoreline forests have been demonstrated to respond to marine subsidies (Trant et al. 2016). I would expect forest understories of the Central Coast to respond to inputs of marine subsidies. However, the Central Coast is productive relative to the arid, nutrient-poor islands and sandy beach ecosystems many subsidy studies have been performed in (e.g., Polis and Sanchez-Pinero 2000, Fariña et al. 2003, Cardona and García 2008). Therefore, the islands the 100 Islands Project has selected provide a test of the effect of subsidies in a terrestrial ecosystem that is both relatively productive and nutrient-limited.

In this thesis, my overarching goal was to understand the interplay between islands and nutrient subsidies, and their combined effects on the species richness of understory plants. In Chapter 2, I look at the potential effect of seaweed wrack subsidies on the relationship between species richness and area, and how shoreline permeability and island size may mediate the impact of wrack subsidies. In the final chapter, I review the implications of my results for the biogeography of plant communities, and for island communities more generally.

Chapter 2: A test of the subsidized island biogeography hypothesis using insular plant communities

Abstract

The theory of island biogeography provides a basis for exploring patterns of diversity on islands. In the decades since the development of the theory, there has been a growing recognition that marine and terrestrial food webs are linked by the flow of subsidies, which may alter the productivity of recipient ecosystems. I tested whether marine subsidies alter the relationship between island area and plant species richness, and if the impact of those subsidies is mediated by landscape-scale habitat characteristics such as island area and shoreline slope. I established a large-scale observational study on 74 small islands (< 3 km^2) on the Central Coast of British Columbia. I measured inputs of marine subsidies through sea wrack accumulations on shorelines, and surveyed island plant communities. I found that 1) wrack biomass was positively associated with island-scale plant species richness, and 2) smaller islands had higher levels of marine-derived nitrogen ($\delta^{15}N$) in soils, and a less pronounced decline in marine-derived nitrogen in soils away from the marine-terrestrial edge. However, I found no evidence that subsidies alter the relationship between species richness and area. Further, I found little evidence that wrack biomass was associated with marine-derived nitrogen in soils, and little evidence for wrack subsidy effects on plot-scale plant species density or composition. The effects of wrack may be obscured by the long-term and consistent inputs of subsidies on islands on the Central Coast. More generally, I found that subsidies are associated with increased species richness independent of island area, and their effect on the relationship between island area and species richness may be context-dependent.

Introduction

Islands have provided insights into fundamental patterns in the fields of ecology and biogeography, including the relationship between area and species richness (Lomolino et al. 2010). Area is a key part of MacArthur and Wilson's (1967) general theory of island biogeography (TIB) along with isolation, and the importance of island area in explaining species richness is well established (Triantis et al. 2012). However, the species richness of small islands is less well-predicted by area below a threshold of island size, a phenomenon called the small island effect (Lomolino and Weiser 2001). Instead, other drivers of species richness may be more important on small islands, including marine subsidies (Anderson and Wait 2001).

There is increasing evidence that island ecosystems are connected to the surrounding marine environment, and that marine subsidies could affect the abundance or diversity of island communities (e.g., Polis and Hurd 1996, Wait et al. 2005, Maron et al. 2006). The degree to which islands are connected to the marine environment depends on characteristics of island shorelines. Islands that are smaller or have more complex shapes have more shoreline relative to their area, and could receive greater inputs of nutrient subsidies than larger or less complex islands (Polis and Hurd 1996, Polis et al. 1997). In addition, the permeability of island shorelines can mediate the deposition and uptake of subsidies (Fariña et al. 2003, Witman et al. 2004, Liebowitz et al. 2016). Permeability is the degree to which the boundary between ecosystems deflects the flow of subsidies, and the boundary characteristics that define it are specific to the type of subsidy (Wiens et al. 1985). Variability among islands of different size in the deposition and uptake of nutrient subsidies could affect the diversity of islands, and alter the relationship between species richness and area expected by TIB. However, most island biogeography studies have ignored variation in resource availability, both within and among islands (Hurlbert and Jetz 2010).

The subsidized island biogeography (SIB) hypothesis links the small island effect to nutrient subsidies and landscape-level factors (Anderson and Wait 2001). The hypothesis predicts that communities on small islands will be more affected by subsidies than those on larger islands. Whereas the TIB assumes that population densities are constant, the subsidized island biogeography hypothesis assumes that population densities may be altered by the input of marine subsidies to an island (Anderson and Wait 2001, Gotelli 2008). Changes in density due to marine subsidy inputs can alter population sizes of island species, thereby changing the extinction rate and ultimately, species richness (Gravel et al. 2011). However, there have been few tests of the SIB hypothesis (e.g., Barrett et al. 2005), and there are still several avenues that deserve more attention, such as the role of subsidies in productive environments (Paetzold et al. 2008) and the mediation of subsidies by permeability (Witman et al. 2004, Marczak et al. 2007) .

I seek to understand how marine subsidies affect diversity and composition on islands, and whether landscape-scale island area and topography (i.e., permeability) mediate the influence of subsidies. To answer these questions, I surveyed 74 islands on the Central Coast of British Columbia. I assessed the effects of seaweed wrack, island area and isolation, and shoreline permeability on understory plant communities. I focused on seaweed wrack as a potential source of marine subsidies to terrestrial plants. Wrack is deposited on coastal shorelines around the world (Polis and Hurd 1996, Dugan et al. 2011, Gómez et al. 2013), and wrack inputs may subsidize terrestrial plants and soils (Cardona and García 2008, Williams and Feagin 2010, Del Vecchio et al. 2013, Villares et al. 2016). I used soil nitrogen and soil $\delta^{15}N$ as proxies for the presence of wrack subsidies in terrestrial soils. Marine organisms are generally enriched in δ^{15}N relative to terrestrial organisms at the same trophic level (Peterson 1987), and δ^{15}N has been used as a tracer of marine-derived sources in numerous subsidy studies.

I predicted that island-scale species richness would increase with higher wrack biomass, and that the effect of wrack would be mediated by shoreline permeability. I also predicted that there would be an interaction between island area and wrack biomass, as suggested by the subsidized island biogeography hypothesis: smaller islands should have a higher intercept and lower slope for the species-area relationship with more wrack biomass inputs. To provide a more stringent test of the island-scale patterns, I used hierarchical models to assess the effects of these variables on plot-scale responses. I predicted that if effects of wrack on species richness were observed at an island-scale, those effects would be present at a plot-scale. Finally, I predicted that an influence of wrack or permeability should also be reflected by changes in plot-scale plant community composition, evenness, and increases in soil nitrogen or δ^{15}N.

Methods

Data Collection

I sampled a total of 74 islands on the Central Coast of B.C. in the summers of 2015 and 2016 (Figure 1). The region occurs in the very wet, hypermaritime subzone of the Coastal Western Hemlock biogeoclimatic zone, which encompasses the coastal islands and a strip of the mainland along the north-central coast of British Columbia (Banner et al. 1993, 2005). The climate is moderated by the influence of the Pacific Ocean, with mild winters, cool summers, and low evapotranspiration potential.

The outer islands of the Central Coast are generally forested, although shoreline edge communities vary, and larger islands on the Central Coast—including several of my study islands—contain bog woodland and open bog in their interiors. Typical forests of the region are relatively open, and are dominated by *Thuja plicata* (western red cedar), *Chamaecyparis nootkatensis* (yellow cedar), and *Tsuga heterophylla* (western hemlock). Common shrub-layer species include *Gaultheria shallon* (salal), *Vaccinium spp*., and *Menziesia ferruginea* (false azalea). Common herb-layer species include *Cornus canadensis* (bunchberry), *Blechnum spicant* (deer fern), and *Maianthemum dilatatum* (false lily of the valley). The bogs of the interiors of larger islands include ericaceous shrubs such as *Kalmia microphylla* (bog-laurel), sedges such as *Trichopohorum cespitosum* (tufted clubrush) and *Eriophorum angustifolium* (cotton-grass), and other typical bog species (e.g., *Drosera rotundifolia* [round-leaved sundew]).

Plant communities directly at the shoreline edge were varied in our study. For example, shoreline forests that are exposed to salt spray and winds are often characterised by an overstory of *Picea sitchensi (*sitka spruce*),* with understories of a variety of species including dense salal and *Calamagrostis nutkatensis* (Pacific reedgrass) (Banner et al. 1993). Dry, rocky shorelines on our study islands had scattered *Pinus contorta* (shore pine), along with *Empetrum nigrum* (crowberry) and *Juniperus communis* (common juniper). Sheltered and steep shorelines often had a dense forest overstory overhanging the water, with typical forest understory vegetation at the edge.

Islands were selected for sampling using two-step cluster analysis in SPSS (IBM Corp. 2015). A set of five descriptors was generated for nearly 1500 islands on the Central Coast: distance from mainland, area, normalised perimeter-to-area ratio, exposure, and the proportion of area occupied by land within a 500 m radius. Cluster analysis identified five clusters of islands based on the set of descriptors. To facilitate sampling logistics, islands were then grouped by geographic proximity into “nodes”, each of which contained islands from multiple cluster groups.

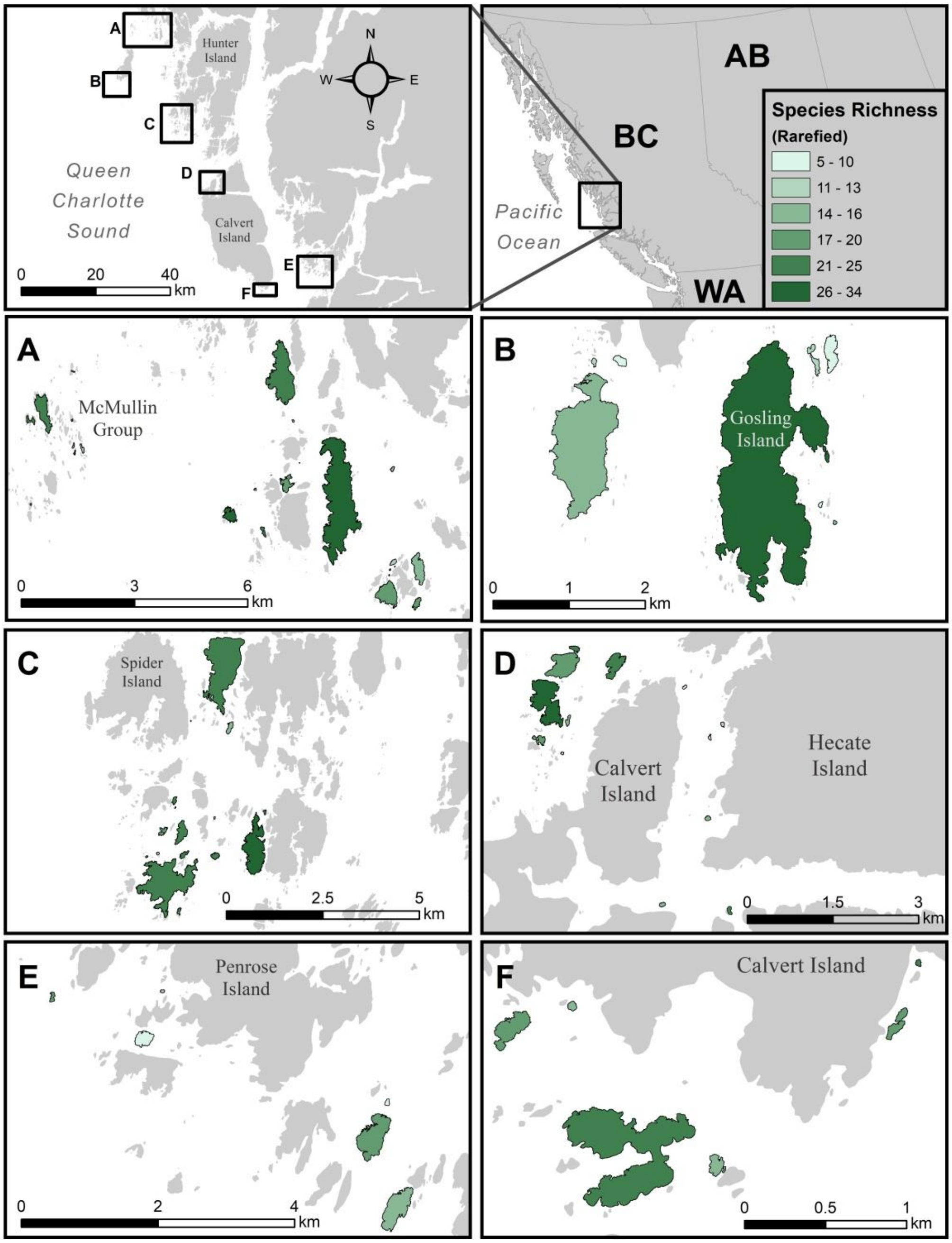

Figure 1. Study region on the Central Coast of British Columbia. Sampled islands are highlighted in green. Darker green indicates higher island-scale species richness (controlled for area sampled).

I established one transect at each of four GPS waypoints corresponding to the four cardinal directions (Appendix S1: Figure S1.1). Each transect was perpendicular to the shoreline and extended up to 40 m into the interior of the island, although this distance decreased on smaller islands (see Appendix S1 for further detail). I established five 1 m^2 quadrats at 10 m intervals along each transect, starting at the shoreline. The shoreline plot was established as close to the upper edge of the intertidal as possible, with the criteria that the majority of the substrate was soil, and not solid rock, water, or other substrates unsuitable for plant growth.

In each quadrat, I measured the percent cover of vascular plant species, as well as abiotic and biotic covariates. I identified vascular plants to the species level when possible, while I recorded both bryophyte cover and lichen cover as single values. Additional percent cover data in 1 m^2 quadrants were collected as part of a concurrent project focusing on subsidy effects on birds (D. Obrist, unpublished data). These additional quadrats were placed at avian point count locations, which were spaced at 250 m intervals and stratified by habitat type. Percent slope of each quadrat was measured using a clinometer. I took three volumetric soil moisture subsamples within each quadrat using a Field Scout TDR 300 Soil Moisture Meter. The soil moisture probe was not functioning for a subset of six islands (n = 97 quadrats). I collected soil samples for these plots, and imputed the missing volumetric values using a regression equation derived from plots with both volumetric and gravimetric soil moisture (see Appendix S1 for more detail).

Remote-sensing was used to derive estimates of forest structure variables and shoreline topography. First, unmanned aerial vehicles (UAV) and LIDAR were used to create terrain models for each island (W. Nijland, unpublished data). Forest structure variables were then derived for each plot, in 10 m^2 grid cells centered on each 1 m^2 quadrat. The forest structure variables included measures of tree height (mean height, max height, and volume) and measures of canopy complexity (surface area ratio and surface volume ratio). These variables were then reduced using principal components analysis (PCA), and scores from the first principal axis (PC1) were used as a single forest structure variable. Low forest structure PC1 scores were associated with taller, more structurally complex forests with higher basal area and canopy cover. See Appendix S1 for further detail on the ordination of forest structure variables.

I used shoreline slope as a permeability metric: lower shoreline slopes may facilitate the transfer of passively-transported marine detritus inland (W. Anderson unpublished data cited in Witman et al. 2004, Talley et al. 2006). Island-scale shoreline slope was measured as the average of the median slope of the ground surface along transects spaced every 5 m along the shoreline. These transects extended from the high tide line to the vegetation edge, perpendicular to the shoreline of the island (W. Nijland, unpublished data). Transect-scale shoreline slope was calculated as the average within a 20 m radius buffer around the transect start-point.

Wrack biomass was measured at shoreline sites centered on the cardinal direction waypoints (i.e., the transect start-points). At each shoreline site, three transects were established: one at the recent high tide line, one at the highest wrack line visible, and one in the terrestrial edge. Wrack biomass for a given site represents the average amount of wrack (g) found in nine 1 m^2 quadrats randomly sampled along the three transects. (S. Wickham, unpublished manuscript). I calculated island-scale wrack biomass as an average across all sites on each island. Wrack biomass was not present at shoreline on 64% of the transects, and on 35% of islands.

To quantify inputs of marine-derived nitrogen to the terrestrial ecosystem, I sampled soil at the shoreline (0 m) and interior (40 m) quadrats of each transect (Appendix S1: Figure S1.1). I sampled 250-500 g of soil from the first 10 cm of soil, with the litter layer removed. Total soil nitrogen was measured using combustion elemental analysis, and was expressed as a percentage of total soil mass (g/100 g). Soil $\delta^{15}N$ was expressed in units of parts per mil (‰). Total nitrogen and nitrogen stable isotope analyses were done at the Government of British Columbia's Analytical Chemistry Laboratory, and the Pacific Forestry Center, respectively.

Response Variables

Island-scale species richness response

To compare species richness between islands, I performed sample-based rarefaction and extrapolation with iNEXT (Hsieh et al. 2016) in R. I incorporated the additional randomly-sampled quadrat data into the rarefaction process, to provide a more complete measure of island species richness (D. Obrist, unpublished data). I converted the percent cover data of each quadrat to incidence data (presence/absence) for the rarefaction process. I standardized to 14 quadrats per island, below the median number of 20 quadrats per island: I chose 14 because it was double the reference sample size of the smallest four islands (n = 7 quadrats), which is the most recommended for reliable extrapolation (Chao et al. 2014).

My measure of island-scale species richness is thus the cumulative species richness per island, found in a standardised 14 m^2 area. Island biogeography studies generally use exhaustive surveys (e.g., Morrison 1997, Cody 2006) or systematic belt transects (e.g., Kohn and Walsh 1994) to survey for species, whereas my quadrat-based sampling design was a trade-off to allow a more intensive look at the impact of marine subsidies on plant communities—particularly at the shoreline edge. Although the post-hoc rarefaction and extrapolation process means my sampling effort is essentially fixed rather than proportional to island size, larger islands had more transects and more randomly-sampled quadrats, and therefore my measure of island-scale species richness still integrates the potential effect of more habitat types being present on larger islands.

Plot-scale community composition response

To derive a measure of community composition at the plot (1 m^2) scale, I performed PCA on the quadrat by species matrix using the vegan package (Oksanen et al. 2015) in R. The scores from the first principal axis (PC1) of the PCA for each 1 m^2 quadrat were used as a univariate response variable, representing community composition. More positive PC1 scores were associated with higher relative abundance of *Gaultheria shallon* (salal); more negative PC1 scores were associated with higher relative abundance of *Maianthemum dilatatum* (false lily of the valley) (Appendix S1: Figure S1.3, Table S1.1). In addition, PC1 scores were strongly negatively correlated with a nitrogen-index (r_s = -0.76, P = <0.001; Appendix S1: Figure S1.4). Therefore, the PC1 scores represent a gradient of soil nitrogen preference: negative scores represent higher nitrogen preference and availability, and more positive scores represent lower nitrogen preference and availability (Klinka et al. 1989). See Appendix S1 for further detail on the ordination.

Plot-scale diversity responses

I used two plot-scale measures of diversity as response variables: species density and evenness. Species density is the number of species per unit area, and depends not only on species richness (number of species per number of individuals), but also on the number of individuals per unit area (Gotelli and Colwell 2001). SIB predicts that species richness will increase due to an increase in density. Species density may allow me to capture the potential effects of both increasing density and increasing species richness with increased productivity, although I cannot parse out their individual effects. Evenness was expressed as a Hill number of order 2. The Hill number of order 2 is equivalent to the Gini-Simpson index (a common diversity metric), but expressed in units of effective species (Jost 2006).

Analysis

Island-scale species richness

To evaluate the influence of subsidies, shoreline permeability and island biogeography variables on island-scale species richness, I fit models that were combinations of different *a priori* hypotheses (see Appendix S1: Table S1.2, Table S1.3 for detailed hypotheses and the complete model set). I included island area and isolation to assess whether patterns in island-scale species richness could be best explained by a combination of island biogeography variables. To test the SIB hypothesis, I included both island-scale wrack biomass and an area by wrack biomass interaction: the SIB hypothesis predicts that the species richness of smaller islands will be disproportionately affected by subsidy inputs (Anderson and Wait 2001). Finally, to test whether permeability mediates the influence of passively-transported wrack subsidies on island ecosystems, I included island-scale shoreline slope and a shoreline slope by wrack biomass interaction.

I performed exploratory analysis following the protocol of Zuur et al. (2010). I log-transformed both island area and average wrack biomass to linearize the relationship with the rarefied species richness response. I scaled and centered all continuous predictors prior to the analysis. I fit models with the lme4 package (Bates et al. 2015) in R, with a random effect of node (island group). I selected the top model using Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002) . I used the MuMIn package (Barton

2017) in R to derive model-averaged parameter estimates from the subset of models with a ΔAICc <2 (Burnham and Anderson 2002). I used the zero-method for model-averaging, which is recommended when the relative strength of the effect of predictor variables on the response is of interest (Grueber et al. 2011). The marginal R^2 (the variance explained by the fixed effects) for each model was obtained from the MuMIn package, using the method of Nakagawa and Schielzeth (2013).

Plot-scale community and nutrient responses

To provide a closer look at the influence of wrack subsidies, shoreline permeability and island biogeography variables on plot-scale (1 m^2 quadrat) vascular plant responses and soil nutrients, I fit hierarchical models using the lme4 package (Bates et al. 2015) in R. The plot-scale responses were PC1 scores (see *Community composition response* section above), species density, evenness, soil nitrogen and soil $\delta^{15}N$.

The plot-scale models were similar to the models generated for the island-scale hypotheses, with some modifications (Appendix S1: Table S1.2, Table S1.4). I included a “local” model that included only plot-scale abiotic and biotic covariates: slope, soil moisture, forest structure, and distance to shore. I used these variables to capture edge effects and other variability, but they were not of principal interest, and so I included them in each subsequent model to control for their effects. I also included interactions between distance to shore and area, shoreline slope, and wrack biomass. I used transect-scale wrack biomass and shoreline slope as the subsidy and permeability variables, respectively. I fit the soil nutrient responses (total soil N and $\delta^{15}N$) to the same models as the vascular plant responses, with further modifications to the model set (see Appendix S1: Table S1.5).

The random structure for all models included island, transect nested within island, and random slopes for distance to shore and wrack habitat, to allow for cross-level interactions (Appendix S1: Table S1.6). I followed the same steps for data exploration, transformation, and model selection as for the island-scale analysis (see *Island Scale Diversity* section above). Plots, transects and islands with missing data were excluded from the analysis: this resulted in a final sample size of 1218 plots, 284 transects and 70 islands for the species density and composition models; and 435 plots, 217 transects, and 69 islands for the soil nitrogen and δ^{15}N models.

Results

Island-scale diversity

97 species of vascular plants were identified in the 1 m^2 quadrats on the 74 islands I sampled (Appendix S2: Table S2.1). Island-scale rarefied species richness ranged from approximately 5 to 34 species (Figure 1), whereas raw species richness (i.e., the number of species in all plots on a given island) ranged from 5 to 54 species.

The top model set (ΔAIC_c <2) for species richness included distance to mainland, area, wrack biomass, and an interaction between area and wrack biomass (Table 1). Both area (Figure 2B) and wrack biomass (Figure 2C) were positively associated with species richness, although area was more important (Figure 2A). However, distance to mainland ($p = 0.31$) and the interaction between area and wrack biomass ($p = 0.08$) had no effect on species richness.

Table 1. Top model sets for (A) island-scale species-richness response, (B) plot-scale species richness, (C) community composition, (D) soil nitrogen and (E) soil δ^{15}N, identified using AIC_c. Shown are models with ΔAIC_c less than 2. All plot-scale models include local covariates (distance to shore, slope, soil moisture, and forest structure) in addition to the variables listed

below. *K* = number of model parameters, ΔAIC$_c$ = change in AIC score from the top model, w$_i$ = AIC$_c$ model weight. Area refers to log$_{10}$ area (m^2); wrack refers to log$_{10}$ wrack biomass (g).

Model rank	**K**	**ΔAIC$_c$**	**w$_i$**	**Marginal R^2**	**Parameters**
A) Island-scale rarefied species richness					
1	7	0.00	0.49	0.30	Wrack, area, distance to mainland, area × wrack
2	6	0.94	0.31	0.27	Wrack, area, distance to mainland
B) Plot-scale species density					
1	17	0.00	0.90	0.18	Area, distance to mainland
C) Plot-scale community composition (PC1 scores)					
1	15	0.00	0.29	0.08	Local model only (distance to shore, forest structure, soil moisture, slope)
2	17	1.19	0.16	0.08	Area, distance to shore, area × distance to shore
3	16	1.40	0.14	0.08	Wrack
4	16	1.57	0.13	0.08	Area
D) Plot-scale soil nitrogen					
1	19	0.00	0.52	0.15	Wrack, area, distance to shore, area × wrack, wrack × distance to shore
2	20	1.82	0.21	0.16	Wrack, area, distance to shore, area × wrack, wrack × distance shore, area × distance to shore
E) Plot-scale soil δ^{15}N					
1	20	0.00	0.65	0.45	Wrack, area, distance to shore, wrack × distance to shore, area × distance to shore, area × wrack
2	17	1.74	0.27	0.45	Area, distance to shore, area × distance to shore

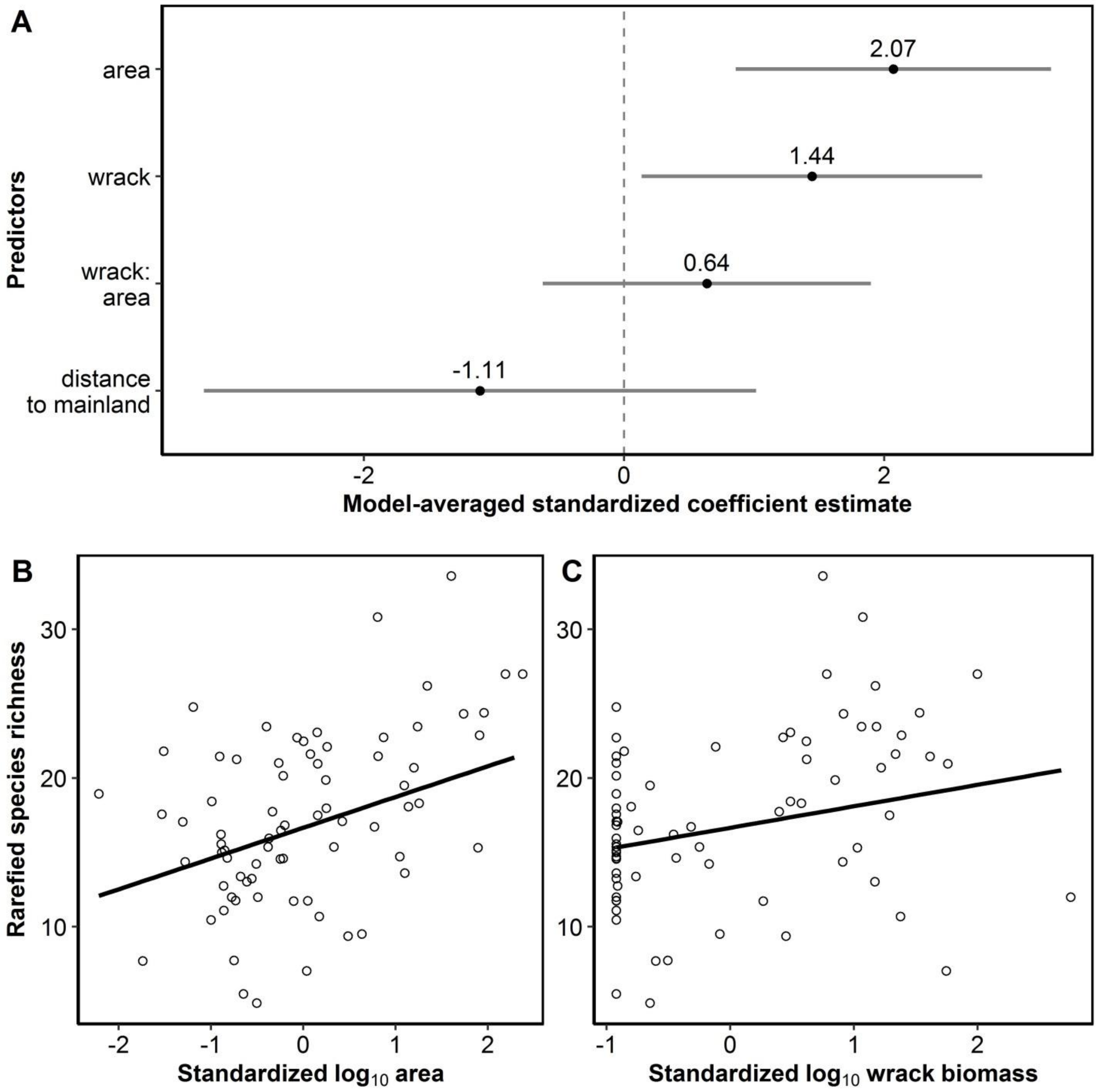

Figure 2. A) Model-averaged, standardized coefficient estimates showing the relative strength of predictors for island-scale rarefied species richness. Area refers to $\log_{10}$ area (m^2); wrack refers to $\log_{10}$ wrack biomass (g). Error bars represent 95% confidence intervals. Species richness is positively predicted by both (B) island area and (C) wrack biomass. Predicted lines are derived from the model-averaged estimates.

Plot-scale community and nutrient responses

The top model for both the plot-scale species density and the evenness responses included distance to mainland and area as predictors, in addition to the local-scale predictors (Table 1). The direction of effects of all predictors was the same for both species density and evenness (although relative strengths of predictors varied), so only the results for species density are presented here (see Appendix S2: Figure S2.1 for coefficients of the top model for evenness).

The top model set (ΔAIC_c <2) for community composition (PC1 scores) included effects of area, wrack biomass, and an interaction between area and distance to shore in addition to the local-scale predictors (Table 1). However, these terms were rarely included in the top model set and only in lower-weighted models. Distance to shore, slope, and soil moisture were the strongest predictors of PC1 scores.

The top model sets for both soil N and soil $\delta^{15}N$ included the same set of predictors: main effects of area and wrack biomass; and interactions between area and distance to shore, area and wrack biomass, and wrack biomass and distance to shore (Table 1). Area was included in both of the top model sets, but wrack biomass and the interactions again appeared rarely, and only in lower-weighted models. Shoreline slope was not included in the top model sets for any of the responses.

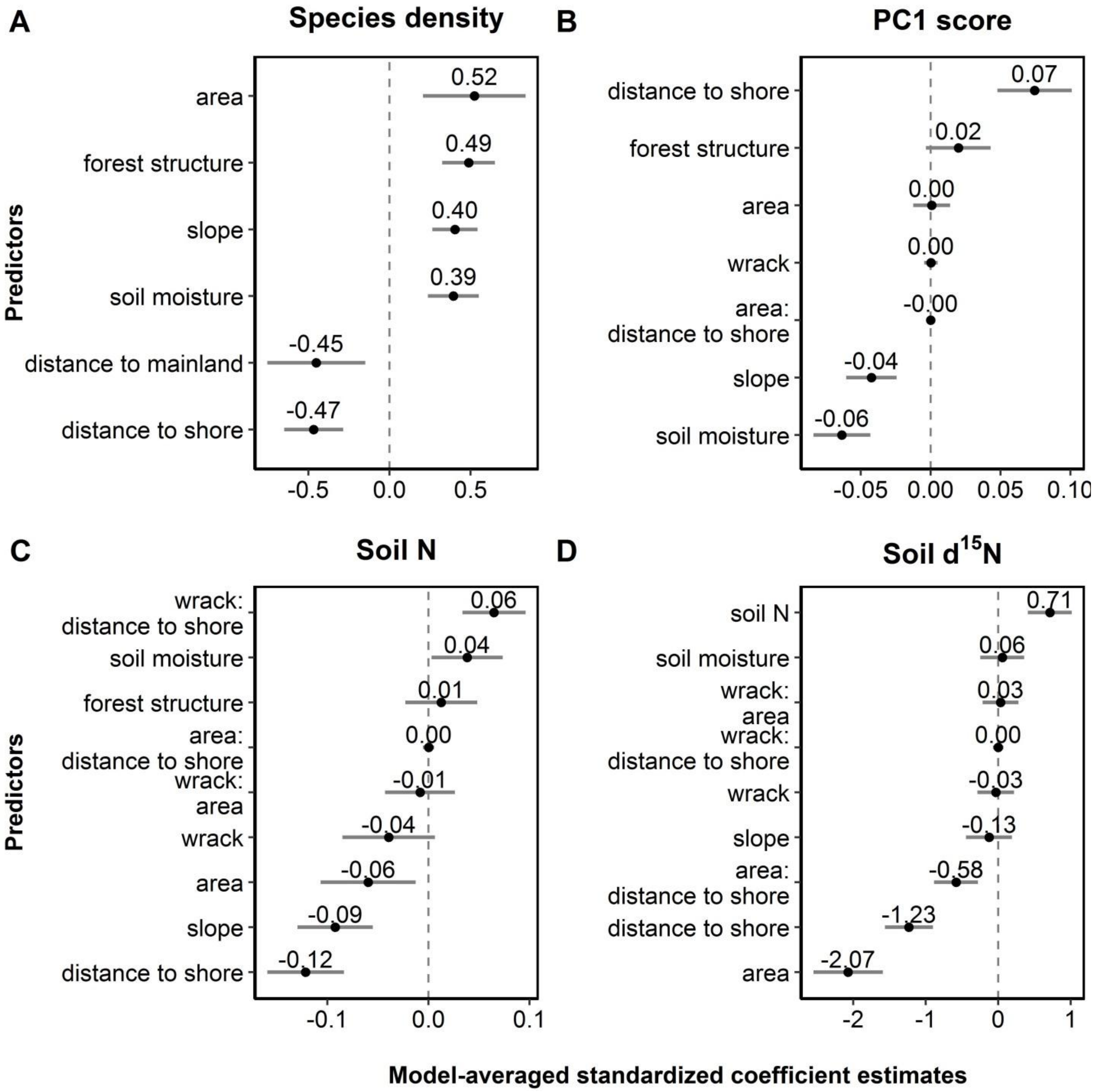

Figure 3. Model-averaged standardized coefficient estimates showing the relative strength of model-averaged predictors from the top models for plot-scale (A) species density, (B) community composition (PC1 scores), (C) total soil N, and (D) soil δ^{15}N. Area refers to $\log_{10}$ area (m^2); wrack refers to $\log_{10}$ wrack biomass (g). Error bars represent 95% confidence intervals.

Island area was the strongest predictor of both species density and soil δ^{15}N, and one of the strongest predictors of soil N (Figure 3). Island CV04 appears as an outlier in the plot of soil N and area (Figure 4C). Species density increased with area, whereas both soil N and soil δ^{15}N decreased with area (Figure 4). The effect of area on soil δ^{15}N was more negative further from shoreline (Figure 4D). In other words, soil δ^{15}N declined with increasing area, but it declined less rapidly with area at shoreline than in the interior of islands. Area had no effect on community composition. Islands TB06, GS01, MM07 and MM08 appear as outliers on the scatterplot of PC1 scores and area: their mean plot community composition values have lower relative abundance of salal and higher relative abundance of false lily of the valley than would be expected for islands of their size (Figure 4B).

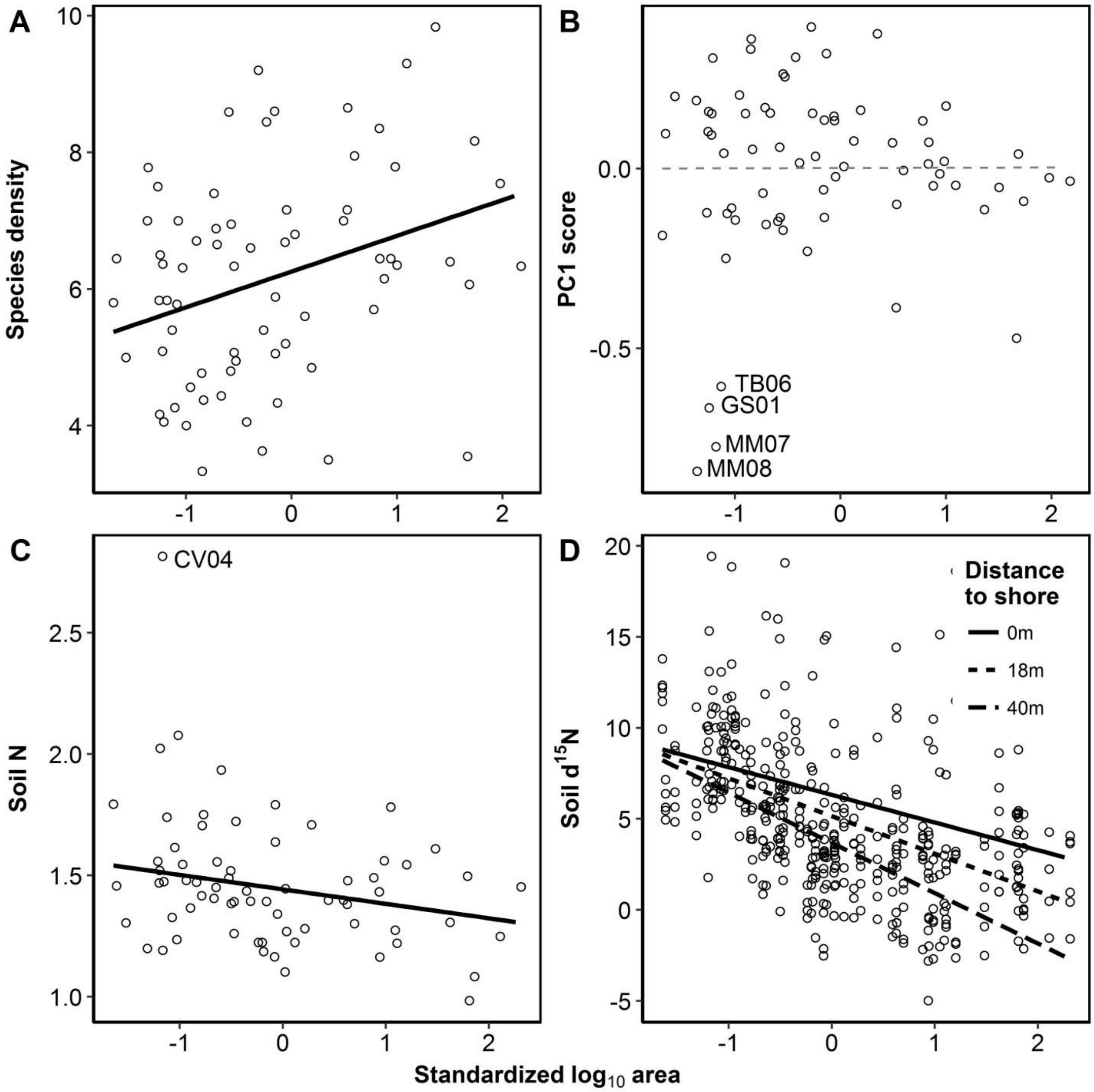

Figure 4. Relationships between plot-scale responses and island area. Plot-scale species density increases with island area (A). There is no effect of area on PC1 scores (B). Both soil N (C) and soil $\delta^{15}N$ (D) decline with island area, but soil $\delta^{15}N$ declines more rapidly with island area further from shore. Predicted lines are derived from coefficient estimates of the top model set for each response. For the relationship between area and richness (A), PC1 scores (B) and soil N (C), mean plot responses per island are plotted for easier visualisation.

Distance to shore was the strongest driver of species density, PC1 scores, and soil N, and the strongest driver of soil $\delta^{15}N$ aside from island area (Figure 3). Species density, total soil N, and soil $\delta^{15}N$ increased closer to shoreline (Figure 5). In addition, plot PC1 scores decreased closer to shoreline, meaning the relative abundance of salal declined and the relative abundance of false lily of the valley increased closer to shoreline (Figure 5B). The effect of distance to shore on soil N was mediated by wrack biomass: in plots along transects with more wrack biomass at shoreline, soil nitrogen declined less rapidly away from shore (Figure 5 C). I assess its effects further in the supplementary material (Appendix S1).

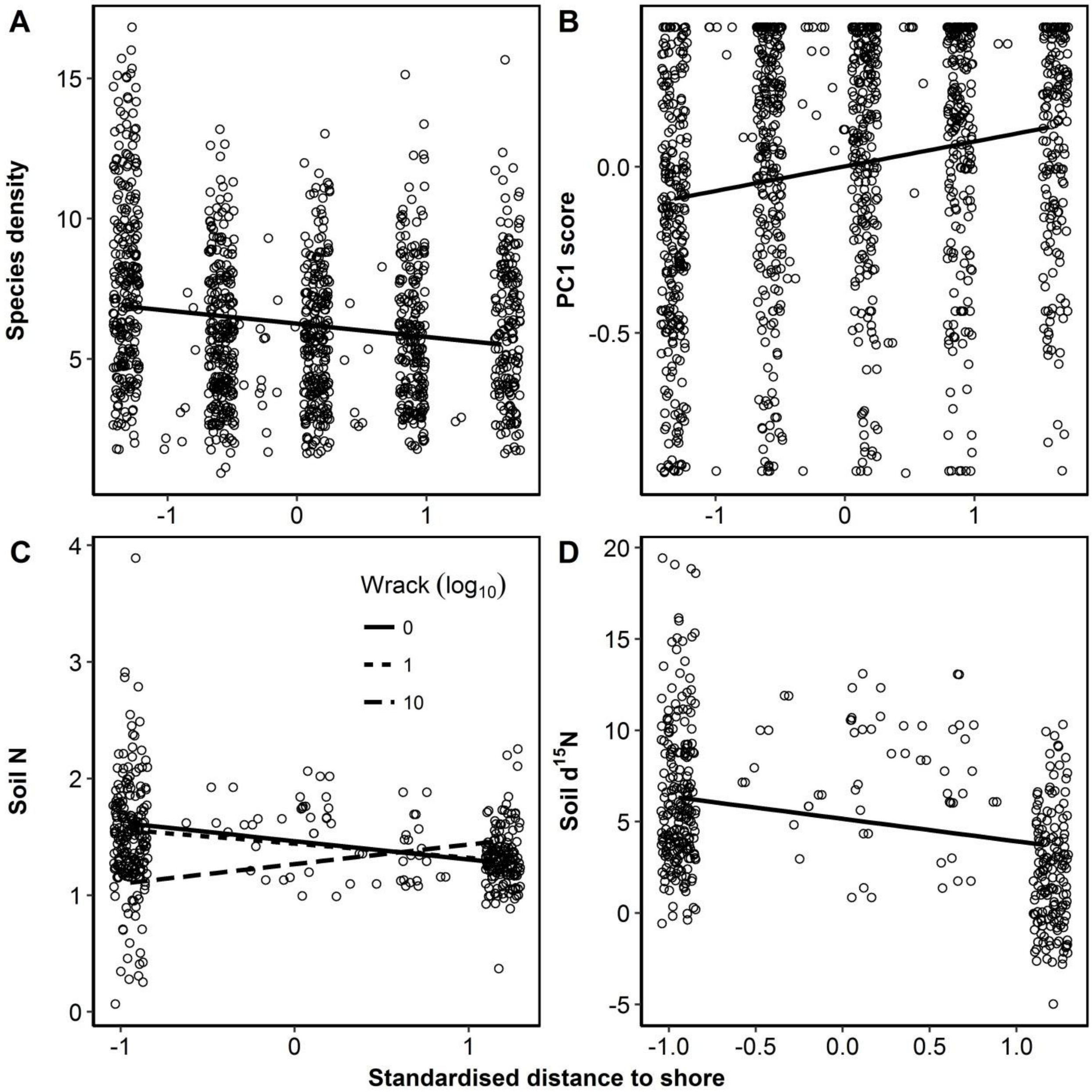

Figure 5. Relationships between plot-scale responses and distance to shore. Plot-scale species density (A) was higher closer to shoreline. PC1 scores (B) were more negative at shoreline. Both soil N (C) and soil δ^{15}N (D) were higher at shoreline, but the decline of soil N with increasing distance to shore becomes less negative when wrack biomass is higher. Predicted lines are derived from coefficient estimates of the top model set for each response.

Discussion

I examined how wrack subsidies affect plant communities on 74 islands on the Central Coast of British Columbia, and whether the influence of wrack subsidies is mediated by island size, shape, and other characteristics. I found that both island area and wrack subsidies were associated with increased island-scale species richness, as I predicted. There was no interaction between wrack subsidies and area, a prediction of the subsidized island biogeography (SIB) hypothesis. However, using hierarchical models, I found that plot-scale soil nutrients and soil $\delta^{15}N$ were higher on smaller islands, indicating that smaller islands may still experience greater inputs of marine subsidies. There were no significant effects of distance to mainland or shoreline slope at either scale.

I found mixed evidence for the SIB hypothesis. A major prediction of the SIB hypothesis is that the species richness of smaller islands will be disproportionately affected by subsidies. Small islands have relatively large perimeter to area ratios, and therefore more edge exposed to the donor ecosystem, per unit area. In turn, more edge exposed to the donor ecosystem can result in greater inputs of marine subsidies per unit area on smaller islands (Witman et al. 2004). Although the top model did include an interaction between island area and wrack biomass, the interaction was not significant, and in the opposite direction than I predicted (Figure 2). Further, mean wrack biomass was moderately positively correlated with island area in my study system (Appendix S1: Figure S1.6). Morrison (2014) made a similar observation in Bahamian archipelagos: small islands had rockier shorelines and less wrack deposition than larger islands. Therefore, Morrison (2014) concluded that small island effects in the Bahamian archipelagoes were not likely due to nutrient subsidies, despite observational and experimental studies in the region that found effects of wrack on plant nutrient status and growth rates (Spiller et al. 2010, Piovia-Scott et al. 2012). Similarly, on the Central Coast, wrack might be more likely to have greater effects on large islands than small islands.

Consistent with the predictions of the SIB hypothesis and Polis and Hurd (1996), smaller islands showed more evidence of marine influence on plot-scale soil N and soil δ^{15} (Figure 4). In addition, soil δ^{15}N values decreased less rapidly with distance to shore on smaller islands than on larger islands (Figure 4D). Both Polis and Hurd (1996) and Maron et al. (2006) found similar patterns: smaller islands had more marine influence, and the effects of marine subsidies decreased less rapidly with distance to shore. This pattern suggests that although wrack is more abundant on larger islands, it could still disproportionately influence the soils of smaller islands.

I found a positive, additive effect of wrack biomass on island-scale species richness. In line with the SIB hypothesis, wrack biomass may directly or indirectly fertilize soils and plants, thereby increasing species richness through increases in the density of individuals (Anderson and Wait 2001). If this were the mechanism, I would expect to see impacts of wrack biomass on plot-scale species density. An alternative mechanism for the effects of wrack subsidies at an island scale may be via increases in niche diversity or spatial heterogeneity of soil resources (e.g., Wait et al. 2005). Spatial variation in wrack deposition could increase beta-diversity within islands, without altering species density at a plot-scale (Anderson et al. 2008). Here, I would expect to see impacts of wrack biomass on plot-scale community composition. In either case, I would also expect to see an effect of wrack on soil nitrogen or soil δ^{15}N signatures. Instead, there was little effect of wrack on plot-scale species density, community composition, or soil nutrients. The weak effects I did observe indicated that soil nitrogen was actually lower at shoreline than in the interior when wrack biomass was higher.

There are several reasons why the effect of wrack at an island-scale may not be reflected by effects at a plot-scale. First, the signal of wrack biomass may be disconnected spatially from my sampling points. Wrack sampling transects paralleled the high tide line along sections of shoreline, whereas my transects started at a single point along that shoreline and extended inland. The small grain size (1 m^2) of my sampling points may have meant that I missed spatial heterogeneity in the deposition and uptake of wrack inputs. In other words, if wrack biomass was distributed non-randomly along transects, the responses might not reflect the measured inputs of wrack biomass at a given site.

Two related problems stem from the clonal growth of the two most common and abundant species in my sampling, salal and false lily of the valley. Both species have extensive underground root systems (Messier and Kimmins 1991, Lezberg et al. 1999), and an individual plant may consist of ramets spread over a large area. Thus, they are able to forage over a much larger area than the scale of the 1 m^2 quadrats I measured, and therefore their abundance may not reflect plot-scale heterogeneity in abiotic conditions (Tamme et al. 2010). In addition, the size of individual plants (distinct from ramet size) of these species is likely larger than my quadrat size, with the consequence that their distribution patterns and associations with other species may not be adequately sampled (Kent 2012). For example, negative associations between salal and other species may simply be because individuals of salal—as both a clonal species and a shrub—are generally larger than a 1 m^2 quadrat. Given the dominance of clonal species on the study islands, larger or nested quadrats, or more replicate quadrats may have been more appropriate.

Second, wrack inputs may be temporally disconnected from my sampling points. The measure of wrack biomass I used represented a specific window of time. Wrack decay can occur rapidly: from 1 to 30 days depending on the species (Mews et al. 2006). Therefore, the measure of wrack biomass I used corresponded roughly to a month of wrack deposition, and may not accurately reflect annual or seasonal inputs to shorelines. At longer time scales, wrack inputs on the Central Coast represent a press rather than a pulse of resources: wrack deposition is relatively stable from season to season (S. Wickham, unpublished manuscript). Furthermore, the nutrient content of wrack is higher in the winter than when we sampled in the summer, when nutrients are used for growth (Villares et al. 2016). Therefore, my short-term measure of wrack biomass may be masked by the influence of diffuse, longer-term inputs of wrack on island shorelines.

Although there was no direct link between my measure of wrack biomass and nutrient and community responses, I found that soil nitrogen, soil $\delta^{15}N$, and species density were all higher closer to shoreline; and shoreline communities had higher relative abundance of false lily of the valley, an indicator of nitrogen-rich sites. However, wrack biomass is likely not the only source of marine subsidies that could increase soil nitrogen and soil $\delta^{15}N$ at shorelines: both marine fog (Weathers and Likens 1997) and sea spray (Art et al. 1974) could act as vectors of marine-derived nitrogen, with most deposition expected at the shoreline edge (Ewing et al. 2009). And although the patterns in vegetation composition and species density were consistent with my predictions for the effects of marine subsidies at shoreline, edge effects may also be responsible for patterns in vegetation change (e.g., species richness is generally higher at forest edges (Murcia 1995)). I attempted to account for some edge effects by including a measure of forest structure and soil moisture in my models, both of which would be expected to change with distance to shore. However, the effect of distance to shore on species density and composition may be driven by additional unmeasured abiotic or biotic variables that vary with distance to shore, including relative humidity, air temperature, light, tree mortality and canopy damage (Murcia 1995). Many of these edge effects have been shown to attenuate at distances within the

40m extent of our transects, potentially explaining our observed effect of distance to shore (Murcia 1995). I investigated the effects of distance to shore further in Appendix S1 and Appendix S2.

Finally, it is possible that wrack biomass is simply correlated with other factors that drive species richness at an island scale. Islands that retain more wrack on average may have certain shoreline or topographical characteristics that could increase habitat diversity. For example, wrack biomass deposition may be higher in concave coves or bays along the shoreline, than in larger flat beaches or on topographical prominences (Duong and Fairweather 2011, Barreiro et al. 2011). On my islands, these concave bays were often associated with topographic lows and freshwater seeps, with surrounding headlands—in other words, islands with more wrack deposition may have had more topographical complexity and corresponding habitat diversity at an island-scale, even if my plot-scale sampling did not detect changes in plant community composition.

In this latter scenario, wrack inputs may indeed be a relatively unimportant source of nitrogen for plants. I assumed that wrack could fertilise shoreline soils: common species of brown and green marine algae contain levels of nitrogen similar to that of animal manure (Villares et al. 2016), and several studies have found evidence for effects of wrack on soil or plant nutrient content, stable isotopes, or growth rates (Williams and Feagin 2010, Spiller et al. 2010, Del Vecchio et al. 2013). However, these studies experimentally applied wrack. On the steep shorelines of my islands, passively-transported wrack or detritus was only rarely observed adjacent to the vegetation edge—instead, wrack may find a more direct route into island food-webs through arthropod detritivores and consumers rather than through non-motile vascular plants (Mellbrand et al. 2011). Most observational studies showing effects of wrack or detritus inputs have looked at arthropod communities (Polis and Hurd 1996, Anderson and Polis 1998, Ince et al. 2007). It would be worth looking at arthropods as a pathway by which wrack is transferred into terrestrial ecosystem, including plants. Although arthropod communities may be more directly subsidized by wrack inputs, the may also serve as vectors of wrack subsidies into terrestrial ecosystems (Mellbrand et al. 2011), and in turn act as subsidies for plant communities (Gratton et al. 2017).

Any effect of wrack on plant communities may be obscured in areas of high terrestrial productivity (Paetzold et al. 2008). Polis and Hurd (1996) predicted that subsidies should be important where marine productivity is high regardless, of terrestrial productivity. However, observational studies that have shown effects of wrack subsidies on soils and plant communities have typically been performed in ecosystems with relatively low terrestrial productivity, such as sandy beaches or dunes (Fariña et al. 2003, Cardona and García 2008, Piovia-Scott et al. 2012). Observational studies that have found evidence for effects of subsidies on plant communities or soils in more productive ecosystems have generally focused on salmon (Bilby et al. 2003, Wilkinson et al. 2005, Bartz and Naiman 2005, Hocking and Reynolds 2011), otters (Crait and Ben-David 2007, Roe et al. 2010), or seabirds (Ellis 2005, Maron et al. 2006). These subsidy sources (and their vectors) may provide more intense inputs of nitrogen, and in locations more suitable for incorporation into soils and plants. Future studies of subsidies on the Central Coast should look at biotic vectors that provide similar types of subsidy inputs. For example, the five islands that were major outliers in the scatterplots of area versus community composition and nitrogen were small, with evidence of both otter and bird (likely eagle) activity. Evidence for subsidies by mediated by birds on these islands included abundant guano on vegetation, nest materials (including wrack) scattered on the forest floor, and plant species associated with nitrogen-rich seabird sites (*e.g.*, *Draba hyperborea*) (Calder and Taylor 1968).

My test of the subsidized island biogeography hypothesis demonstrated that wrack subsidies influence species richness at an island-scale, although evidence for the mechanism by which wrack increases species richness was equivocal. Taken at face-value, the effect of wrack on species richness indicates that future studies of island biogeography would do well to consider the effect of subsidies in conjunction with island area, on species richness. Any external factors, such as subsidies, that alter the productivity or niche diversity of islands could be drivers of patterns of species richness on islands (Hurlbert and Jetz 2010). In addition, I found evidence that the signature of marine nitrogen in soils is higher and more pervasive on small islands. However, wrack did not alter the relationship between species richness and area as expected, and is actually more abundant on larger islands on the Central Coast. Instead, the effect of subsidies on islands of varying sizes may be context-specific, and depend not only on the subsidy source and its vector, but also on characteristics of the recipient ecosystem.

Chapter 3: General conclusion

Context

The broad objective I introduced in the General Introduction to this thesis was to better understand the implications of the link between island ecosystems and the surrounding marine environment. In particular, I wanted to understand whether subsidies alter the relationship between species richness and area, a key part of the theory of island biogeography (TIB; MacArthur and Wilson 1967). I found that inputs of marine subsidies were nearly as important as island area in explaining variation in species richness on islands. My results add to the weight of evidence that the link between islands and the marine environment is an area that deserves attention for understanding large-scale patterns of species richness.

Some of the first research to investigate the implications of the linkage between terrestrial island ecosystems and the marine environment was done by Gary Polis and others in the Gulf of California. The dry and unproductive islands of the Gulf of California provided an ideal testing ground for understanding the effects of marine subsidies on terrestrial communities of plants (Anderson and Polis 1999, Wait et al. 2005), arthropods (Anderson and Polis 1998, Polis and Sanchez-Pinero 2000), reptiles (Barrett et al. 2005) and mammals (Rose and Polis 1998, Stapp and Polis 2003). Polis et al. (1997) also applied principles of landscape ecology to their island work in the Gulf of California, recognising that island characteristics such as the perimeter-to-area ratio could mediate the effects of marine subsidies on terrestrial communities (Polis and Hurd 1996).

From their work in the Gulf of California, Anderson and Wait (2001) proposed an extension to the theory of island biogeography: the subsidized island biogeography (SIB) hypothesis. Broadly, the SIB hypothesis proposes that subsidies can alter the relationship between species richness and area for small islands. The hypothesis has been invoked as a possible explanation of patterns of diversity on small islands that deviate from the expected species-area curve (e.g., Anderson and Wait 2001, Morrison 2005, 2014). However, little empirical work has been done to explicitly test the predictions of the SIB hypothesis. Barrett et al. (2003) performed one of the few empirical tests of SIB, wherein they found little evidence for effects of seabird guano subsidies, nor any difference between the species-area relationship for lizards on small and large islands.

General implications

In Chapter 2, I provided a test of the SIB hypothesis, and looked specifically at how seaweed wrack subsidies may affect the relationship between vascular plant species richness and island area. My results indicate that wrack subsidies are a potential driver of species richness on islands of British Columbia's Central Coast. However, rather than altering the species-area relationship, as predicted by the SIB hypothesis, inputs of wrack increased species richness across the range of island sizes sampled. My results reinforce previous research that suggests nutrient subsidies affect island communities, although the mechanism was unclear. My results also confirmed the basic predictions that stemmed from the application of landscape ecology to island ecosystems: that small islands should experience higher per unit area inputs of subsidies, and that subsidies should decline less rapidly away from shoreline on small islands (Polis and Hurd 1996, Polis et al. 1997). I found that smaller islands had higher average plot-scale soil nitrogen and $\delta^{15}N$, and $\delta^{15}N$ decreased less rapidly away from shoreline on smaller islands. The connection of these patterns of soil nutrients to species richness and wrack deposition was not clear, however.

My results suggest that subsidies do not necessarily affect the relationship between species richness and area. In other words, wrack subsidies were associated with increased species richness across the range of island sizes that I surveyed: subsidies did not disproportionately affect the diversity of small islands, as was predicted by the SIB hypothesis. My results are similar to those of Barrett et al. (2003), who found little evidence for an interaction between seabird subsidies and island area. This implies that subsidies can have a broader range of effect on the species richness of islands than previously suggested, and that their effects may not be limited to "small" islands.

Both the theoretical context, and the implications of my results, fit into the framework of species-area and species-energy relationships. The relationship between species and energy, and the relationship between species and area have a similar foundation (Hurlbert and Jetz 2010). Both hypothesize that species richness is driven by the total numbers of individuals in an area. This is one of the basic assumptions of the TIB that I discussed in the introduction: larger islands can support more individuals, and can therefore support more species. Species-energy theory posits that the number of individuals that a given area can support is also driven by variation in available energy (a synonym for resource availability). In other words, holding area constant, increased resource availability should increase the number of individuals that can be supported in a given area, resulting in increased species richness (Hurlbert and Jetz 2010). The SIB hypothesis can be seen as a more specific hypothesis that relates to these ideas: subsidies increase resource availability on islands, and therefore increase the density and species richness of islands. In fact, the SIB references productivity-diversity-area relationships (Anderson and Wait 2001).

Hurlbert and Jetz (2010) analysed the effects of variation in energy and area on species richness, using a global dataset of breeding birds. They assessed the strength of support for a set of models that included interactions between energy and area, and independent effects of energy and area. The questions they asked are similar to the ones that I asked, and that the SIB asks: do resource availability and area affect species richness independent of one another? Or does resource availability interact with area, altering the relationship between species richness and area? Hurlbert and Jetz (2010) found that the model with the most widespread, global support included independent effects of energy and area on species richness. This reinforces the broader implications of my results. Islands, habitat fragments, and ecosystems of all sizes may be influenced by subsidies, if those subsidies are able to influence the overall energy available to the communities that inhabit them (Jonsson et al. 2011).

What are the consequences of the effect of subsidies on plant diversity in the larger context of island communities? The 100 Islands Project is interested in studying the effects of subsidies on multiple trophic levels, including plants, invertebrates, mammals, and birds. Holt (2010) noted that island biogeography theory has typically been focused on the “horizontal” aspects of island communities—that is, the effects of island area, isolation, and species interactions on members of a single trophic level. Although I focused on plant communities in isolation, a holistic view of island communities would recognize the linkages between trophic levels. The 100 Islands Project is well situated to address how the effect of marine subsidies on one trophic level—such as plants—may propagate throughout the food web. Indeed, one of the major questions in island biogeography today is how trophic interactions affect the diversity of island communities (Patiño et al. 2017).

The trophic theory of island biogeography (TTIB) integrates these linkages between trophic levels into island biogeography theory (*e.g.*, Holt 2010, Gravel et al. 2011). Species of higher trophic levels are predicted to have a steeper species-area slope, due to their relatively small population sizes and reliance on the presence of prey of lower trophic levels (Holt 2010, Gravel et al. 2011). In other words, species of higher trophic levels are more sensitive to changes in island area. Smaller islands are therefore predicted to have less consumers and shortened food chains (Roslin et al. 2013).

As I have shown, inputs of wrack subsidies can increase island-scale plant species richness independent of area. Under the predictions of the TTIB, this increased plant species richness could have bottom-up influences on the richness of higher trophic levels through several mechanisms. Wrack subsidies may increase the productivity or density of plant communities. In turn, higher productivity of primary producers could translate into higher densities of populations at higher trophic levels, increasing species richness through effects on population sizes (Holt 2010). Alternatively, higher plant species richness may provide greater niche diversity for both plant herbivores and species that utilize vegetation as habitat, thereby altering consumer species richness and composition (Jonsson et al. 2009, Hurlbert and Jetz 2010, Harvey and MacDougall 2014). Ultimately, subsidized islands may support more species of higher trophic levels than expected for their area, through bottom-up effects mediated by increased plant species richness.

Future questions

My observational study across a large spatial extent provides both a foundation and questions for future work on the Central Coast of British Columbia, and on island ecosystems in general. The evidence for the mechanism by which wrack subsidies increase plant species richness was equivocal, and observational or experimental studies could help understand whether and how wrack subsidies have a causal effect on island-scale plant species richness. Experimental applications of wrack have found effects on both substrate and plant nitrogen, δ^{15}N, and plant growth rates (Cardona and García 2008, Spiller et al. 2010, Piovia-Scott et al. 2012, Del Vecchio et al. 2013). However, these experiments were performed in relatively unproductive ecosystems, similar to the Gulf of California research by Polis and others. Experimentally confirming an effect of wrack subsidies on both nutrient levels and plant or community-level responses on the Central Coast would be helpful for understanding the mechanisms by which wrack affects plant species richness.

Although there was no direct link to my measure of wrack subsidies, soil nutrients indicated higher nitrogen and $\delta^{15}N$ closer to shore, evidence of the input of subsidies. On the Central Coast of British Columbia, additional research needs to be done on other potential sources of subsidies. Marine fog (Ewing et al. 2009), sea spray (Art et al. 1974), and biotic vectors such as bald eagles (personal observation; B. Miller, unpublished data) and river otters (Roe et al. 2010) may be important sources of nutrients to islands. One avenue for disentangling the uptake of various marine subsidies in plant communities may be through the use of isotopic mixing models (Boecklen et al. 2011). Isotopic mixing models utilise the unique isotopic signatures of prey items to quantify their contribution to the consumer's diet, and have been used to identify sources of nitrogen for plants (Helfield and Naiman 2001, Millett et al. 2003, Mayor et al. 2012).

More generally, my results highlight the importance of context for future studies of marine subsidies, and their effects on the relationship of species richness and area. Marine subsidies do not necessarily affect small islands disproportionately, as predicted (Polis et al. 1997, Anderson and Wait 2001). Instead, subsidies could affect islands of all sizes equally, or even larger islands disproportionately. The relationship between subsidies, species richness, and area depend on multiple interacting factors: the subsidy, its vectors, the specific characteristics that define permeability for those vectors, and the distribution of those characteristics across study islands (Witman et al. 2004). For example, my measure of permeability did not prove to be a mediator of the wind and wave-driven influx of wrack to islands. Instead, shoreline substrate may be a better predictor of the permeability of island shorelines to wrack inputs (S. Wickham, unpublished manuscript), and shoreline substrates may be correlated with island size. Ultimately, more wrack was deposited on larger islands in our study region. Researchers looking for an effect of marine subsidies on the biogeography of island systems should carefully consider all of these factors when designing studies.

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Appendix S1: Supplementary methods and figures

Data Collection

On 33 of 74 islands, I sampled exactly four transects with five plots on each transect. However, on islands larger than 0.5 km^2, I added transects (the number scaled with size), up to a maximum of four additional transects. In addition, on smaller islands (when the distance from a shoreline to an opposite shoreline was estimated to be 60 m or less) I established a single transect to span the island along that axis. For the smallest islands, I established four shoreline (0 m) quadrats, and as many interior quadrats as possible while maintaining a 10 m spacing between quadrats (Appendix S1: Figure S1.1). The 0 m quadrat was established as close as possible to the shoreline, with the criteria that the majority of the substrate was soil.

UAV and LIDAR data was used to generate several remotely-sensed forest structure variables in 10 m^2 grid cells surrounding each 1 m^2 quadrat. These variables were measures of canopy height (mean and max canopy height, volume) and canopy complexity (surface volume ratio, and surface area ratio). *Volume* is related to canopy height metrics and is a measure of the volume under the canopy surface. Canopy complexity is a measure of the regularity of the canopy surface: that is, whether the canopy surface is even, or whether it is characterised by unequal canopy heights, gaps, etc. Greater complexity is thought to be associated with older stands (Lefsky et al. 1999). *Surface volume ratio* is the ratio of the volume under the canopy to the volume under a box that is the same height as the top of the canopy surface. *Surface area ratio* is the ratio of the surface area of the canopy to the surface area of an orthogonal, flat surface. This has also been called “rumple”, and has been shown to be correlated with increasing stand age (Kane et al. 2010).

I then used PCA to derive a single variable representing forest structure at the plot scale. The first principal axis explained 69% of the variation in the individual forest structure variables, and was negatively correlated with all of the variables, representing the height and structural complexity of the overstory. Plot PC1 scores were also negatively correlated with field-based forest structure metrics, which were collected using the point-centered quarter method (Mitchell 2015) centered on each plot: basal area, $r(1187) = -0.37$, $p < 0.001$; stem density, $r(1187) = -0.08$, $p < 0.01$; and canopy cover, $r(666) = -0.34$, $p < 0.001$. In other words, plots with lower combined "forest structure" (axis 1) values were surrounded by taller and more structurally complex forests, with higher stem density, basal area and canopy cover.

Soil moisture imputation

The Field Scout TDR 300 soil moisture probe was not functioning for a subset of six islands (n = 97 quadrats). I collected a soil sample at each of these quadrats and calculated the gravimetric moisture content following a standard protocol. With a working Field Scout TDR 300, I then measured both gravimetric and volumetric soil moisture for a set of quadrats (n = 44), and used a beta regression model based on those quadrats to predict volumetric soil moisture for the missing volumetric soil moisture values ($\beta = 0.0035$, $P < 0.001$, pseudo-$R^2 = 0.54$; Appendix S1: Figure S1.2).

Community composition ordination

I applied a Hellinger transformation to the raw quadrat by species matrix using prior to the PCA analysis. The Hellinger transformation standardizes by "site" (quadrat) totals; thus the distances between quadrats are based on differences between quadrats in the relative abundances of species in each quadrat, rather than differences in absolute abundance (Legendre and Gallagher 2001). Legendre and Gallagher (2001) recommend this measure for data sets containing many zeroes. By standardising by quadrat total, the Hellinger distance removes the influence of double-zeroes on Euclidean distance, while still weighting common species more heavily than rare species (Legendre and Gallagher 2001).

There is—and has been, for quite some time—debate in the literature as to the most appropriate ordination technique to use for vegetation data, although other methods are now generally seen as more appropriate for vegetation data than PCA in most cases (Kent 2012). However, I saw PCA as a compromise, and I consciously chose to use it rather than other indirect methods such as non-metric multidimensional scaling (NMDS), or direct methods such as canonical correspondence analysis (CCA) and distance-based redundancy analysis (dbRDA). I chose PCA over NMDS because I wanted to capture the main variation in my vegetation data along a single axis, which NMDS does not necessarily do (Kent 2012). And I chose to use PCA over direct (constrained) ordination techniques such as CCA and dbRDA because the complex nested and hierarchical nature of my data and analysis was more efficiently dealt with using linear mixed effects models, with PC1 axis scores as a univariate response variables.

The first principal axis explained 30% of the variation in the Hellinger-transformed community data (Appendix S1: Figure S1.3). *Gaultheria shallon* was strongly positively correlated (r = 0.85; Appendix S1: Table S1.1) with the first principal axis, while *Maianthemum dilatatum* was negatively correlated (r = -0.49; Table S1.1). Together, the two species explained 96% of the variation within the first principal axis (Appendix S1: Table S1.1). To assess whether the major gradient in community composition reflected nitrogen preferences, I calculated quadrat scores for a nitrogen-indicator index (Klinka et al. 1989). PC1 and nitrogen-indicator index scores were strongly negatively correlated (r_s = -0.76, P = <0.001; Appendix S1: Figure S1.4). Therefore, my PC1 scores likely reflected a major gradient of nutrient availability/preference, similar to other ordinations in the Coastal Western Hemlock zone by Hocking and Reynolds (2011) and Courtin et al. (1988) (and in both, salal and false lily of the valley also loaded strongly in opposite directions).

Distance to shore and nutrient effects

To further assess the effect of distance to shore and wrack subsidies on plant community responses, I fit structural equation models (SEM) using the plot-scale abiotic and biotic variables used in the "local" model suite. Piecewise structural equation models, with random effects of island and transect, were fit using lme4 (Bates et al. 2015) and piecewiseSEM (Lefcheck 2016) in R.

I wanted to assess two hypotheses. First, I wanted to assess the relative importance of the direct and indirect pathways by which distance to shore influences plant communities (Appendix S1: Figure S1.5). If the effects of distance to shore in the hierarchical models were due primarily to the effect of the permeability of wrack subsidies, I would expect a) a strong direct effect of soil nutrients, b) a strong indirect effect of distance to shore mediated by subsidies, and c) that the sign of the indirect pathway mediated by nutrient subsidies should be the same as the sign of the direct pathway observed in the hierarchical models. That is, if the negative influence of distance to shore on species richness was driven by subsidies, I would expect the indirect pathway mediated by subsidies to be stronger than other direct and indirect effects of distance to shore, and it would have to have a negative effect on species richness.

Second, I wanted to test whether there was evidence for a direct effect of total soil N and soil $\delta^{15}N$ (as proxies for the presence of wrack subsidies in terrestrial soils) on plant community responses. Although I did not hypothesize that soil $\delta^{15}N$ would have effects of its own independent of nitrogen, it may indicate the presence of marine subsidies even when total soil N does not vary. See Appendix S2 for the results of the SEM analysis.

Figures

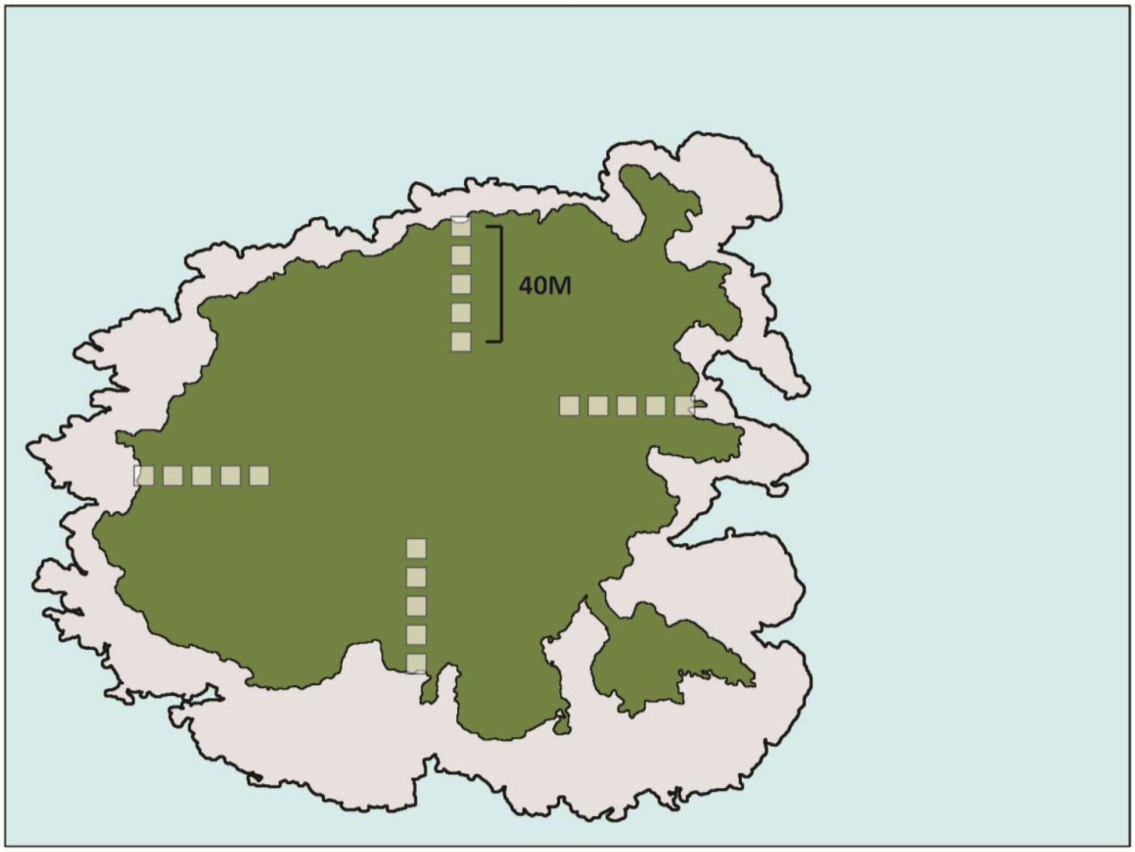


Figure S1.1. Study design for the field-based observational sampling. Transects were established at each of the four cardinal directions. 1 m^2 plots were spaced 10 m apart along transects that extended 40 m, from the shoreline towards the interior of islands. Soil samples were collected at the shoreline and interior plots on each transect.

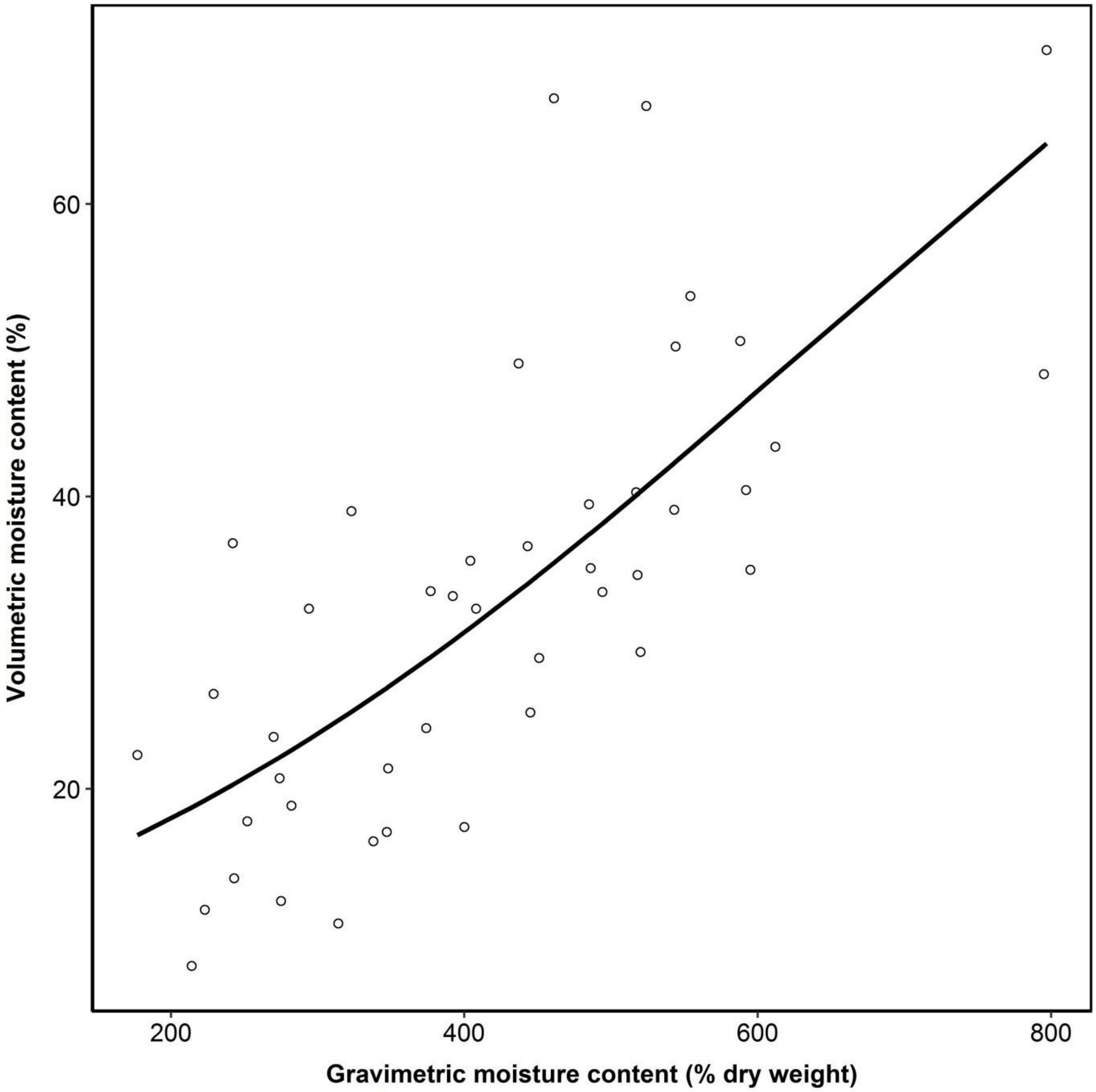


Figure S1.2. Volumetric moisture content, measured by the TDR 300 Soil Moisture Meter, increases with gravimetric moisture content expressed as % of dry soil weight (n = 44). Predicted line is derived from a beta regression model (β = 0.0035, $P < 0.001$, pseudo-$R^2 = 0.54$, n = 44). The model was used to predict volumetric moisture content for plots that were not measured with the soil moisture meter.

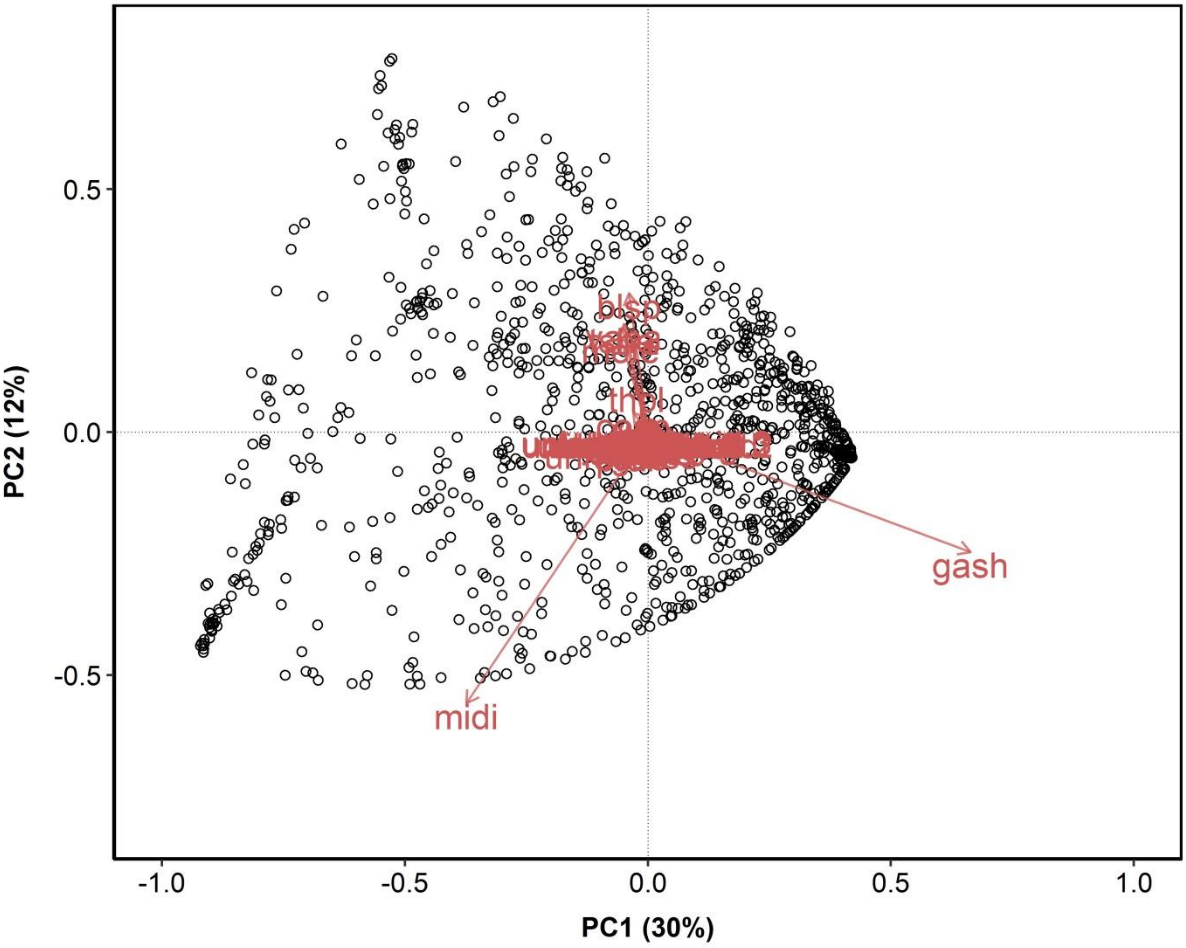


Figure S1.3. PCA biplot of the Hellinger-transformed community matrix. The variance explained by each principal component axis is shown. Points represent quadrats (n = 1281). ‘Gash’ is the species code for *Gaultheria shallon*; ‘midi’ is the species code for *Maianthemum dilatatum*.

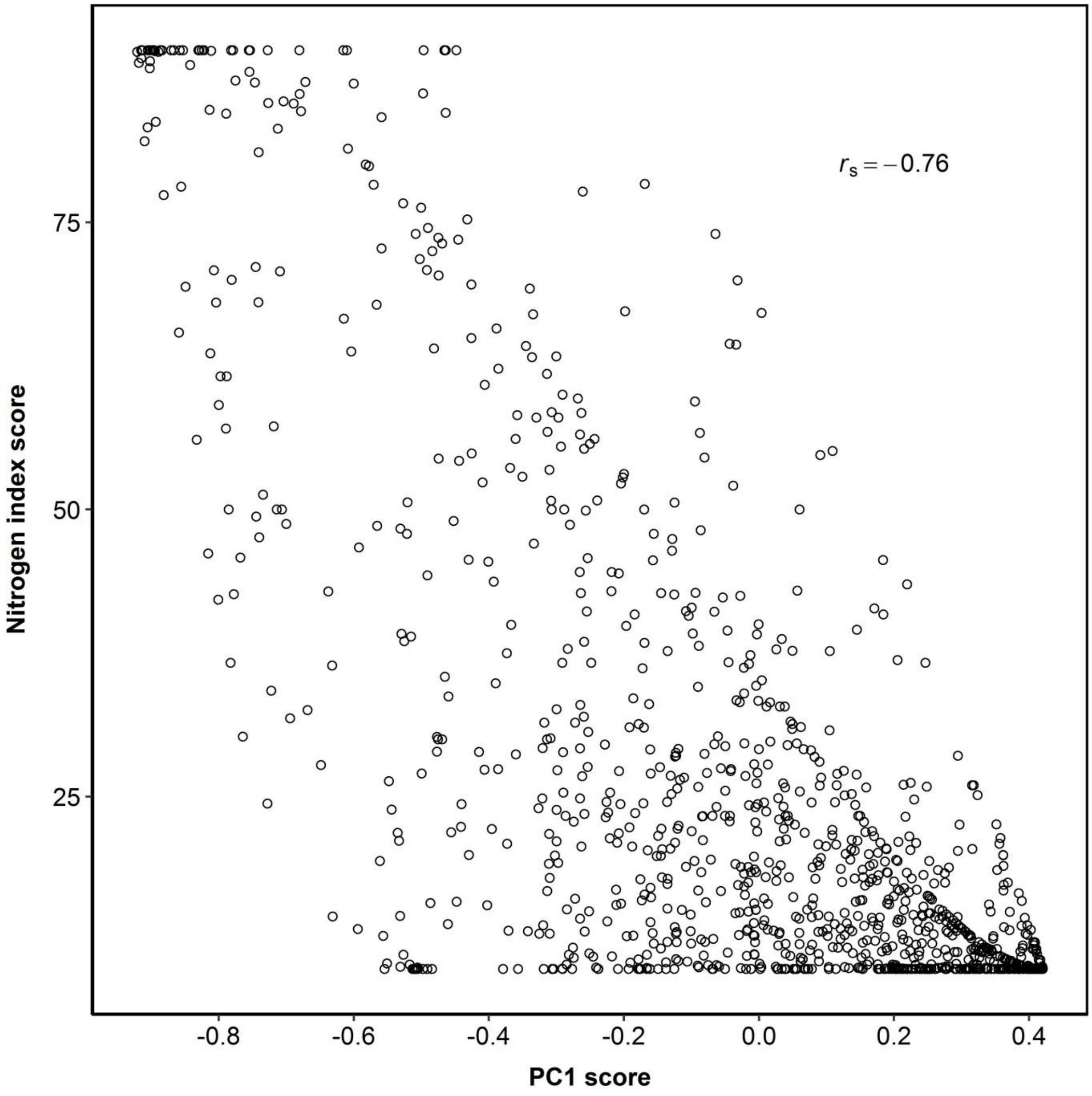


Figure S1.4. Relationship between plot scores on PCA axis 1 and nitrogen-indicator index from Klinka et al. (1989). Correlation coefficient is Spearman's rank correlation ($p < 0.001$).

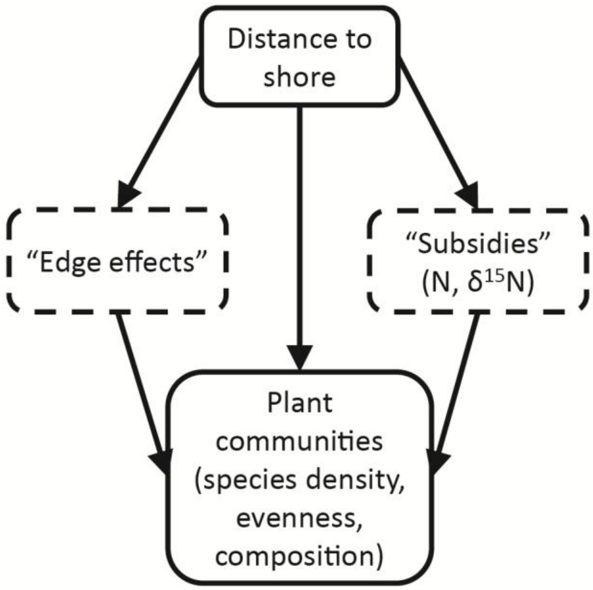


Figure S1.5. Conceptual SEM metamodel illustrating hypothesized pathways for the effect of distance to shore on plant community responses (species density, composition, evenness), mediated by edge effects or wrack subsidies.

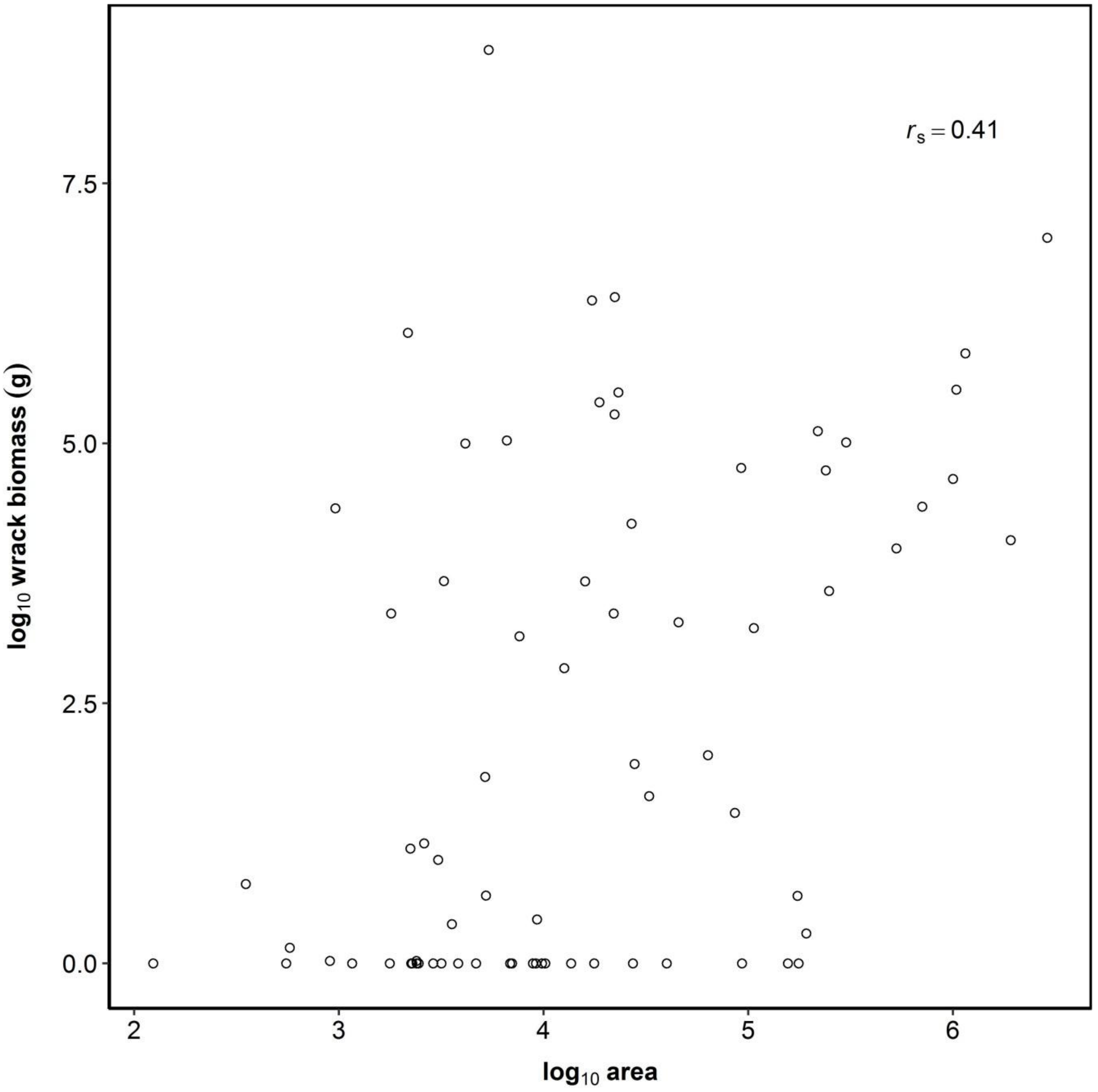


Figure S1.6. Relationship between $\log_{10}$ island area (m^2) and $\log_{10}$ wrack biomass (g) (n = 74). Correlation coefficient is Spearman's rank correlation (*P*<0.001)

Tables

Table S1.1. Top loadings of the first principal component. Sign indicates whether the variable (species) is positively (+) or negatively (-) correlated with the first principal component. R^2 is the square of the loading.

Species	|Loading|	Sign (+/-)	R^2
Gaultheria shallon	0.849	+	0.73
Maianthemum dilatatum	0.497	-	0.23

Table S1.2. Conceptual hypotheses for the variables included in the model sets for island-scale species richness (Table S1.3) or plot-scale nutrient and plant community responses (Table S1.4, S1.5).

Parameter	Hypothesis	Prediction
Island and transect-scale variables, and cross-scale interactions		
Area	Larger islands support larger population sizes, and may have higher habitat diversity (MacArthur and Wilson 1967, Kohn and Walsh 1994). Conversely, smaller island have higher P:A ratios, and are therefore more affected by passive inputs of marine subsidies, whether measured or unmeasured (Polis and Hurd 1996, Maron et al. 2006, Marczak et al. 2007)	Island-scale and plot-scale species richness will increase with island size. Plots on smaller islands will have higher soil nitrogen and δ^{15}N, and composition will shift towards nitrogen-rich indicator plants.
Distance to mainland	Islands that are less isolated from sources of propagules will experience higher colonisation rates and lower extinction rates (rescue effect)	Island-scale species richness and plot-scale species density will increase with decreasing distance to mainland.

	(MacArthur and Wilson 1967, Cody 2006)	
Wrack	Wrack acts as a subsidy for terrestrial soils and plants (Spiller et al. 2010, Piovia-Scott et al. 2012, Del Vecchio et al. 2013, Villares et al. 2016)	Wrack subsidies will be associated with higher species richness, a shift in community composition to nitrogen-rich indicators, and higher soil nitrogen and $\delta^{15}N$ (these predictions are what I refer to when I mention effects of wrack subsidies)
Wrack × shoreline slope	The effect of subsidies are mediated by shoreline slope (Witman et al. 2004, Talley et al. 2006, Hocking and Reynolds 2011).	Islands and plots along transects with lower shoreline slope will *be more affected by wrack subsidies* (see predictions for wrack above)
Wrack × area	Smaller islands have more edge exposed to the marine environment, and will be more affected by inputs of subsidies (Polis and Hurd 1996, Anderson and Wait 2001)	Island and plot-scale responses on smaller islands will be *more affected by wrack subsidies*
Shoreline slope	Gentler shorelines are more permeable to passive inputs of subsidies (Witman et al. 2004, Talley et al. 2006)	Islands and plots along transects with lower shoreline slopes will be *more affected by wrack subsidies*

Plot-scale variables and cross-scale interactions

Distance to shoreline	Distance to shoreline captures the influence of subsidies, whether measured or unmeasured (Ben-David et al. 1998, Bilby et al. 2003, Wilkinson et al. 2005, Maron et al. 2006, Cardona and García 2008, Ewing et al. 2009)	Plot-scale responses will vary with distance to shore: soil nutrient and species density responses will be higher due to subsidy inputs; species composition will shift toward nitrogen-rich indicators

Wrack × distance to shore	The effect of subsidies decreases with distance from the source (Wilkinson et al. 2005, Maron et al. 2006)	The *effect of wrack biomass* on soil nutrient and community responses will be greatest at shoreline
Area × distance to shore	The interior of smaller islands is closer to more adjacent shoreline than the interior of larger islands (Polis and Hurd 1996)	On smaller islands, there will be less of an effect of distance to shore on soil nutrient and plant community responses
Distance to shore × shoreline slope	The effect of distance to shore will be mediated by shoreline slope	There will be less of an effect of distance on soil and community responses when shoreline slopes are lower
Forest structure	Overstory forest structure affects plant communities and soil nitrogen (McKenzie et al. 2000, Van Pelt and Franklin 2000, Frelich et al. 2003, Barbier et al. 2008, Diver 2010)	Just controlling for the effect as a covariate
Soil moisture	Soil moisture can affect plant communities in general (Graves et al. 2006), and is a driver of community change on the Central Coast of B.C. (Asada et al. 2003, Lamb and Megill 2003) and nutrient responses (through denitrification potential; Pinay et al. 2003)	Just controlling for the effect as a covariate
Slope	Slope could affect plant communities (Asada et al. 2003) and nutrient responses, through its effect on soil moisture and/or denitrification potential. (Davidson and Swank 1986).	Just controlling for the effect as a covariate

Table S1.3. Statistical model set developed to select for the best suite of predictors of rarefied island plant species richness. Area refers to $\log_{10}$ area (m^2); wrack refers to $\log_{10}$ wrack biomass (g).

Statistical model
Island biogeography
Area + distance to mainland
Subsidy
Wrack biomass
Subsidy and permeability
Wrack*shoreline slope
Subsidy and island biogeography
wrack + area + distance to mainland
Wrack*area + distance to mainland
Wrack + wrack*shoreline slope + area + distance to mainland
Wrack*area + wrack*shoreline slope + distance to mainland

Table S1.4. Statistical model set developed to select for the best suite of predictors of plot-scale plant community responses (PC1 scores, species density, and evenness). Area refers to $\log_{10}$ area (m^2); wrack refers to $\log_{10}$ wrack biomass (g). Local covariates are included in *every* model, but are only shown in the "local" model here, to save space.

Statistical model
Local
Soil moisture + forest structure + distance to shore + slope
Island biogeography
Area
Area + distance to mainland
Subsidy
Wrack
Wrack*distance to shore
Wrack*area
Area*distance to shore
Wrack*distance to shore + wrack*area
Wrack*distance to shore + wrack*area + area*distance to shore
Subsidy and permeability
Wrack*distance to shore + wrack*shoreline slope
Wrack*area + wrack*shoreline slope
Wrack*distance to shore + wrack*shoreline slope + wrack*area
Wrack + wrack*shoreline slope
Distance to shore*area + distance to shore*shoreline slope
Wrack*distance to shore + wrack*shoreline slope + wrack*area + area*distance to shore + shoreline slope*distance to shore

Table S1.5. Details of models used for nutrient responses. Only the differences between the plant community model set (Table S3) and the nutrient model set are presented.

Statistical model	Conceptual model
Local	
Soil moisture + distance to shoreline + slope +forest structure*	Local covariates have direct effects on soil nutrients. Forest structure was hypothesized to be driven by soil nutrient inputs rather than being a driver, so it was excluded. Total %N was included in the δ^{15}N model to account for denitrification potential.
Subsidy	
Area	Area/PA has an effect on soil nutrients; islands with a larger PA ratio (and smaller area) have higher soil nutrients per unit area. Note: statistically speaking, this is the same formulation as the biogeographical hypothesis for plant communities.

*not included in δ^{15}N models

Table S1.6. Random effects structure used for models.

Scale	Response type	Random effects
Island	Richness	(1| node)
Plot	Composition, evenness, species density	(distance to shore + $\log_{10}$ wrack biomass | island) + (distance to shore | island/transect)
	Soil nutrients	(distance to shore + $\log_{10}$ wrack biomass | island) + (distance to shore | island/transect)

Appendix S2: Supplementary results

Table S2.1. Vascular plant species encountered on 74 islands on the Central Coast of B.C, in a) 1281 1 m^2 quadrats along 40 m transects starting at shoreline, and b) in 296 randomly sampled 1 m^2 quadrats (only species not found along the transects are listed here). Nomenclature follows the *Illustrated Flora of British Columbia* (Douglas et al. 1998-2002). For each species encountered in 1 m^2 quadrats along transects (i.e. excluding any species encountered in randomly sampled quadrats), their percent frequency both in quadrats (n = 1281) and on islands (n = 74) is presented. The raw count of occupied plots and islands is in brackets.

Latin name	Common name	Family	Plot % Frequency (n / 1281)	Island % Frequency (n / 74)
a) Quadrats along 40 m transects (n = 1281)				
Achillea millefolium	Yarrow	Asteraceae	1.1 (14)	16 (12)
Angelica lucida	sea-watch	Apiaceae	5 (64)	34 (25)
Aquilegia formosa	red columbine	Ranunculaceae	0.16 (2)	3 (2)
Arabis eschscholtziana	Escholtz's hairy rockcress	Brassicaceae	0.23 (3)	4 (3)
Asplenium viride	green spleenwort	Aspleniaceae	0.47 (6)	5 (4)
Athyrium filix-femina	lady fern	Dryopteridaceae	1.3 (17)	16 (12)
Blechnum spicant	deer fern	Blechnaceae	17 (221)	46 (34)
Boschniakia hookeri	Vancouver groundcone	Orobanchaceae	0.23 (3)	4 (3)
Calamagrostis nutkatensis	Pacific reedgrass	Poaceae	14 (174)	70 (52)

Calypso bulbosa	fairy-slipper	Orchidaceae	0.16 (2)	3 (2)
Cardamine oligosperma	little western bitter-cress	Brassicaceae	0.08 (1)	1 (1)
Carex lyngbyei	Lyngbye's sedge	Cyperaceae	0.08 (1)	1 (1)
Carex obnupta	slough sedge	Cyperaceae	0.86 (11)	8 (6)
Carex pluriflora	many-flowered sedge	Cyperaceae	0.78 (10)	11 (8)
Carex sitchensis	Sitka sedge	Cyperaceae	0.16 (2)	3 (2)
Castilleja miniata	common red paintbrush	Orobanchaceae	2.1 (27)	27 (20)
Chamaecyparis nootkatensis	yellow-cedar	Cupressaceae	0.23 (3)	3 (2)
Cladothamnus pyroliflorus	copperbush	Ericaceae	0.16 (2)	1 (1)
Claytonia sibirica	Siberian miner's-lettuce	Montiaceae	0.08 (1)	1 (1)
Conioselinum gmelinii	Pacific hemlock-parsley	Apiaceae	6.3 (81)	47 (35)
Coptis asplenifolia	three-leaved goldthread	Ranunculaceae	0.08 (1)	1 (1)
Cornus spp.	various; likely Alaskan bunchberry	Cornaceae	22 (287)	57 (42)
Dodecatheon pulchellum	few-flowered shootingstar	Primulacaea	0.16 (2)	1 (1)
Dryopteris expansa	spiny wood fern	Dryopteridaceae	1.7 (22)	20 (15)
Empetrum nigrum	crowberry	Ericaceae	4 (51)	43 (32)

Epilobium angustifolium	fireweed	Onagraceae	0.08 (1)	1 (1)
Equisetum arvense	common horsetail	Equisetaceae	0.08 (1)	1 (1)
Equisetum spp.	various	Equisetaceae	0.16 (2)	1 (1)
Fragaria chiloensis	coastal strawberry	Rosaceae	2.7 (34)	31 (23)
Fritillaria camschatcensis	northern rice-root	Liliaceae	3.1 (40)	31 (23)
Galium aparine	cleavers	Rubiaceae	0.23 (3)	4 (3)
Galium trifidum	small bedstraw	Rubiaceae	0.47 (6)	7 (5)
Galium triflorum	sweet-scented bedstraw	Rubiaceae	0.16 (2)	3 (2)
Gaultheria shallon	salal	Ericaceae	87 (1114)	99 (73)
Goodyera oblongifolia	rattlesnake-plantain	Orchidaceae	0.39 (5)	3 (2)
Juncus arcticus	arctic rush	Juncaceae	0.23 (3)	4 (3)
Leymus mollis	dune wildrye	Poaceae	1 (13)	10 (7)
Linnaea borealis	twinflower	Caprifoliaceae	6.8 (87)	27 (20)
Listera caurina	northwestern twayblade	Orchidaceae	2.9 (37)	27 (20)
Listera cordata	heart-leaved twayblade	Orchidaceae	11 (137)	50 (37)
Loiseluria procumbens	alpine-azalea	Ericaceae	0.08 (1)	1 (1)
Lonicera	black twinberry	Caprifoliaceae	3.8 (49)	30 (22)

involucrata				
Luzula multiflora	many-flowered wood-rush	Juncaceae	0.16 (2)	3 (2)
Lycopodium clavatum	running club-moss	Lycopodiaceae	0.16 (2)	1 (1)
Lysichiton americanus	skunk cabbage	Araceae	0.78 (10)	11 (8)
Maianthemum dilatatum	false lily of the valley	Asparagaceae	58 (744)	99 (73)
Malus fusca	Pacific crab apple	Rosaceae	2.9 (37)	34 (25)
Menziesia ferruginea	false azalea	Ericaceae	29 (377)	82 (61)
Mimulus guttatus	yellow monkey-flower	Phrymaceae	0.47 (6)	7 (5)
Moneses uniflora	single delight	Ericaceae	0.62 (8)	10 (7)
Oploplanax horridus	devil’s club	Araliaceae	1.2 (15)	8 (6)
Picea sitchensis	Sitka spruce	Pinaceae	5.3 (68)	50 (37)
Pinguicula vulgaris	common butterwort	Lentibulariaceae	0.08 (1)	1 (1)
Pinus contorta	shore pine	Pinaceae	0.23 (3)	3 (2)
Plantago macrocarpa	Alaska plantain	Orchidaceae	0.16 (2)	3 (2)
Plantago maritima	seaside plantain	Plantagineacea	0.78 (10)	12 (9)
Platanthera spp.	various	Plantaginaceae	6.8 (87)	3
Platanthera	slender rein	Orchidaceae	0.62 (8)	8 (6)

stricta	orchid			
Polypodium glycyrrhiza	licorice fern	Polypodiaceae	3.8 (49)	38 (28)
Polystichum munitum	sword fern	Dryopteridaceae	0.78 (10)	11 (8)
Potentilla villosa	villous cinqefoil	Rosaceae	0.39 (5)	7 (5)
Prenanthes alata	western rattlesnake-root	Asteraceae	15 (190)	78 (58)
Pteridium aquilinum	bracken fern	Denstaedtiaceae	4.6 (59)	27 (20)
Pyrola picta	white-veined wintergreen	Ericaceae	0.08 (1)	1 (1)
Ranunculus occidentalis	western buttercup	Ranunculaceae	0.08 (1)	1 (1)
Rhamnus purshiana	cascara	Rhamnaceae	0.62 (8)	5 (4)
Rhododendron groenlandicum	Labrador tea	Ericaceae	0.31 (4)	4 (3)
Ribes divarticum	coastal black gooseberry	Grossulariaceae	0.08 (1)	1 (1)
Ribes lacustre	black gooseberry	Grossulariaceae	0.16 (2)	1 (1)
Rosa nutkana	Nootka rose	Rosaceae	0.16 (2)	1 (1)
Rubus parviflorus	thimbleberry	Rosaceae	0.55 (7)	3 (2)
Rubus pedatus	five-leaved bramble	Rosaceae	0.39 (5)	4 (3)
Rubus spectabilis	salmonberry	Rosaceae	4.9 (63)	32 (24)
Sagina maxima	coastal pearlwort	Caryophyllaceae	0.78 (10)	12 (9)

Sisyrinchium littorale	shore blue-eyed grass	Iridaceae	1 (13)	14 (10)
Stellaria crispa	crisp starwort	Caryophyllaceae	0.16 (2)	3 (2)
Streptopus amplexifolius	clasping twistedstalk	Liliaceae	6.9 (89)	47 (35)
Taxus brevifolia	western yew	Taxaceae	1.4 (18)	16 (12)
Thuja plicata	western red-cedar	Cupressaceae	12 (148)	65 (48)
Tiarella trifoliata (var. *trifoliata* & var. *laciniata)*	three-leaved foamflower, cut-leaved foamflower	Saxifragaceae	3.5 (45)	22 (16)
Triantha glutinosa	sticky false asphodel	Tofieldiaceae	0.08 (1)	1 (1)
Trientalis europaea subsp. *arctica*	northern starflower	Myrsinaceae	2.7 (34)	35 (26)
Tsuga heterophylla	western hemlock	Pinaceae	14 (177)	62 (46)
Vaccinium caespitosum	dwarf blueberry	Ericaceae	0.08 (1)	1 (1)
Vaccinium ovalifolium	oval-leaved blueberry	Ericaceae	1.6 (21)	20 (15)
Vaccinium parvifolium	red huckleberry	Ericaceae	30 (379)	84 (62)
Veratrum viride	green false hellebore	Melanthiaceae	0.16 (2)	3 (2)
Vicea nigricans ssp. *gigantea*	giant vetch	Fabaceae	1.7 (22)	22 (16)

b) randomly sampled quadrats (n = 296)

Coptis trifolia	threeleaf goldthread	Ranunculaceae
Drosera rotundifolia	round-leaved sundew	Droseraceae
Gentiana douglasiana	swamp gentian	Gentianaceae
Kalmia microphylla	western bog-laurel	Ericaceae
Lycopodium dendroideum	ground-pine	Lycopodiaceae
Myrica gale	Sweet gale	Myricaceae
Piperia unalascensis	Alaska rein orchid	Orchidaceae
Plantathera dilatata	white bog orchid	Orchidaceae
Potentilla anserina	silverweed	Rosaceae
Sanguisorba officinalis	great burnet	Rosaceae
Vaccinium oxycoccos	bog cranberry	Ericaceae

Distance to shore and nutrient effects

The structural equation model that contained pathways between total N, δ^{15}N, and community composition fit the data better (AIC$_c$ = 101.5, χ^2 = 20.4, df = 16, p = 0.20) than the model without those pathways (AIC$_c$ = 112.1, χ^2 = 35.8, df = 20, p = 0.02). The same was true with species density as a response: the data fit better with the nutrient pathways included (AIC$_c$ = 101.5, χ^2 = 20.4, df = 16, p = 0.20) than without them (AIC$_c$ = 117.4, χ^2 = 41.1, df = 20, p = 0.004). As in the hierarchical models, species density and evenness displayed similar patterns, and the results for species evenness are in Appendix S2: Figure S2.2). Total N did not have significant direct effects on any of the three responses, whereas δ^{15}N presence in soils was negatively associated with all three responses (Appendix S2: Figure S2.3). Species density was lower in the presence of δ^{15}N, whereas community composition had higher relative abundance of false lily of the valley and lower relative abundance of salal in the presence of δ^{15}N. The direct effect of distance to shore still had the strongest effect on each of the responses, even with soil nutrients included in the model (Appendix S2: Figure S2.3). In addition, the indirect effect of distance to shore mediated by soil nutrients on species density was opposite in sign to that of the direct effect (Appendix S2: Figure S2.3).

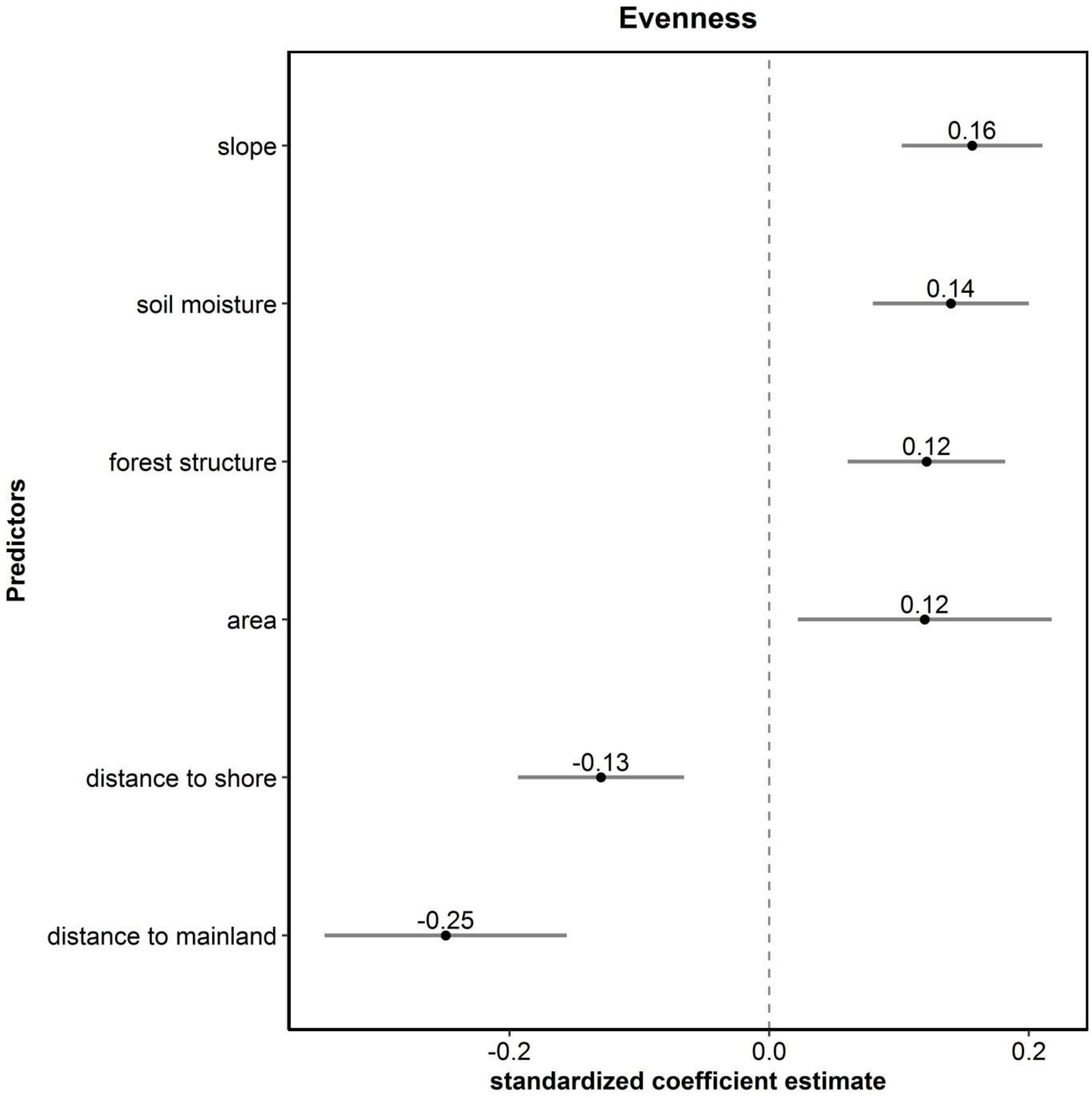
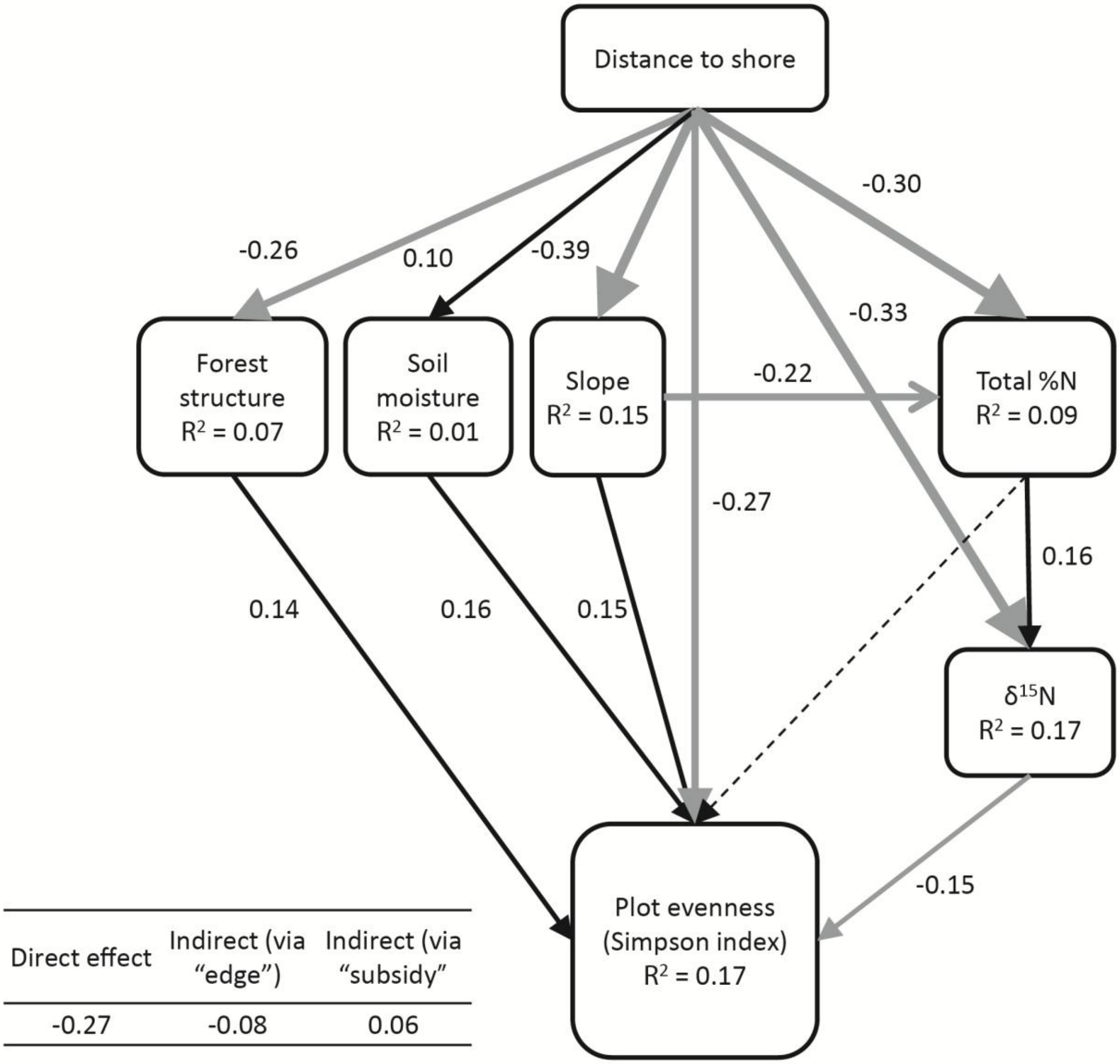
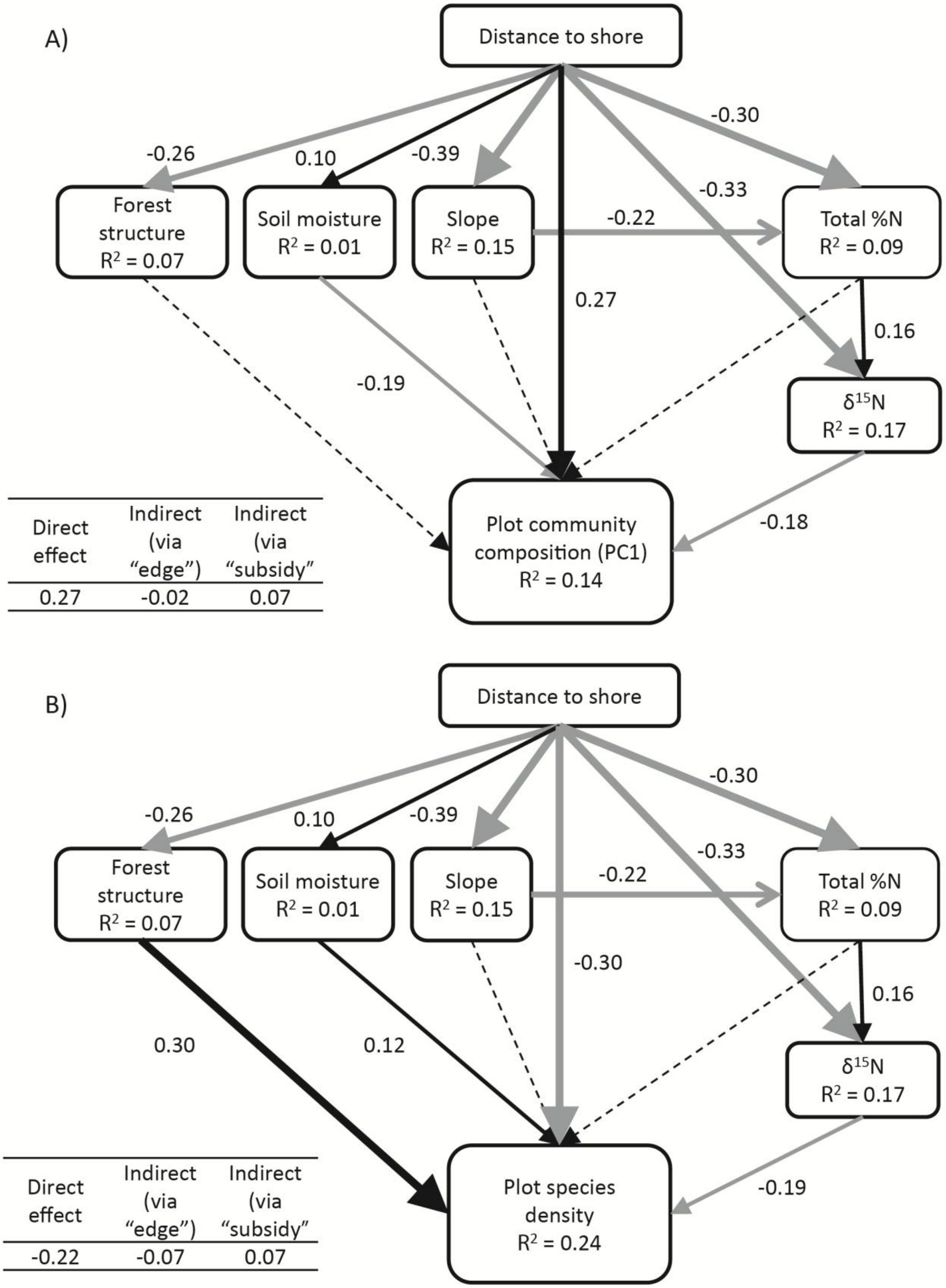


Figure S2.1. Model-averaged **s**tandardized coefficient estimates showing the relative strength of predictors from the top model for evenness (Hill number of order 2). Area refers to $\log_{10}$ area (m^2). Bars represent 95% confidence intervals.



Direct effect	Indirect (via "edge")	Indirect (via "subsidy"
-0.27	-0.08	0.06

Figure S2.2. Path model showing the relative strength of the direct and indirect pathways through which distance to shore affects community plot-scale evenness. Path coefficients represent the standardized regression coefficient. Arrow width is proportional to standardized coefficient weight. Black arrows represent positive relationships; grey arrows represent negative relationships; and dotted arrows are non-significant pathways. The table next to each path model summarizes the strength of the direct effect of distance to shore; the indirect pathways mediated by edge effects (the sum of the indirect pathways through forest structure, soil moisture and slope); and the indirect pathways mediated by subsidies (the sum of the indirect pathways through soil nitrogen and soil $\delta^{15}N$).



A)

Direct effect	Indirect (via "edge")	Indirect (via "subsidy"
0.27	-0.02	0.07

B)

Direct effect	Indirect (via "edge")	Indirect (via "subsidy"
-0.22	-0.07	0.07

Figure S2.3. Path model showing the relative strength of the direct and indirect pathways through which distance to shore affects community composition (A) and species density (B). Path coefficients represent the standardized regression coefficient. Arrow width is proportional to standardized coefficient weight. Black arrows represent positive relationships; grey arrows represent negative relationships; and dotted arrows are non-significant pathways. The table next to each path model summarizes the strength of the direct effect of distance to shore; the indirect pathways mediated by edge effects (the sum of the indirect pathways through forest structure, soil moisture and slope); and the indirect pathways mediated by subsidies (the sum of the indirect pathways through soil nitrogen and soil $\delta^{15}N$).

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