

Ecological effects of marine subsidies to temperate islands

by
Debora S. Obrist

Bachelor of Science, University of Victoria, 2015

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy

in the
Department of Biological Sciences
Faculty of Science

© Debora S. Obrist 2022
SIMON FRASER UNIVERSITY
Fall 2022

Copyright in this work rests with the author. Please ensure that any reproduction or re-use is done in accordance with the relevant national copyright legislation.

Declaration of Committee

Name: **Debora S. Obrist**

Degree: **Doctor of Philosophy**

Thesis title: **Ecological effects of marine subsidies to temperate islands**

Committee: **Chair:** Wendy Palen
Professor, Biological Sciences

John D. Reynolds
Supervisor
Professor, Biological Sciences

David G. Green
Committee Member
Professor, Biological Sciences

Leithen M'Gonigle
Committee Member
Associate Professor, Biological Sciences

Chelsea Little
Examiner
Assistant Professor, Environmental Science and
Resource and Environmental Management

Tara Martin
External Examiner
Professor, Forest and Conservation Science
University of British Columbia

Ethics Statement

The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

- a. human research ethics approval from the Simon Fraser University Office of Research Ethics

or

- b. advance approval of the animal care protocol from the University Animal Care Committee of Simon Fraser University

or has conducted the research

- c. as a co-investigator, collaborator, or research assistant in a research project approved in advance.

A copy of the approval letter has been filed with the Theses Office of the University Library at the time of submission of this thesis or project.

The original application for approval and letter of approval are filed with the relevant offices. Inquiries may be directed to those authorities.

Simon Fraser University Library
Burnaby, British Columbia, Canada

Update Spring 2016

Abstract

Sometimes referred to as “nature’s laboratories”, islands have long been used to test fundamental ecological theories. One highly influential theory, MacArthur and Wilson’s (1967) *Theory of Island Biogeography*, provided an early framework for predicting species diversity according to island size and distance from mainland. Since then, further studies have considered the additional effects of climate, habitat diversity, *in situ* evolution, and invasive species, among others. Although islands are generally well-studied, most work has considered islands as entirely isolated entities. In 2001, the *Subsidized Island Biogeography Hypothesis* was proposed. This theory considers islands as meta-ecosystems; their ecologies may be fundamentally impacted by inputs from the surrounding marine habitat. Marine inputs can increase the quantity of resources available on islands, which may lead to an increase in productivity. This increased productivity affects the diversity and composition of island communities. Depending on the direct and indirect recipients of marine inputs, island trophic dynamics might also be affected. In this thesis, I study the effects of marine inputs on island species diversity, community composition, and food webs on 99 islands on the Central Coast of British Columbia, Canada. Specifically, in Chapter 2, I evaluate the effects of marine subsidies on terrestrial breeding bird species richness and total density. I find higher species richness on both larger islands and those receiving fewer marine-derived nutrients. Meanwhile, bird densities are higher on smaller islands and those with more marine-derived nitrogen in the soil. To evaluate the mechanisms behind these patterns, in Chapter 3, I dig deeper into species-level responses to marine inputs and island characteristics. I find that bird species distributions are just as well explained by marine influences as classically studied island biogeography parameters. Finally, to better understand ecosystem level effects of marine subsidies, I evaluate nutrient enrichment in six trophic levels across island food webs, and trace marine-derived nutrients from the soil into upper-level consumers. Overall, in this thesis, I connect fundamental ecological theories about species distributions on islands with theories about marine subsidies and demonstrate the value of considering island ecosystems in a meta-ecosystem framework rather than as isolated entities.

Keywords: island biogeography; avian ecology; spatial subsidies; marine-derived nutrients; food webs; biodiversity

Acknowledgements

First, I am incredibly grateful to both the Haíłzaqv and Wuikinuxv Nations, on whose territories this research took place. The ecosystems I fell in love with during my time on the central coast have been shaped by Indigenous stewardship since time immemorial and I feel so fortunate to have experienced their beauty.

I want to extend an enormous thank my supervisor, John Reynolds. Thanks for taking a chance on me; despite seeking a person with a masters in avian ecology and an extensive stats background, you ended up hiring a recent undergrad amateur birder with no idea what a linear regression was. I have certainly learned a great deal from you. I am immensely grateful for the encouragement, scientific discussion, and beer you have provided to me over the last six years. Thank you also to my two committee members, David Green and Leithen M'Gonigle. I have truly appreciated your input, knowledge, and support throughout this thesis. I also thank Chelsea Little and Tara Martin for serving on my defense as the internal and external examiners, and I look forward to our discussions.

I would like to extend my thanks to Natural Sciences and Engineering Research Council and to the Department of Fisheries and Oceans Canada for funding this research. I also thank Simon Fraser University for funding through graduate fellowships and for travel awards to attend scientific conferences.

I am immensely appreciative of my two unofficial UVic “co-supervisors”, Chris Darimont and Brian Starzomski. I feel incredibly privileged to have been able to work with you two and learn from you. You’ve both been highly influential in the way that I think about and communicate science.

I was fortunate that my thesis work was part of a larger, collaborative group of fellow 100 Islands post-docs and grad students. In time, I will (maybe) forgive you all for abandoning me by defending your respective theses way before I finished mine. This project was greatly enriched as a result of collaborations and friendships with Norah Brown, Katie Davidson, Chris Ernst, Owen Fitzpatrick, Pat Hanly, Becky Miller, Wiebe Nijland, and Sara Wickham. Thank you also to Luba Reshitnyk, Cal Humchitt, and all the 100 Islands field technicians, particularly the bird crew. Jeremiah Kennedy, thank you for

running the bird crew in the first season, and for teaching me so much about birds. Kate Prince, thank you for your help with banding permits in the final year, and for being such a calming presence during hectic field times. Thanks also to Ian Thomas, Blair Dudeck, Janine McManus, Rob White, and Julian Heavyside; without you all, this fieldwork would literally not have been possible (because I don't know how to drive boats or how to catch birds).

I was lucky enough to be part of an amazing lab group throughout my PhD. Thanks to the Reynolds Lab members: Allison Dennert, Jane Pendray, Sean Godwin, Kirsten Wilcox, Marlene Wagner, Emma Atkinson, Pat Hanly, Chris Ernst, Jess Walsh, Eric Hertz, Jess Edwards, Celeste Kieran, Nico Muñoz, Mike Price, and Elly Guertz. Special thanks to Jane Pendray, for your help with field season planning and willingness to eat samosas with me. To Sandra Vishloff, for your patience answering questions about finances and permits. To Allison Dennert, for being an incredibly supportive labmate who is always willing to workshop ideas and answer endless plant ecology and stats questions. Finally, to Pat Hanly, without whom this thesis would probably have taken at least twice as long. In addition, I was part of the Earth to Ocean research group, which has been a wonderful opportunity to collaborate and exchange ideas, but also to develop lifelong friendships. I am grateful for my E2O friends and colleagues, as well as other folks I have spent time with because of my time at SFU: Fiona Francis, Jamie Yin, Hannah Watkins, Colin Bailey, Michael Arbeiter, Dan Greenberg, Sarah Johnson, Blake Danis, Maya Guttman, Sara Tremblay Boyer, Tess Forstner, Rachel Munger, Lena Ware, Rylee Murray, Steven Brownlee, Claire Attridge, Sherry Young, Julie Charbonneau, and many others.

Thanks also to my parents, for your motivation in finishing this thesis, and to my friends, for motivating me to stop working on my thesis and going outside instead. A delicate balance was struck and I think it was for the best. I especially want to thank Fiona Francis and Dylan Smyth for being key influencers in these pursuits over the last few years. Finally, a million thanks to my partner Matt, for his continuous, unwavering support ever since we met. Thanks for putting up with me daily and being my COVID-cockroach house-work-from-home desk mate while we were stuck at home together in 2020. I'm glad we have finally both made it through to the end of our grad school journeys, and I am so excited to continue to whatever comes next together.

Table of Contents

Declaration of Committee	ii
Ethics Statement	iii
Abstract	iv
Acknowledgements	v
Table of Contents	vii
List of Figures	ix
Chapter 1. General introduction	1
1.1. History of island biogeography	1
1.2. The Theory of Island Biogeography	2
1.3. The Subsidized Island Biogeography Hypothesis	4
1.4. Marine subsidies and their ecological effects	5
1.5. Contributions	7
Chapter 2. Marine subsidies mediate patterns in avian island biogeography	9
2.1. Abstract	9
2.2. Introduction	9
2.3. Material and methods:	12
2.3.1. Study area	12
2.3.2. Terrestrial breeding birds	12
2.3.2. Nutrient subsidies	12
2.3.4. Environmental covariates	14
2.3.5. Data Analysis	15
Avian Species Richness	15
Avian Density	15
2.4. Results	16
Avian species richness	16
Avian Density	16
2.5. Discussion	17
Chapter 3. Equivalent roles of marine subsidies and island biogeography in shaping island bird communities	21
3.1. Abstract	21
3.2. Introduction	22
3.3. Material and methods	26
3.3.1. Study area	26
3.3.2. Field surveys and data collection	27
Terrestrial breeding birds	27
Nutrient subsidies	28
Other environmental covariates	29
3.3.3. Statistical analysis	30
Hierarchical modeling of species communities (HMSC)	30

	Fitting and evaluating the model	30
3.4.	Results	31
	3.4.1. Variance partitioning	32
	3.4.2. Environmental filtering.....	33
	3.4.3. Species' traits.....	35
	3.4.4. Co-occurrence patterns.....	36
3.5.	Discussion	37
Chapter 4. Biogeographic features mediate marine subsidies to island food webs		
	webs	42
4.1.	Abstract	42
4.2.	Introduction.....	42
4.3.	Material and methods	45
	4.3.1. Study area.....	45
	4.3.2. Field collections and measurements	46
	Soil and plant samples	47
	Invertebrate samples	47
	Bird samples	48
	4.3.3. Stable isotope analysis.....	48
	4.3.4. Island characteristics and wrack biomass.....	49
	4.3.5. Data analysis	49
	Enrichment analyses: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$	49
	Subsidy analysis: %N	50
	Path analysis	51
4.4.	Results	52
	Enrichment analysis: $\delta^{15}\text{N}$	52
	Enrichment analysis: $\delta^{13}\text{C}$	53
	Subsidy analysis: %N	54
	Path analysis	55
4.5.	Discussion	57
Chapter 5. General discussion		
	61	61
5.1.	“Wrack myopia” and the river otter realization.....	62
5.2.	The context-dependent nature of marine subsidies	65
5.3.	Does the unimodal productivity-diversity relationship even exist?	66
5.4.	The meta-ecosystem in conservation	68
5.5.	Concluding remarks.....	69
References.....		71
Appendix A. Supporting information for Chapter 2		95
Appendix B. Supporting information for Chapter 3		102
Appendix C. Supporting information for Chapter 4		111

List of Figures

- Figure 2.1. Outer islands in the Central Coast region of British Columbia, Canada. Circles surround island groups that were studied. Each group contains between 6 and 17 study islands. 13
- Figure 2.2. Model-averaged predictions for species richness (a,b) and bird density (d,e) as a function of the area and forest-edge soil $\delta^{15}\text{N}$, holding all other variables constant at their observed means. Shaded areas represent 95% confidence intervals. Model-averaged, standardized coefficients are ranked in descending order of their relative variable importance (RVI) (c,f). For species richness (c), the RVIs are: area (1.00), forest-edge soil $\delta^{15}\text{N}$ (0.87), all others (less than 0.43). For density(f), the RVIs are: area (0.99), forest-edge soil $\delta^{15}\text{N}$ (0.99), area \times forest-edge soil $\delta^{15}\text{N}$ (0.92), all others (less than 0.33). Error bar represents 95% confidence interval of model-averaged coefficient estimate. 17
- Figure 3.1. (a) Map showing the location of studied islands on the Central Coast of British Columbia, Canada. (b) Map showing island groups that were sampled together for sampling feasibility. (c) sRPAS image of two islands in the Goose Group of islands with six point count locations shown in yellow. 26
- Figure 3.2. Rank abundance of terrestrial breeding bird species detected in at least 20 study plots across 89 islands on the Central Coast of British Columbia, Canada. Inset images represent the three most common species, making up nearly 46% of all observations – (a) Orange-crowned warbler, (b) Pacific wren, and (c) Pacific-slope flycatcher. 32
- Figure 3.3. Proportions of variance explained by different grouping variables. The “marine influence” grouping includes wrack biomass, $\delta^{15}\text{N}$ of the soil at the edge of the island, distance to shore, and the proportion of shoreline that is rocky, while “island characteristics” includes island area, habitat heterogeneity, and isolation. The “interaction” component is the proportion of variance explained by the interaction between island area and $\delta^{15}\text{N}$ of the soil. The “random: pcid” term is the amount of variance explained by the random effect of point count ID – i.e., the proportion of variance explained in species interactions at the point count level and the unmeasured environmental parameters at the point count level. The “random: island” term represents the variance accounted for by the random effect of island. The “random: spatial” term represents variance explained by the point count’s spatial coordinates – i.e., unexplained additional variance that arises due to certain points being closer together in space than others. Species 4-letter code key is in Figure 2. 34
- Figure 3.4. Species level responses to environmental parameters (posterior means) in terrestrial breeding birds on the Central Coast of British Columbia, Canada. This plot only shows estimates where the posterior probability of the coefficients $> 95\%$. Species 4-letter code key is in Figure 2. 35
- Figure 3.5. Trait level responses to environmental parameters (posterior means) in terrestrial breeding birds on the Central Coast of British Columbia, Canada. This plot shows all estimates: none had a posterior probability of

	the coefficients > 95%. The intercept (Column 1) represents birds that feed and nest on the ground.....	36
Figure 3.6.	Terrestrial breeding bird species co-occurrences on 89 islands on the Central Coast of British Columbia, Canada. These results come from a joint species distribution model, which fits species co-occurrences simultaneously with species responses to environmental parameters. (a) Co-occurrences at a plot (point count location) level, and (b) co-occurrences at the level of the entire island. Species 4-letter code key is in Figure 3.2.	37
Figure 4.1	Stable isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N} \pm \text{SE}$ in soil, plants, and animals on islands on the central coast of British Columbia, Canada. Plots are separated into tertiles according to island size: small (0.00012-0.016 km ²), medium (0.016-0.22 km ²), and large (0.22-2.88 km ²).	46
Figure 4.2	Standardized coefficient estimates from taxon-specific model-averaged linear mixed effects models for (a) $\delta^{15}\text{N}$ and (b) $\delta^{13}\text{C}$. Bars represent 95% confidence intervals around estimates.	53
Figure 4.3	Effects of island area (m ²) and distance to shore (m) on $\delta^{15}\text{N}$ (a, b) and $\delta^{13}\text{C}$ (c, d) values of island soil, plants, invertebrates, and songbirds. Shaded areas represent 95% confidence intervals around taxon-specific model-predicted means.	54
Figure 4.4	(a) Standardized coefficient estimates from taxon-specific model-averaged linear mixed effects models for %N. Bars (a) and shaded areas (b, c) represent 95% confidence intervals around estimates. Modeled relationships between $\delta^{15}\text{N}$ and %N in (b) songbirds, invertebrate beetles, isopods, and weevils, and in false lily-of-the-valley, salal, and soil (c). ...	55
Figure 4.5	Structural equation models showing pathways of (a) $\delta^{15}\text{N}$ and (b) $\delta^{13}\text{C}$ enrichment through soil, and island plants and animals. Highlighted (darker) paths with associated path coefficients are statistically significant at the 95% level.....	56
Figure 5.1	A) and B) show two of the studied islands on the Central Coast of British Columbia, Canada. The steep, rocky shorelines seen here are characteristic of many of the islands in this study. C) and D) show examples of North American river otter (<i>Lontra canadensis</i>) latrines.....	64

Chapter 1.

General introduction

1.1. History of island biogeography

Islands have an innate simplicity, variability, and abundance that has prompted ecologists to use them as model systems to test hypotheses about why species occur where they do in space and time for the last quarter millennium. The field of island biogeography has certainly come a long way since 1781, when Carolus Linnaeus's *Center of Origin* theory provided an early explanation to the global distribution of species. Linnaeus claimed that during the Great Flood, Noah's Ark had come to rest on insular Mount Ararat, a Turkish mountain with many elevational zones (Browne 1983). Species were unchanging throughout time but were pre-adapted to particular elevational zones. As waters from the Flood receded, species spread out to habitats to which they were adapted to across the globe. Around the same time but along a slightly different line of thinking, Georges-Louis Leclerc, Comte de Buffon proposed what would later become known as *Buffon's Law*: that environmentally similar but geographically isolated regions are composed of distinct biotas (Lomolino et al. 2009). This theory is noteworthy because it implied that it was impossible for all species to come from the same centre of origin. Then, in 1778, Johann Reinhold Forster set the foundations for island biogeography with his observations made on a voyage with Captain James Cook: that larger islands were generally more diverse than smaller ones (Forster 1778). Forster suggested that this phenomenon might be due to increases in resource availability, habitat diversity, and variability in insolation, essentially providing the precursors for extensive future work on species-area relationships, the area-per-se versus habitat diversity argument (e.g., Ricklefs and Lovette 1999), and species-energy theory (Lomolino et al. 2009). Indeed, Forster's work paved the way for the seminal *Theory of Island Biogeography* (TIB; MacArthur and Wilson 1967). TIB is the cornerstone to our modern understanding of species distributions on islands.

1.2. The Theory of Island Biogeography

The theory proposed by MacArthur and Wilson (1967) describes the number of species on an island as a dynamic equilibrium driven by an isolation-dependent immigration rate, and an area-dependent extinction rate. This theory was groundbreaking for several reasons. First, the concept of rate-dependent species richness was novel because previously, it was thought that all islands started out devoid of species, and over time, they would “fill up” until a static saturation point was reached (Schoener 2009). Islands of similar habitat type and size had equal potential species diversity—more isolated islands would just take longer to saturate. TIB instead suggested that due to variable immigration and extinction rates, the potential species richness on a more isolated island is likely lower than on an island of the same size near mainland. Second, TIB posits that there is continuous turnover in species, as immigration and extinction are processes that continue happening (albeit at different rates) once an island reaches saturation. Although the equilibrium species richness on island would remain relatively constant, there would be continuous turnover in species compositions throughout time. Examples of island species in dynamic equilibrium have since been found across taxa—from plants and ants in the Bahamas (Morrison 2002; 2003), arthropods on Floridian mangrove islands (Simberloff and Wilson, 1969), to birds on the Channel Islands (Jones and Diamond, 1976) and the Aegean Sea (Foufopolous and Mayer, 2007). Overall, TIB catalyzed a transition in the field of biogeography, and in ecology more generally, from a largely descriptive field to one grounded in analytical approaches (Losos and Ricklefs 2009). This has allowed for rapid progress and opened the door to a wealth of new ideas.

Since its inception, TIB has been highly influential in both ecological and evolutionary contexts (Patiño et al. 2017, Whittaker et al. 2017), stimulating thousands of studies on the topic of islands and island analogues (Laurance 2009). On the ecological side, TIB has been modified and expanded to consider the roles of climate (Kalmar and Currie, 2006), habitat diversity (Ricklefs and Lovette, 1999), latitude (Kissling et al. 2012), invasive species (Blackburn et al., 2016), primary productivity (i.e., *species-energy theory*; Wright 1983), and disturbance (Fox and Fox 2000), to name just a few. TIB has also spurred more in-depth analyses on dispersal limitations that may affect immigration rates (Sheard et al. 2020), and on the competitive interactions which may shape island communities (Diamond 1975, Gilpin and Diamond 1976). On the

evolutionary side, TIB has been expanded to explicitly consider *in-situ* speciation (Gillespie and Baldwin 2010), adaptive radiation (Losos et al. 1998), and variation in phylogenetic diversity (Pyron and Burbrink 2014). For instance, the *general dynamic theory* considers the influence of island age on potential for *in-situ* speciation (Whittaker, Triantis and Ladle, 2008).

Another reason TIB has been so influential is due to the ubiquity of island analogues worldwide; indeed, TIB has been expanded far beyond oceanic islands. This theory has been used as a framework to improve our understanding of and attempt to manage an abundance of fragmented landscapes. It has been used to evaluate freshwater pond and lake communities (Lassen 1975, Browne 1981), and isolated mountain ranges (Brown 1978). It has even been used to characterize species diversity in “kurgans”—ancient burial grounds of steppe ecosystems surrounded by croplands in the Ukraine (Dembicz et al. 2021), and microbial communities in self-contained cryoconite holes in glaciers (Darcy et al. 2018). Although TIB seems to describe many ecological communities well, Simberloff and Abele (1976) implored careful consideration prior to broad application of TIB as a conservation tool due to its generality and potentially idiosyncratic results. Despite this plea, TIB has guided much of the management ideas on both reserve design (Diamond 1976, Wilcox and Murphy 1985, McNeill and Fairweather 1993, Kitahara and Fuji 1997) and forestry practices (Forman et al. 1976, Laurance et al. 2002), although the utility of TIB in these endeavours has recently again come under scrutiny (e.g., Laurance 2008, Fahrig 2013, Mendenhall et al. 2014).

Although the species-area relationship is frequently touted as one of ecology’s only “laws” (Schoener 1976), the species-area relationship often breaks down on small islands due to a phenomenon known as the *small island effect* (Lomolino and Weiser 2001, Triantis et al. 2006). Below a certain area threshold, species richness has been found to vary independently of area in a number of studies, including those examining flora of the Kapingamarangi Atoll in the Carolina Islands (Niering 1963) and in the Bahamas (Morrison 2014), in plants, lizards, and invertebrates in Puerto Rican islands (Heatwole and Levins 1973), and in Oniscidian fauna in the Mediterranean (Gentile and Argano 2005). A recent global analysis of approximately 700 islands found that the *small island effect* is a widespread phenomenon that may depend on biological traits and functional groups (Schrader et al. 2020). Similarly, another global synthesis detected

evidence of the *small island effect* in approximately 40% of habitat islands worldwide (Wang et al. 2018). To facilitate understanding this, at least three possible mechanisms have been proposed (summarized by Menegotto et al. 2019). First, since stochastic events are more frequent on very small islands, such small islands may experience high extinction rates that do not correlate with island size (Whittaker 1995). Second, it is possible that islands below a certain size have more homogeneous, harsh environments that can only be tolerated by a few species (Triantis et al. 2003, 2006). Finally, the *Subsidized Island Biogeography Hypothesis* (SIB; Anderson and Wait 2001) proposes that due to inputs of nutrients, organisms, and detritus from the surrounding marine habitat, small islands may experience more variability in resource availability, resulting in variability in species densities, allowing associated species richness to vary independently from island size.

1.3. The Subsidized Island Biogeography Hypothesis

Rather than considering islands as isolated entities, SIB expands on the classical TIB framework by considering islands as part of meta-ecosystems (Loreau et al. 2003). SIB builds on previous observations that movements of marine subsidies (i.e., nutrients, detritus, and organisms) from marine to terrestrial ecosystems have the potential to alter dynamics of recipient communities (Polis et al. 1997, Anderson et al. 2008). Indeed, researchers in the Sea of Cortez found that islands receive more energy from marine inputs than from *in-situ* terrestrial primary productivity on an annual basis (Polis and Hurd 1996). Shore-cast macroalgal and carrion deposits were found to provide additional sources of food for semi-terrestrial invertebrates on island shorelines, which, through bottom-up processes, provided more food resources for upper-level consumers on these islands (Polis and Hurd 1995, 1996). This provides the basis for SIB; that marine subsidies result in increased amounts of resources available on islands, facilitating an increase in productivity. SIB relies on the assumption of a unimodal relationship between productivity and diversity, a relationship whose existence has been greatly debated in the literature (e.g., Waide et al. 1999, Mittelbach et al. 2001, Adler et al. 2011, Fraser et al. 2015, Grace et al. 2016). SIB suggests that as productivity on an island increases, either through *in situ* productivity or arising from marine inputs, the island is able to host more species in higher densities (Montagano et al. 2019), effectively decreasing extinction rates due to stochastic processes and resource

limitations (Preston 1962). However, beyond the “hump” of the unimodal curve, the added pressures of competition accrue, and extinction rates increase again. Certain species capitalize on the additional resources and become competitive, to the exclusion of other species. Depending on where island communities fall on this unimodal productivity-diversity relationship, the slopes of species-area curves on small islands (defined as $<3 \text{ km}^2$ by Anderson and Wait 2001) receiving marine inputs would either be steeper or shallower than expected for unsubsidized islands. An important note about SIB is that it predicts stronger effects of marine subsidies on smaller islands than larger ones due to increased per-unit-area effects. Essentially, due to larger perimeter-to-area ratios, more of the area on smaller islands is closer to shore and therefore has the potential to receive more marine inputs (Anderson and Wait 2001).

Very few empirical tests of SIB have been done, and those that have been done have yielded mixed results. In the Bahamas, Barrett et al. (2003) created species-area curves for lizards on subsidized and unsubsidized islands, and found that, albeit not statistically significant, the slope was lower for subsidized islands than unsubsidized islands. This finding suggested that species richness may be raised on smaller islands due to an input of marine nutrients. However, a global analysis found that marine primary productivity (a proxy for potential marine inputs) had no observed effect on angiosperm diversity on 790 islands ranging from 4×10^{-6} to $102,000 \text{ km}^2$ (Menegotto et al. 2019). In contrast, two studies conducted on temperate islands in coastal Canada found decreased plant and terrestrial bird species richness on islands with higher levels of marine-derived nitrogen in the soil, another proxy for marine inputs (Obrist et al. 2020—Chapter 2 in this thesis, Obrist et al. 2022). For plants, this effect was only detectable on the plot level, and not the island level, implying that the effects of marine inputs may be scale dependent (Obrist et al. 2022). Instead of comparing subsidized versus unsubsidized islands, these two studies measured a number of different metrics of marine inputs that were island and even plot specific.

1.4. Marine subsidies and their ecological effects

The variable results of tests of SIB are not surprising, given the context-dependent nature of spatial subsidies (Subalusky and Post 2019), including both those delivered through donor-controlled processes (e.g., Polis and Hurd 1996), and those that result from animal-mediated transfers (McInturf et al. 2019). Donor-controlled

subsidization tends to be passive, and the resulting ecological effects of marine subsidies vary widely depending on characteristics of both the donor and recipient habitats. For instance, kelp forests and seagrass beds act as donor habitats to sandy beach ecosystems around the world (Hyndes et al. 2022). The amount of standing stock in these kelp forests and seagrass beds determines how much kelp is available to potentially subsidize nearby beach ecosystems (Liebowitz et al. 2016, Pedersen et al. 2020). Trophic dynamics in donor habitats, such as urchin grazing (Rogers-Bennett and Catton 2019), can affect the standing stock. Processes including tides, waves, wind, and storm events at sea can affect the quantity and timing of transportation of these subsidies to terrestrial communities (Spiller et al. 2010, Barreiro et al. 2011). In addition, the physical characteristics of recipient habitats can affect rates of subsidy delivery and retention (Wiens et al. 1985). For instance, on islands on the Central Coast of British Columbia, Canada, more wrack is retained on shorelines with more sand, gravel, and pebble substrate (i.e., less rock substrate; Wickham et al., 2020). Beach morphology (Orr et al. 2005) and exposure to major winds and currents (Liebowitz et al. 2016) also affect the amount and type of subsidy that is retained.

Although subsidies actively delivered by animal vectors are still mediated by donor and recipient habitat characteristics, behavioural patterns exhibited by the vectors of these nutrients can elicit unique effects on ecosystems (McInturf et al. 2019, Subalusky and Post 2019). In contrast with abiotic processes, animal vectors can facilitate nutrient transports against energy gradients. As a result, animal-mediated subsidies may not be subject to the same physical barriers that affect passive subsidy processes. An archetypal example is the Pacific salmon, which swim upstream from the ocean for hundreds of kilometers before they spawn and die, effectively fertilizing riparian ecosystems, stimulating a wide range of ecological responses (Walsh et al. 2020). Secondly, animals can respond to patterns resulting from nutrients that they provide and adjust their behaviours accordingly. These adjustments can result in feedback loops, both positive and negative, with the potential to form nutrient hotspots. In the Chagos Archipelago, for example, nutrient-rich seabird guano leaches into adjacent marine ecosystem, increasing coral reef productivity, resulting in increased food availability for seabirds (Graham et al. 2018). Finally, animals can interact with one another, which can affect their nutrient-depositing behaviours. For instance, coastal North American river otters feed on fish and invertebrates in the ocean, and deposit

feces, urine, and anal excretions used for scent-marking on shoreline latrine sites (Ben-David et al. 1998). The purpose of the scent-marking depends on each individual's sex and social status; for nonsocial otters, scent-marking likely facilitates mutual avoidance of a site (e.g., for territory defense), but for social otters, scent-marking may stimulate aggregations because it indicates sites with higher food abundance (Ben-David et al. 2005, Crowley et al. 2012).

Regardless of whether deposited by active or passive means, subsidies are highly variable in amount, quality, timing, and duration (Subalusky and Post 2019), and can thus elicit a wide range of consumer responses (Marczak et al. 2007, Piovia-Scott et al. 2019). Consistent, low amounts of inputs tend to support ecosystem stability, while large pulses of inputs can destabilize ecosystems through stronger trophic cascades (Huxel and McCann 1998, Leroux and Loreau 2008). For example, a recent simulation of a soil-plant-arthropod food web revealed a tendency towards bottom-up effects with increased subsidy amount (McCary et al. 2021). In general, the effects of subsidies tend to be lower in higher trophic levels of food chains due to mobility and/or a more generalized diet (Marczak et al. 2007).

Overall, it is difficult to obtain an understanding of the effects of subsidies without thoroughly evaluating an ecological community in a holistic way. We can gain some insights by examining species richness, but it is worth evaluating species level responses to understand the mechanisms driving patterns. Additionally, determining the pathways of nutrients through meta-ecosystems can facilitate a better understanding of the ecological effects resulting from spatial subsidies crossing from one ecosystem into those adjacent.

1.5. Contributions

In this thesis, I tested hypotheses concerning the effects of marine subsidies on (1) species richness and total bird densities, (2) avian community composition, and (3) island food webs on temperate islands on in the Central Coast region of British Columbia, Canada. I conducted this research as part of the Hakai Institute's 100 Islands research program—a program whose intent was to shed light on some of the lesser-known ecological processes occurring at the land-sea interface, and on the pathways that connect the marine and terrestrial realms. As part of this program, in Chapter 2, I

evaluate the effects of classical island biogeography parameters (i.e., area and isolation), and three metrics of marine subsidies (forest-edge soil $\delta^{15}\text{N}$, shoreline substrate, and shore-cast macroalgal biomass) on the rarefied species richness and total bird densities. I present evidence that islands that are larger, and those that have lower amounts of $\delta^{15}\text{N}$ in forest-edge soils, host more species but lower total densities of birds. In Chapter 3, I examine bird species community composition to evaluate the mechanism behind decreased species richness on islands with higher amounts of forest-edge soil $\delta^{15}\text{N}$. Specifically, I use a novel modelling approach to distinguish between environmental filtering and biotic interactions as the mechanisms structuring species communities. I find evidence that bird species communities are predominantly shaped by environmental filtering and infer that the nature of the subsidy has an effect. Lastly, in Chapter 4, I use stable isotopes to evaluate the pathways of marine-derived nutrients from the sea into upper-level consumers. I first fit hierarchical mixed effects models to evaluate the mechanisms driving ^{15}N -enrichment in samples taken from 6 trophic groups (soil, plants, detritivorous, herbivorous, and carnivorous invertebrates, and insectivorous songbirds). I found that all samples across all groups were enriched on smaller islands, and closer to shore, but that distance from shore was less important on smaller islands, which experience greater per-unit-area effects of marine subsidies. Next, I fit a series of structural equation models to trace the pathway of nutrients up the food web and found evidence that marine nutrients enter the food web by fertilizing the soil before being taken up by plants and moving through the food web all the way into upper-level consumers. This work increases our understanding of the rarely studied connections between marine and terrestrial ecosystems, particularly on temperate islands. Collectively, the research presented in this thesis facilitates a deeper understanding of how island characteristics and nutrient inputs from the surrounding marine ecosystem can affect patterns in biodiversity, species distributions, and flows of nutrients through island food webs. As a result, this thesis ties together key theories in island biogeography, landscape ecology, and food web ecology.

Chapter 2.

Marine subsidies mediate patterns in avian island biogeography¹

2.1. Abstract

The classical *Theory of Island Biogeography* (TIB), which predicts species richness using island area and isolation, has been expanded to include contributions from marine subsidies, i.e., *subsidized island biogeography theory* (SIB). We tested the effects of marine subsidies on species diversity and population density on productive temperate islands, evaluating SIB predictions previously untested at comparable scales and subsidy levels. We found that the diversity of terrestrial breeding bird communities on 91 small islands (~0.0001 to 3 km²) along the Central Coast of British Columbia, Canada was correlated most strongly with island area, but also with marine subsidies. Species richness increased and population density decreased with island area, but isolation had no measurable influence. Species richness was negatively correlated with marine subsidy, measured as forest edge soil $\delta^{15}\text{N}$. Density, however, was higher on islands with higher marine subsidy, and a negative interaction between area and subsidy indicates that this effect is stronger on smaller islands, offering some support for SIB. Our study emphasizes how subsidies from the sea can shape diversity patterns on islands and can even exceed the importance of isolation in determining species richness and densities of terrestrial biota.

2.2. Introduction

The *Theory of Island Biogeography* (TIB; MacArthur and Wilson, 1967) predicts that species richness on islands is driven by an immigration rate, determined by island isolation, and an extinction rate, which depends on island size. TIB has been expanded

¹ A version of this chapter appears as Obrist, D.S., Hanly, P.J., Kennedy, J.C., Fitzpatrick, O.T., Wickham, S.B., Ernst, C.M., Nijland, W., Reshitnyk, L.Y., Darimont, C.T., Starzomski, B.M., and Reynolds, J.D. (2020) Marine subsidies mediate patterns in avian island biogeography. *Proceedings of the Royal Society B: Biological Sciences*, 287:20200108.

to consider other factors that mediate the effects of area and isolation, including speciation (Gillespie and Baldwin 2010), variability in primary productivity (Wright 1983), climate (Kalmar and Currie 2006), exposure to prevailing winds and ocean currents (Weigelt and Kreft 2013), habitat diversity (Lack 1969, Ricklefs and Lovette 1999), invasive species (Blackburn et al. 2016), and spatial subsidies (Polis and Hurd 1996, Anderson and Wait 2001, Barrett et al. 2003, Menegotto et al. 2019).

Nutrient-limited habitats often receive subsidies from adjacent ecosystems (Loreau et al. 2003). Nutrient transfers can be controlled by the donor habitat or result from foraging by recipient-habitat species (Richardson et al. 2010), and can have large impacts on nutrient-limited islands. Subsidized island biogeography (SIB) theory predicts that insular species richness will either increase or decrease with subsidy input, depending on where islands lie on a unimodal productivity-diversity curve (Rosenzweig and Abramsky 1993). While classical TIB assumes constant population densities across islands regardless of size, spatial subsidies can shift species densities (Gende and Willson 2001, Christie and Reimchen 2008, Field and Reynolds 2011, Hocking and Reynolds 2011, Wagner and Reynolds 2019). As subsidies increase productivity, islands can support denser populations, reducing extinction risk from demographic stochasticity and thereby increasing expected diversity. Conversely, beyond some productivity threshold, a few species at high densities may outcompete others, leading to lower diversity (Rosenzweig and Abramsky 1993). SIB posits that these effects are amplified on smaller islands because subsidies have a higher per-unit-area effect on productivity (Anderson and Wait 2001).

Since the inception of SIB, studies have shown that the productivity-diversity relationship is likely scale and system dependent (Mittelbach et al. 2001, Cusens et al. 2012). SIB has mostly been investigated on dry, arid islands at low latitudes (Polis and Hurd 1996, Barrett et al. 2003), with one recent exception that found no influence of marine productivity on island diversity at global or regional scales (Menegotto et al. 2019). No empirical tests have been conducted in more productive temperate island systems, but nutrients from salmon carcasses are established drivers of songbird (Gende and Willson 2001, Christie and Reimchen 2008, Field and Reynolds 2011, Wagner and Reynolds 2019), invertebrate (Hocking and Reimchen 2002), and plant communities (Hocking and Reynolds 2011) in mainland coastal temperate rainforests. In addition, there is a surprising lack of research on subsidy effects on bird communities,

despite the avian focus of many island biogeography studies (MacArthur and Wilson 1967, Lack 1969, Diamond et al. 1976, Diamond and Mayr 1976, Gilpin and Diamond 1976, Haila et al. 1983, Ricklefs and Lovette 1999, Kalmar and Currie 2006).

Here, we conducted the first empirical test of the effects of marine subsidies on classical TIB predictions on temperate rainforest islands. We quantified marine subsidies and tested their effects on terrestrial breeding bird communities on 91 small islands (<3 km²) along the Central Coast of British Columbia, Canada. We used hierarchical models to test the importance of classical TIB predictors (island area and isolation) relative to island-specific predictors of subsidy acquisition and retention (shore-cast macroalgal biomass, shoreline substrate, and forest-edge soil nutrients) on avian species richness and density. This approach provides a finer resolution than previous studies where island subsidies were treated as binary (i.e., presence/absence), or where island subsidies were predicted from mainland accumulations (Polis and Hurd 1996). Our study region contains nearly 1,500 islands, many of which are too small and topographically simple to host salmon-bearing streams, but they could receive nutrient transfers from foraging bald eagles (*Haliaeetus leucocephalus*) and river otters (*Lontra canadensis*), and from shoreline seaweed deposits. Nearly all surveyed islands had evidence of river otters (>90%), whose activities have been observed to subsidize temperate coastal forests through excrement and food scraps (Ben-David et al. 1998, Roe et al. 2010). Furthermore, the northeastern Pacific Ocean exhibits some of the highest levels of primary productivity in the world, resulting in large kelp forests (Steneck et al. 2002). In the Bahamas, shore-cast macroalgal deposits directly increase terrestrial productivity, and the diversity and abundance of shoreline invertebrates and their predators (Spiller et al. 2010).

Consistent with TIB, we predicted that island area would be a strong predictor of terrestrial bird species richness, with a minimal effect on density (MacArthur and Wilson 1967). We did not expect isolation to have an effect because birds are unlikely to be dispersal-limited on nearshore islands (Lack 1969, Kalmar and Currie 2006). We predicted that species richness and density would be higher on heavily subsidized islands, as populations with more individuals have lower extinction rates and higher equilibrium species richness (Christie and Reimchen 2008, Field and Reynolds 2011, Wagner and Reynolds 2019). Depending on where these islands fall on the unimodal productivity-diversity curve, we also anticipated that additional subsidies could move the

system towards an equilibrium with fewer species (Anderson and Wait 2001). We tested the hypothesis that islands with more macroalgal deposition, higher $\delta^{15}\text{N}$ in forest-edge soils, and greater receptivity to subsidies (less rocky shoreline) would host more species and more birds per-unit-area.

2.3. Material and methods:

2.3.1. Study area

We surveyed 91 islands in the Central Coast region of British Columbia, Canada (Figure 2.1.; 51° 26' to 52° 3' N and 127° 41' to 128° 28' W). This area is in the very wet, hyper-maritime subzone of the Coastal Western Hemlock biogeoclimatic zone, which receives over 3,000 mm precipitation annually (Pojar et al. 1987). We selected islands representative of the region's biogeographical and geomorphological variation (Table 2S) with a maximum area of 3 km² for sampling feasibility. We defined an island as a landmass with terrestrial vegetation that is separated from neighbouring landmasses during high tide.

2.3.2. Terrestrial breeding birds

We surveyed terrestrial breeding birds on each island with 10-minute point count surveys between early May and mid-July in either 2015, 2016, or 2017. We spaced point counts at least 250 m apart to maintain independence (Ralph et al. 1995). Two surveys were conducted at each location, approximately one month apart, to account for detection differences in early and late season migrant species. To reduce the effects of edge habitat we avoided placing points within 50 m of the shore. Point counts were not conducted during rain or wind speeds above 3 on the Beaufort scale. To minimize inter-observer bias, surveyors were selected based on their ability to identify birds of British Columbia.

2.3.2. Nutrient subsidies

We considered nutrient subsidies from three factors: (1) the biomass of beach-cast seaweeds (wrack); (2) the proportion of shoreline classified as "rocky", a metric inversely related to an island's ability to receive and retain wrack (Wickham et al. 2020);

and (3) forest-edge soil $\delta^{15}\text{N}$, a composite measure of other marine-derived nutrients vectored by wind, water, and animals (e.g., river otter feces and food scraps, sea spray, and seabird guano).

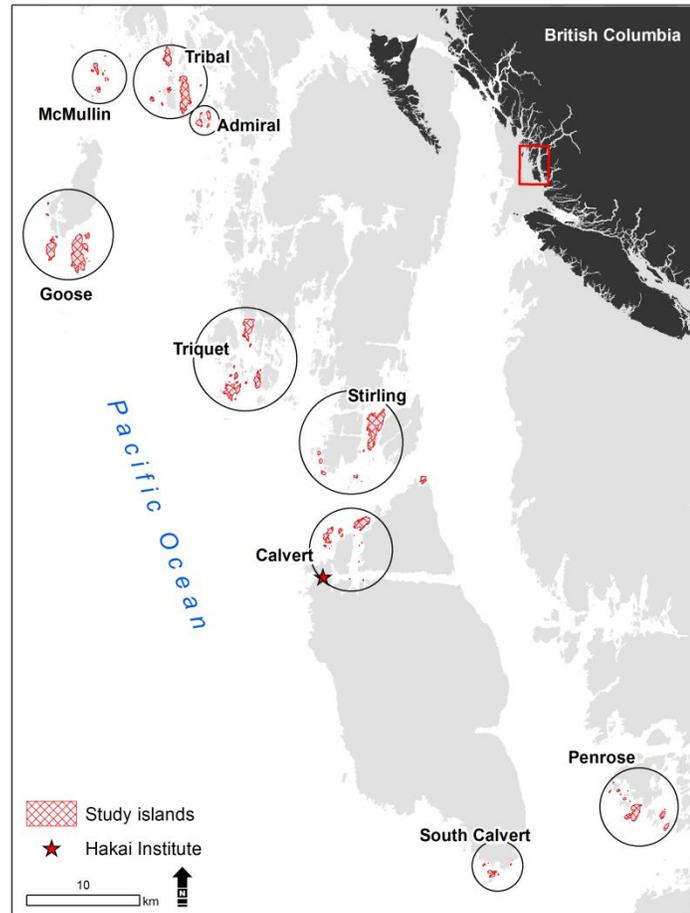


Figure 2.1. Outer islands in the Central Coast region of British Columbia, Canada. Circles surround island groups that were studied. Each group contains between 6 and 17 study islands.

To measure wrack biomass, we placed two 20 m transects parallel to the water at four locations on every island, representing the north, east, south, and west-most points. We placed one transect on the most recent high tide line, and one at the most recent storm line - the highest wrack line on the beach. We weighed wrack in three randomly placed 1 m² quadrats along each transect (Wickham et al. 2020). Wrack wet weights were calibrated to dry weight by species (Wickham et al. 2019). To linearize the

data for analysis at an island level, we used the square root of the mean wrack biomass of the 24 biomass measurements per island.

Shoreline substrate is the most important predictor of wrack retention on islands in this region; wrack accumulates less on rocky shorelines than on other substrates (i.e., boulder, cobble, gravel, and sand; Wickham et al. 2020). To calculate the proportion of rocky shoreline on each island, we used ESRI ArcMap 10.3 to categorize shoreline substrate at 5 m intervals around each island using raster data collected with small remotely piloted aerial systems (sRPAS) at 10 cm resolution.

We used forest-edge soil $\delta^{15}\text{N}$ as a direct measure of marine subsidies before they attenuate throughout the island. Previous studies on these islands showed that soil $\delta^{15}\text{N}$ decreases significantly with increased distance from shore (O. Fitzpatrick, unpublished data), implying marine origin (Maron et al. 2006). Levels of $\delta^{15}\text{N}$ also tend to be higher at river otter activity sites (Crait and Ben-David 2007, Roe et al. 2010) and near eagle nesting trees (Miller 2019). Soil samples were taken from vegetated sites adjacent to the shoreline at each of the four cardinal directions on each island and analysed for stable isotopes. To obtain a single measure for each island, we averaged these four $\delta^{15}\text{N}$ values. Interestingly, there was a moderate negative correlation between island area and forest-edge soil $\delta^{15}\text{N}$, despite all points being adjacent to the shoreline (Figure 3S).

2.3.4. Environmental covariates

We measured island area and the normalized difference vegetation index (NDVI) with WorldView-2 satellite imagery. By combining NDVI and visual inspection of sRPAS imagery, we distinguished five habitat categories on our islands: dense/closed-canopy forest, light/open-canopy forest/dense shrub, light shrub/grass, bog (vegetation and water), and woody debris/snags. We determined the relative proportion of these habitats on each island and calculated the Shannon diversity index to represent heterogeneity (Shannon 1948). We calculated distance to the nearest island large enough (120,245 m^2) to act as a functional “mainland” to represent isolation (methods in SI).

2.3.5. Data Analysis

Avian Species Richness

To account for missed detections and unequal numbers of point counts on islands of different sizes, we estimated species richness with Chao1 (Gotelli and Colwell 2011) using the ‘vegan’ package (Oksanen et al. 2019) in R. We only considered birds detected within 50 m of the observer to minimize errors in distance estimation, differences in species detectability, and double-counting. To investigate factors influencing species richness on an island-level scale, we fit a series of linear mixed-effects models (LMMs) representing a suite of hypotheses and evaluated them using Akaike’s information criterion (AICc), corrected for small sample sizes. We compared an area-only model with models containing isolation, habitat heterogeneity, and both (Table A3). Since these parameters did not improve model fit, we dropped them from further analyses.

To assess the relative importance of each remaining variable (RVI) we model-averaged a set of LMMs with all possible subsets of island area, forest-edge soil $\delta^{15}\text{N}$, proportion of rocky shoreline, and wrack biomass (kg/m^2) using the ‘lme4’ package in R (Bates et al. 2015). We scaled and centred all independent variables, log-transformed island area and estimated species richness, and square root-transformed wrack biomass to linearize the relationship prior to standardizing. We included interactions between area and both direct subsidy measures: forest-edge soil $\delta^{15}\text{N}$ and wrack biomass. Since substrate is the best predictor of shoreline wrack accumulation, we also considered an interaction between proportion of rocky shoreline and wrack biomass. Assuming that rocky shoreline could influence subsidy vectors that affect forest-edge soil $\delta^{15}\text{N}$, we considered this interaction as well. We assumed the combined effect of wrack biomass and forest-edge soil $\delta^{15}\text{N}$ was additive. All models included year and a random effect of node (a cluster of nearby islands sampled in one survey period).

Avian Density

We followed the same procedures to analyze patterns in avian density. First, we used AICc to confirm that generalized linear mixed-effects models (GLMMs) containing isolation, habitat heterogeneity, or both were not more informative than a model with area alone (Table 4S). We then used the candidate models from the species richness

analysis to determine the effects of subsidies on avian density. We fit a series of GLMMs with each island's raw bird abundance (sum of all individuals within 50 m of observers) as the response. The total area surveyed per island was included as an offset term. Since we wanted to predict relative densities to make comparisons across islands, we did not account for variation arising from differences in detectability.

2.4. Results

Avian species richness

We conducted 566 point counts in 283 locations on 91 islands and detected 32 species of terrestrial breeding birds (Table S1). Raw species richness ranged from 0 to 20 species, and estimated species richness (Chao1) ranged from 0 to 30 species.

As predicted, island area was the strongest predictor of terrestrial bird species richness (Figure 2.2.a; RVI: 1.00). The effect of area was nearly 3.5 times stronger than the effect of forest-edge soil $\delta^{15}\text{N}$ (Figure 2.2.b; RVI: 0.87). Average-sized islands (16 571 m²) are predicted to host 8.23 ± 1.13 (model-averaged estimate \pm 95% CI) species, whereas islands one order of magnitude larger (159 485 m²), or smaller (1 722 m²) would host 13.27 ± 1.19 and 5.11 ± 1.18 species, respectively. Forest-edge soil $\delta^{15}\text{N}$ had a negative relationship with bird species richness, with approximately one species lost for every 3‰ increase above the mean (6.8‰). All other variables had low RVIs and 95% confidence intervals that overlapped with zero (Figure 2.2.c).

Avian Density

Bird densities on islands ranged from 0 to 171 individuals per hectare (median = 19.1; mean = 26.5 ± 5.3). Island area was a strong negative predictor of density (Figure 2.2.d; RVI: 0.99). Forest-edge soil $\delta^{15}\text{N}$ and the interaction between island area and soil $\delta^{15}\text{N}$ were also highly important (RVI: 0.99 and RVI: 0.92, respectively). The effect of island area was nearly twice as strong as that of soil $\delta^{15}\text{N}$; however, the effect of $\delta^{15}\text{N}$ was not significant due to the large uncertainty (Figure 2.2.f). The interaction between island area and soil $\delta^{15}\text{N}$ was significant, and nearly as strong as the effect of island area itself. The interaction coefficient was negative indicating that this marine subsidy effect decreased with island area. An average-sized island is predicted to host 20.7 ± 4.1 individuals per hectare versus 17.2 ± 4.0 and 25.0 ± 5.8 individuals per hectare for islands

one order of magnitude larger and smaller, respectively. Forest-edge soil $\delta^{15}\text{N}$ had a positive relationship with bird relative density (Figure 2.2.e), with a single standard deviation increase ($\sim 3\text{‰}$) above the mean resulting in an increase of over two individuals per hectare (23.0 ± 5.5).

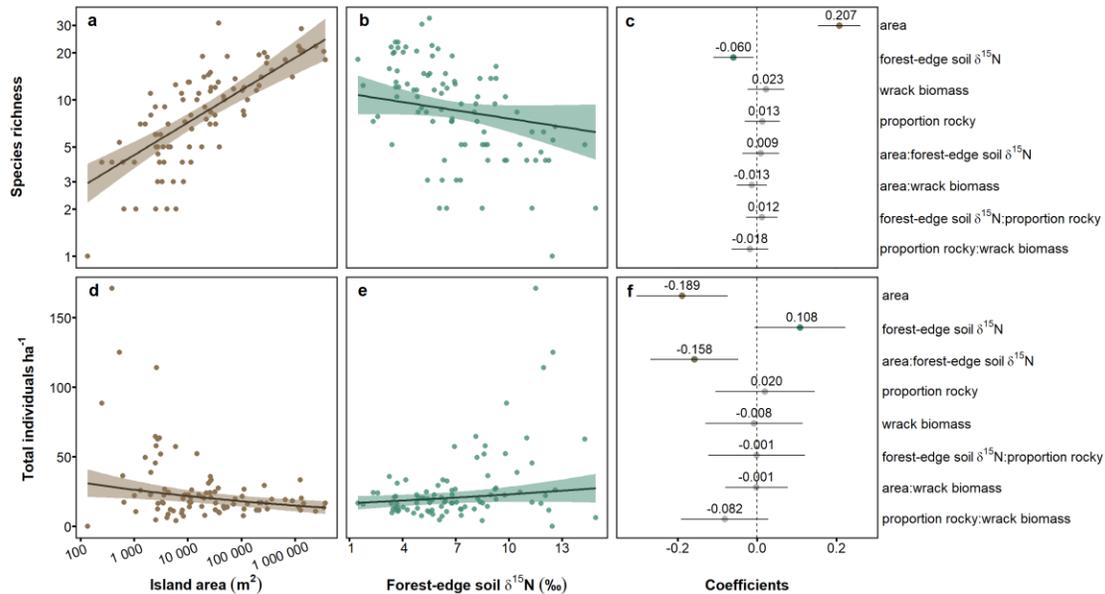


Figure 2.2. Model-averaged predictions for species richness (a,b) and bird density (d,e) as a function of the area and forest-edge soil $\delta^{15}\text{N}$, holding all other variables constant at their observed means. Shaded areas represent 95% confidence intervals. Model-averaged, standardized coefficients are ranked in descending order of their relative variable importance (RVI) (c,f). For species richness (c), the RVIs are: area (1.00), forest-edge soil $\delta^{15}\text{N}$ (0.87), all others (less than 0.43). For density(f), the RVIs are: area (0.99), forest-edge soil $\delta^{15}\text{N}$ (0.99), area \times forest-edge soil $\delta^{15}\text{N}$ (0.92), all others (less than 0.33). Error bar represents 95% confidence interval of model-averaged coefficient estimate.

2.5. Discussion

We explored how cross-ecosystem spatial subsidies mediate classical island biogeography predictions for terrestrial breeding bird species richness and population density on 91 islands on the Central Coast of British Columbia, Canada. In accordance with classical TIB (MacArthur and Wilson 1967), island area was the most important predictor of terrestrial bird species richness (Figure 2a). We found that nutrient subsidies affect this relationship: islands heavily subsidized by marine nutrients had fewer species

(Figure 2b). Accordingly, our study system cannot be reduced to the two classical TIB predictors: isolation was not an important predictor of bird species richness, and one measure of marine subsidy (forest-edge soil $\delta^{15}\text{N}$) was the second most important predictor of bird species richness. In addition, while TIB makes no predictions about how population density varies with island area, we found lower densities of birds on larger islands, and higher densities on more subsidized islands (Figure 2d, e). We found that the effect of subsidies on density was stronger on smaller islands.

Overall, we found little support for subsidized island biogeography (SIB) theory as a standalone predictive framework for understanding the influence of subsidies on bird species richness. One of the key predictions of this theory is that smaller islands are disproportionately affected by marine subsidies due to a larger perimeter-to-area ratio. A larger interface between land and sea should increase the potential for marine input, leading to increased terrestrial productivity, higher population densities, and lower extinction rates, with the potential to affect species diversity (Rosenzweig and Abramsky 1993, Anderson and Wait 2001). In our study, species richness on smaller islands was not disproportionately affected by marine subsidies, but smaller, more subsidized islands hosted more dense populations. Since these islands are relatively productive, one possibility is that additional nutrients push the community towards the downward-sloping side of the hypothetical unimodal productivity-diversity curve. Theoretically, higher productivity could increase species richness up to a certain threshold, beyond which species richness decreases due to exclusion by competitively dominant species (Grime 1973). Although this relationship has received strong support in early productivity-plant-diversity literature (Grace 1999) and mixed support in productivity-animal-diversity literature (Waide et al. 1999, Mittelbach et al. 2001), more recent re-analyses of productivity-diversity relationships suggests that unimodal and negative relationships between diversity and productivity are extremely rare in both plants and animals, at all spatial scales (Cusens et al. 2012).

Our results differ from similar studies in the Pacific Northwest, where nutrients derived from Pacific salmon are associated with higher species richness and population densities at mainland sites (Field and Reynolds 2011, Wagner and Reynolds 2019). This is likely due to the source of subsidy. While the underlying mechanism is the same, (i.e., soils are enriched and stimulate plant productivity), salmon provide a large, predictable flux of nutrients without disturbing coastal vegetation or increasing songbird predation

risk. Given their ubiquity in our system, is likely that $\delta^{15}\text{N}$ enrichment in forest-edge soils results from river otter activity, which is more variable in intensity and duration (Olson et al. 2008). Although river otter feces can directly fertilize riparian plant communities (Ben-David et al. 1998), otters could drive behavioural changes as birds actively avoid direct predation and/or nest predation. Alternatively, otters can reduce the structural complexity of coastal vegetation (Roe et al. 2010), an important predictor of bird diversity (Macarthur and Macarthur 1961). An additional contribution to the observed pattern may relate to marine exposure. Plant communities on many of our islands reflect their windswept, salt-sprayed environment with dwarfed trees and dense shrub thickets (Banner et al. 1993). Marine nutrients are deposited on land through marine fog, wind, and sea spray, which may raise soil $\delta^{15}\text{N}$ while creating unfavourable conditions for many bird species. We also considered that certain species/feeding guilds could be driving patterns in our study; our data suggest that the insectivore guild may be important but there is too much uncertainty to draw meaningful conclusions (Figure 4S).

Habitat diversity was not related to island-scale avian diversity, despite contrary findings elsewhere at a range of spatial scales (Macarthur and Macarthur 1961, Haila et al. 1983, Ricklefs and Lovette 1999, Stein et al. 2014). Either our coarse categorizations did not capture habitat components that underly avian habitat affinities, or our species pool is not particularly sensitive to habitat variation. Habitat diversity is also unimportant for arboreal arthropods in Florida mangroves (Simberloff 1976), snakes on Eastern Nearctic islands (Burbrink et al. 2015), and vascular plants on Swedish islands (Rydin and Borgegård 1988).

Finally, we found no support for the prediction that wrack biomass or shoreline substrate affect bird species richness or density on islands. Wrack decays in 1 to 30 days (Mews et al. 2006), and wrack deposition in this region is significantly lower in July than during winter (Wickham et al. 2020); the wrack biomasses we recorded may not represent annual or seasonal input. It is also possible that any subsidizing effects of wrack and shoreline substrate are dwarfed by the effects of river otters and other unmeasured sources (e.g., fog and sea spray) contributing to soil $\delta^{15}\text{N}$.

Subsidies may not directly increase productivity in our system. Soils are nitrogen limited; we observed total nitrogen levels of 0.9 to 2.4‰, which is comparable to those of other nitrogen-limited forests in the Pacific Northwest (0.7 to 3.8‰). We observed a

greater $\delta^{15}\text{N}$ range on islands compared to mainland coastal forests (1.2 to 15.3‰ vs. -2.9 to 6‰, respectively (Quesnel and Lavkulich 1980, Prescott et al. 1993, 2000, Chang et al. 1996, Chang and Preston 2000)), which suggests that insular soil nitrogen is largely marine derived. Islands with higher $\delta^{15}\text{N}$ also had higher levels of total nitrogen ($R^2 = 0.08$, $p < 0.001$). However, the $\delta^{15}\text{N}$ signal is noisy, and levels can also be affected by soil fractionation processes.

We provide a novel test of subsidized island biogeography on avian diversity on 91 islands that vary in area and levels of marine subsidy. We show that marine subsidies increase avian density but decrease species richness in a productive temperate island ecosystem. These results suggest that marine subsidies can cascade to higher trophic levels and alter diversity in a manner infrequently observed for animals (i.e., a negative relationship between productivity and diversity). In agreement with SIB, we find that small island communities are more strongly influenced by subsidies. While these results neither prove nor disprove the subsidy-richness relationship proposed by SIB (Anderson and Wait 2001), they confirm that subsidies play an important role in shaping insular biodiversity, even relative to biogeographic variables like isolation and habitat diversity.

Chapter 3.

Equivalent roles of marine subsidies and island biogeography in shaping island bird communities²

3.1. Abstract

Species distributions across islands are shaped by dispersal limitations, environmental filters, and biotic interactions, but the relative influence of each of these processes has rarely been assessed. Here, we evaluate avian community composition in a meta-ecosystem framework by examining the relative contributions of island characteristics, marine subsidies, species traits, and species interactions to bird community composition. Specifically, we surveyed terrestrial breeding birds and their island habitats in the Central Coast region of British Columbia, Canada. We observed 3,610 individuals of 32 bird species on 89 islands that spanned multiple orders of magnitude in area (0.0002-3 km²). We fit a spatially explicit joint species distribution model to estimate the relative contributions of island physical characteristics, island-specific inputs of marine subsidies, species' traits, and biotic interactions on species distributions. Biogeographic characteristics included island area, isolation, and habitat heterogeneity, while marine influence was represented by forest-edge soil $\delta^{15}\text{N}$, wrack biomass, shoreline substrates, and distance to shore. This approach also allowed us to estimate how much variation in distributions resulted from species' biological traits (i.e., body mass, feeding guild, feeding height, and nesting height). Bird species distributions were determined almost equivalently by island characteristics (23.5% of variation explained) and marine influence (24.8%). We detected variation in species-specific responses to both island biogeographic characteristics and marine influences, but no significant effect of any biological trait examined. Additionally, we found evidence that the environmental filter plays a larger role in species distributions than biotic interactions, implying that these communities are not shaped through competition. Although most island biogeographic studies focus only on islands' physical characteristics, we found evidence for an

² A version of this chapter appears as Obrist, D.S., Hanly, P.J., Kennedy, J.C., Fitzpatrick, O.T., Wickham, S.B., Ernst, C.M., Nijland, W., Reshitnyk, L.Y., Darimont, C.T., Starzomski, B.M., and Reynolds, J.D. (*In Review*) Equivalent roles of marine subsidies and island biogeography in shaping island bird communities. *Journal of Biogeography*.

equivalent role of marine subsidy in structuring island bird communities. Our study demonstrates that disentangling the effects of island biogeographic characteristics, marine inputs, and biotic interactions is a useful next step in understanding species distributions on islands.

3.2. Introduction

Species distributions across landscapes, including islands, are a key focus in ecology. In fact, understanding how species distributions are shaped by island biogeography was the number one question offered by a group of 29 ecologists in a 50-year retrospective of the field of island biogeography (Patiño et al. 2017). In addition to stochastic processes, species distributions are predominantly driven by three deterministic mechanisms: dispersal limitations, environmental filtering, and biotic interactions (Hutchinson 1957, van der Valk 1981, Kraft et al. 2015, Zurell 2017). Environmental filtering refers to whether a population can persist under the environmental conditions of a locale, while biotic interactions include competition, facilitation, predation, and other interactions that can either increase or decrease a species' chance of survival in an area. It has been an on-going challenge to disentangle the effects of dispersal, environmental filters, and biotic interactions on species distributions (Pollock et al. 2014). Although the general statistical framework was developed nearly 25 years ago (Chib and Greenberg 1998), the more recent application of joint species distribution models in ecological studies has facilitated the possibility of a deeper understanding of the processes underlying community assembly (Warton et al. 2015, Ovaskainen et al. 2017).

The three mechanisms driving species distributions are deeply intertwined with the ecological processes underlying the immigration and extinction rates of island species, which are central to predicting species richness according to the classical *Theory of Island Biogeography* (TIB, MacArthur & Wilson, 1967). Immigration rates are affected by island isolation, and vary between species of different dispersal abilities, whereas extinction rates are determined by island size—an important component in determining species' responses to environmental conditions and the outcomes of biotic interactions. Essentially, two species can co-exist on an island if some environmental conditions are tolerated by both species, enough resources exist for both, or they facilitate each other's presence (i.e., through mutualism or commensalism). They may

not overlap on islands that are remote and therefore difficult to disperse to, where they cannot tolerate the environmental conditions, or where they exclude one another through competition for shared resources (Cazelles et al. 2016). Ultimately, the relative contributions of dispersal limitations, environmental filtering, and biotic interactions depend both on the physical characteristics of islands and the biological traits of species living on them.

Spatial subsidies can alter resource availability in recipient ecosystems through the cross-ecosystem movement of nutrients, detritus, and organisms, shifting recipient community dynamics (Anderson, Wait, & Stapp, 2008; Polis, Anderson, & Holt, 1997). Marine subsidization (i.e., marine-derived nutrients that subsidize terrestrial ecosystems) can occur either through passive, donor-controlled processes (e.g., wind and waves washing up marine detritus), or active and animal-mediated means (e.g., through egestion, excretion, gametes, or carcass deposition; Subalusky & Post, 2019). One modification of TIB, the *Subsidized Island Biogeography Hypothesis* (SIB), suggests that an input of marine-derived nutrients may vary productivity in a way that facilitates the co-occurrence of either more or fewer species on an island than would be predicted by TIB alone (Anderson & Wait, 2001). The mechanisms behind SIB are yet another balancing act of the processes that determine patterns in species distributions. Assuming a unimodal productivity-diversity relationship, beyond a certain level of productivity, biotic interactions become more important than the local environmental conditions (i.e., the habitat filter). Specifically, in nutrient-poor environments, SIB suggests that nutrient inputs will result in increased productivity, providing limiting nutrients such that more species can co-occur. This phenomenon occurs on Sardinian beaches, where macroalgal deposits have been found to increase species richness in foredune plant communities (Del Vecchio et al. 2017). In contrast, at high productivity, some species will become competitively dominant, resulting in a decrease in species diversity. This is seen on salmon-rich streams in British Columbia, Canada, where nutrient-loving plant species dominate riparian communities, effectively decreasing plant species richness (Hocking and Reynolds 2011). Additionally, the relationship between productivity and diversity is predicted to be stronger on smaller islands due to higher per-unit-area effects of marine inputs (i.e., relatively more of the island is close to shore; Anderson & Wait, 2001), making small islands the ideal model system to test predictions about the effects of marine influence on island species distributions.

Since its proposal, empirical tests of SIB have been few and have yielded mixed support. Barrett, Wait, & Anderson (2003) found that the slope of the species-area curve was lower on subsidized than unsubsidized desert islands, suggesting that subsidies facilitate higher lizard diversity, but only on islands smaller than 1 km². Obrist et al. (2020) found a decrease in terrestrial bird species richness on temperate islands with higher levels of marine subsidies, suggesting a potential role for competition on more productive islands. On a global scale, however, Menegotto, Rangel, Schrader, Weigelt, and Kreft (2019) found no evidence for SIB, reporting no effects of marine productivity on island plant diversity. These mixed results suggest that the effects of marine subsidies on terrestrial ecosystems may be scale- and system-dependent, which may affect aspects of species communities that are not captured if only alpha diversity is evaluated. The mechanisms underlying the effects of marine subsidies may be revealed through the evaluation of species level responses.

Understanding species level responses to environmental conditions and biotic interactions provides insights on broader patterns of biodiversity, but these responses also depend on the spatial scale of investigation. At larger scales, dispersal limitations and environmental filters may be more important than biotic interactions in structuring species communities. This is exemplified in a recent global scale analysis, where climate and isolation were found to be the most important drivers of island bird assemblages (Sato et al. 2020). These effects depended on feeding guilds and habitat; indeed, such species-specific traits can influence species distributions across environmental gradients due to variations in available niche spaces (Carnicer et al. 2012, Kissling et al. 2012). In contrast, on smaller scales, both local environmental conditions and biotic interactions become more important. For example, in the Central Coast region of British Columbia (BC), Canada, several bird species prefer habitat on streams with higher abundances of spawning salmon (Field and Reynolds 2011, Wagner and Reynolds 2019). However, there are competitive trade-offs in accessing those higher quality habitats; Pacific wrens living on streams with more salmon-derived nutrients show higher rates of counter-singing than those in watersheds with fewer salmon (Wilcox et al. 2021). Determining the relative influence of these spatially dependent mechanisms on islands is an important next step in understanding how island species are assembled.

Here, we assess how marine subsidies might influence the mechanisms that structure terrestrial breeding bird species communities on 89 islands in the Central

Coast region of BC, Canada. We fit a spatially explicit joint species distribution model (JSDM) to estimate the relative contributions of island physical characteristics (island area, isolation, and habitat heterogeneity), island-specific measures of marine influence (forest-edge soil $\delta^{15}\text{N}$, distance to shore, wrack biomass, and proportion of rocky shoreline), species' traits (body mass, feeding guild, nesting height, and feeding height), and biotic interactions on bird community composition. Islands on the Central Coast of BC are surrounded by a nutrient-rich, productive ocean, and typically receive nutrient subsidies in the forms of beach-cast seaweeds, and through animal-mediated fecal and food scrap depositions, particularly those from North American river otters (*Lontra canadensis*). Our previous work on these islands showed that the subsidizing effect of river otter activity provided a stronger signal than wrack deposition when predicting terrestrial bird species richness. We found higher densities of birds on islands with more marine-derived nutrients (measured through forest-edge soil $\delta^{15}\text{N}$, an isotopic measure of marine influence)—islands that also experienced lower species richness. This effect was stronger on smaller islands than larger ones (Obrist et al. 2020). As such, we predicted that marine subsidies would also play a significant role in species distributions, although the mechanism was unclear. This prompted us to generate two hypotheses about how communities are structured: 1) the biotic interaction hypothesis—terrestrial breeding bird communities on islands are structured through interspecific competition, or 2) the habitat filter hypothesis—bird species are distributed on islands according to their environmental preferences and/or tolerances. This second hypothesis encapsulates the possibility that the process leading to increases in marine subsidies can only be tolerated by certain species; for example, river otter activities subsidize terrestrial vegetation but simultaneously cause major habitat disturbances (Ben-David et al. 1998, Roe et al. 2010). In reality, these two hypotheses encompass processes that are likely happening in unison to some degree, but our analysis evaluates the relative contribution of each mechanism. In evaluating these hypotheses, we hope to unite key theories about island biogeography, spatial subsidies, and species-specific responses to environmental gradients.

3.3. Material and methods

3.3.1. Study area

We surveyed terrestrial breeding bird communities on islands in the Central Coast region of BC, Canada (Figure 3.1.; 51° 26' to 52° 3' N and 127° 41' to 128° 28' W). A table with the observed bird species, including names in both local languages—Haítzaqv̓la (Haítzaqv̓) and 'Uik̓ala (Wuikinuxv̓)—and relative abundances can be found in Appendix B:Table B1. Islands in this region are surrounded by a highly productive marine environment, with some of the largest kelp forests in the world (Steneck et al. 2002). As part of the very wet, hyper-maritime subzone of the Coastal Western Hemlock biogeoclimatic zone, these coastal temperate rainforests receive over 3000 mm of precipitation annually (Pojar et al. 1987).

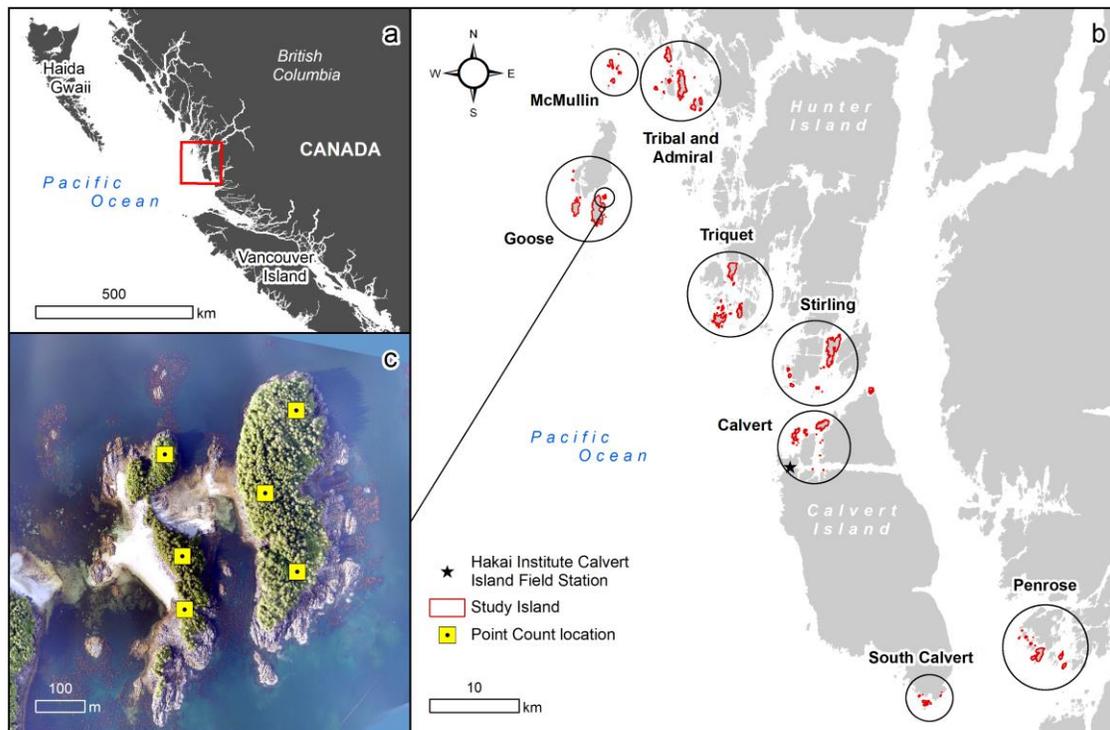


Figure 3.1. (a) Map showing the location of studied islands on the Central Coast of British Columbia, Canada. (b) Map showing island groups that were sampled together for sampling feasibility. (c) sRPAS image of two islands in the Goose Group of islands with six point count locations shown in yellow.

To select a representative sample of islands to survey out of the 1470 islands in the region, we used a two-step, unsupervised clustering analysis, which employs a probability-based distance measure, in SPSS statistical software (V23, IBM). We considered five descriptors per island to assess geographical and geomorphological similarities: distance from mainland, area, wave exposure according to the British Columbia ShoreZone dataset (Howes et al. 1994), normalized (size-independent) perimeter-to-area ratio, and percentage of area occupied by surrounding landmasses within 500 m of each island. All metrics (besides exposure) were derived using WorldView2 satellite imagery with 2 m resolution. All data were standardized to z-scores prior to clustering to ensure approximately equal weight for all variables. This process begins with an initial partition of the data, followed by a hierarchical clustering of these partitions. The Schwartz Bayesian Criterion (BIC) detected five clusters of island types, ranging from 134 to 432 islands per type (results in Appendix B: Table B12). We visually examined the results and found distinct island groups for which multiple islands of each cluster type were present. Within each island group of 9-17 islands (Figure 1b), we selected islands that maximized the within-group variation to ensure a range of island size and coastline geomorphology. We surveyed up to a maximum island area of 3 km² for sampling feasibility.

3.3.2. Field surveys and data collection

Terrestrial breeding birds

We conducted two 10-minute point count surveys at 301 locations across 99 islands, approximately one month apart to account for detection differences in early and late season migrant birds. Retaining only islands with a complete set of environmental parameters left us with 283 locations across 91 islands. Finally, to improve model fit, we removed the two islands (TB04: 124 m² and CV05: 3560 m²) with no observations of species abundant enough to include in the model (see section 2.3.2 below), which left 281 locations across 89 islands for analysis. The number of point counts on each island was roughly proportional to the size of the island. Chosen point count locations covered the different habitat types on each island. To maintain independence among point counts, we chose locations approximately 250 m apart, although sometimes they were closer together on smaller islands. To account for this, and for differences among species in detectability, we only included observations from within 50 m of the observer

for analysis. We intended to reduce the effects of edge habitat by placing points more than 50 m inland, but due to the small size of most of the islands, 56% of point counts occurred within 50 m of a shoreline. We did not survey during rain or high winds (wind speed above 3 on the Beaufort scale). Our field teams were chosen based on high competency to identify birds of BC by sight and sound, and initial comparisons with multiple observers in the field confirmed that inter-observer variation was minimal. At the start of each field season, observers calibrated distances to birds observed using range finders on trial point counts. On the 99 islands surveyed, we conducted surveys between late April and early July in 2015 (n = 40 islands), 2016 (n = 33 islands), or 2017 (n = 26 islands); each island was surveyed twice in only one year.

We obtained data on bird species feeding guild and body mass from the EltonTraits 1.0 database (Wilman et al. 2014). For feeding guild, we used the “Diet-5Cat” column in this database, which groups species into one of five categories according to the dominant source of that species’ diet: “Plant and Seeds”, “Fruits and Nectar”, “Invertebrates”, “Vertebrates and Fish and Carrion”, and “Omnivore”. We also categorized birds into four feeding heights (ground, ground/lower canopy, lower canopy, and upper canopy) and two nesting heights (ground versus off-ground) based on individual species accounts on the Birds of the World database (Billerman et al. 2020).

Nutrient subsidies

As in Obrist et al. (2020), we quantified marine inputs in three ways: (1) by weighing beach-cast seaweeds (wrack) on each island; (2) by estimating the proportion of rocky shoreline on each island; and (3) by measuring the amount of marine-derived nitrogen ($\delta^{15}\text{N}$) in island soils. The third measure represents multiple sources of marine-derived nutrients, including sea spray and animal vectors (e.g., river otter feces, urine, and abandoned prey items).

We measured wrack biomass in three quadrats along two transects at four locations (3 x 2 x 4) on each island – at the north, east, south, and west-most points. Each transect was 20 m long and parallel to the water. The first was placed at the most recent high tide line, and the second at the highest wrack line on the beach (most recent storm line). These wrack lines have the potential to be similar, or to differ greatly, based on weather conditions, tidal heights, shoreline substrate, or season. The three quadrats were placed randomly along transects to capture the heterogeneous nature of wrack

subsidies in an unbiased way. In each quadrat, we weighed wrack by species, and calibrated wet weights to dry weights (Wickham, Darimont, Reynolds, & Starzomski, 2019). For our analyses, we linearized this parameter by taking the square root of the mean wrack biomass in the 24 plots per island.

Shoreline substrate affects the ability of islands to receive and retain wrack and wrack-like subsidies. Rocky substrates retain less wrack on these islands when compared to boulder, cobble, gravel, and sandy substrates (Wickham et al., 2020). We used small remotely piloted aerial systems (sRPAS) to collect raster imagery of islands at 10 cm resolution. We then manually categorized shoreline substrate at 5 m intervals around each island using ESRI ArcMap v. 10.3 to calculate the proportion of shoreline on each island that is classified as “rocky”.

To quantify the amount of marine-derived nitrogen on islands, we took soil samples from four shore-adjacent plots on each island, corresponding to the sites where we measured wrack biomass. Samples weighed 250-500 g and were taken from the upper 10 cm of soil with the litter layer removed. Stable isotope analysis was done at the Pacific Forestry Centre in Saanich, BC. We used the average $\delta^{15}\text{N}$ of these four soil samples as an estimate of marine input on an island. Because $\delta^{15}\text{N}$ fractionates $\sim 3.4\text{‰}$ per trophic level, this forest-edge soil $\delta^{15}\text{N}$ can be used as a rough estimate for marine inputs from animal vectors—upper level consumers that cross the land-sea interface to feed. River otters are prolific on these islands, feeding on fish and marine invertebrates in the sea but returning to extensive latrine sites and dens on land where they deposit feces, urine, and uneaten prey items. Several studies have shown that values of $\delta^{15}\text{N}$ in the soil are higher at river otter activity sites (Crait & Ben-David, 2007; Roe et al., 2010; Christopher Ernst 2017, *unpublished data*). In addition to river otters, other subsidy sources are also likely to impact soil $\delta^{15}\text{N}$; for instance, both marine fog (Weathers and Likens 1997) and sea spray (Art et al. 1974) could act as abiotic vectors of marine-derived nitrogen.

Other environmental covariates

We obtained measures for island area and the normalized difference vegetation index (NDVI) using WorldView-2 satellite imagery. To estimate habitat heterogeneity, we combined NDVI and visual inspection of sRPAS imagery to distinguish five habitat categories: dense/closed-canopy forest, light/open-canopy forest/dense shrub, light

shrub/grass, bog (vegetation and water), and woody debris/snags. We used the Shannon diversity index of the relative proportion of each habitat type on each island as habitat heterogeneity. Since study islands are continental, and often close to other large islands (see Figure 1a), we chose to represent isolation by calculating the point at which the bird species-area curve approaches its asymptote (i.e., the area required for an island to act as a functional “mainland”) and calculating the distance to the nearest island of that size (120,245 m²). Details are in the Supplemental Information.

3.3.3. Statistical analysis

Hierarchical modeling of species communities (HMSC)

To evaluate how communities are structured, we fit a joint species distribution model (JSDM) with Bayesian inference using the ‘*Hmsc*’ package in R v. 4.1.1 (Ovaskainen et al. 2017, Tikhonov et al. 2020, R Core Team 2021). This approach, termed the “Hierarchical Modeling of Species Communities”, allows for the concurrent estimation of species responses to a matrix of environmental covariates, across samples and their responses to one another, for all species simultaneously. This type of model also attributes variation in species’ abundances to differences in how species’ biological traits respond to environmental parameters. Correlations in residuals among species’ occurrences are used to infer biotic interactions. The HMSC framework has a distinct advantage over previous versions of JSDM-fitting frameworks as it enables the use of different statistical distributions for presence-absence, count, percent cover, and biomass data. Additionally, it allows the user to fit nested, hierarchical spatiotemporal models (Tikhonov et al. 2020). Since this type of model is newly applied, we provide thorough details of the fitting process in the Supplementary Information, closely following steps laid out in Ovaskainen et al. (2017), who developed the original framework, and Stark et al. (2020), who applied it to eelgrass epifaunal communities.

Fitting and evaluating the model

We fit a Poisson-distributed model by running two Markov chain Monte Carlo (MCMC) chains with 40,000 iterations, a burn-in of 1000 samples, and thinning to retain every 10th iteration. We assessed MCMC convergence both visually and quantitatively by inspecting mixing of the chains and by evaluating effective sample size and the potential scale reduction factor (PSRF, Appendix B: Figure B2). PSRF values close to 1

indicate minimal difference between chains (Brooks and Gelman 1998). We examined the model's explanatory power by calculating a series of model fit statistics: the root mean square error (RMSE), a pseudo- R^2 value appropriate for Poisson-distributed models, and the area under the receiver operating characteristic curve (AUC) (Appendix B: Table B3). Finally, we evaluated the model's predictive power through three-fold cross validation (Appendix B: Table B4).

Next, we used variance partitioning to assess the explanatory power of groups of predictor values to evaluate their importance in structuring avian communities. To do this, we grouped together environmental parameters that could fit under the "island characteristics" heading: island area, isolation, and habitat heterogeneity; ones that related to "marine influence": forest-edge soil $\delta^{15}\text{N}$, distance to shore, wrack biomass, and proportion of rocky shoreline. We kept separate the interaction between island area and soil $\delta^{15}\text{N}$, as well as survey year. Variance partitioning also allowed us to calculate the variance explained by each level of random effect that we analyzed, including point count ID, island, and where the point count lies in space (XY coordinates).

After removing species that were present in fewer than 5% of plots (Stark et al. 2020), plus three additional relatively uncommon species that resulted in poor model fits, we retained detections of 3425 individuals belonging to 16 species over the three summers (Figure 3.2.). Nearly 48% of the detections belonged to the three most common species: orange-crowned warbler, Pacific wren, and Pacific-slope flycatcher. The reported mean adult mass (averaged across sexes) ranged from 3.5 g (rufous hummingbird) to nearly 400 g (American crow) (Dunning Jr. 2007). All birds belonged to either the omnivore or insectivore feeding guild classified by the EltonTraits 1.0 database (Wilman et al. 2014). Other traits that we considered in our analysis are where they feed, from ground to upper-canopy, and whether they nest on or off the ground.

3.4. Results

The model explained the variance in species distributions better for some species than others, with a mean pseudo- R^2 (squared Spearman correlation between observed and predicted values times the sign of the correlation for Poisson-distributed models) of 0.36. The fit was poorest for American robin with a pseudo- R^2 of only 0.02,

and best for fox sparrow with a pseudo-R² of 0.61. Pseudo-R² for all species can be found in Appendix B: Table B3.

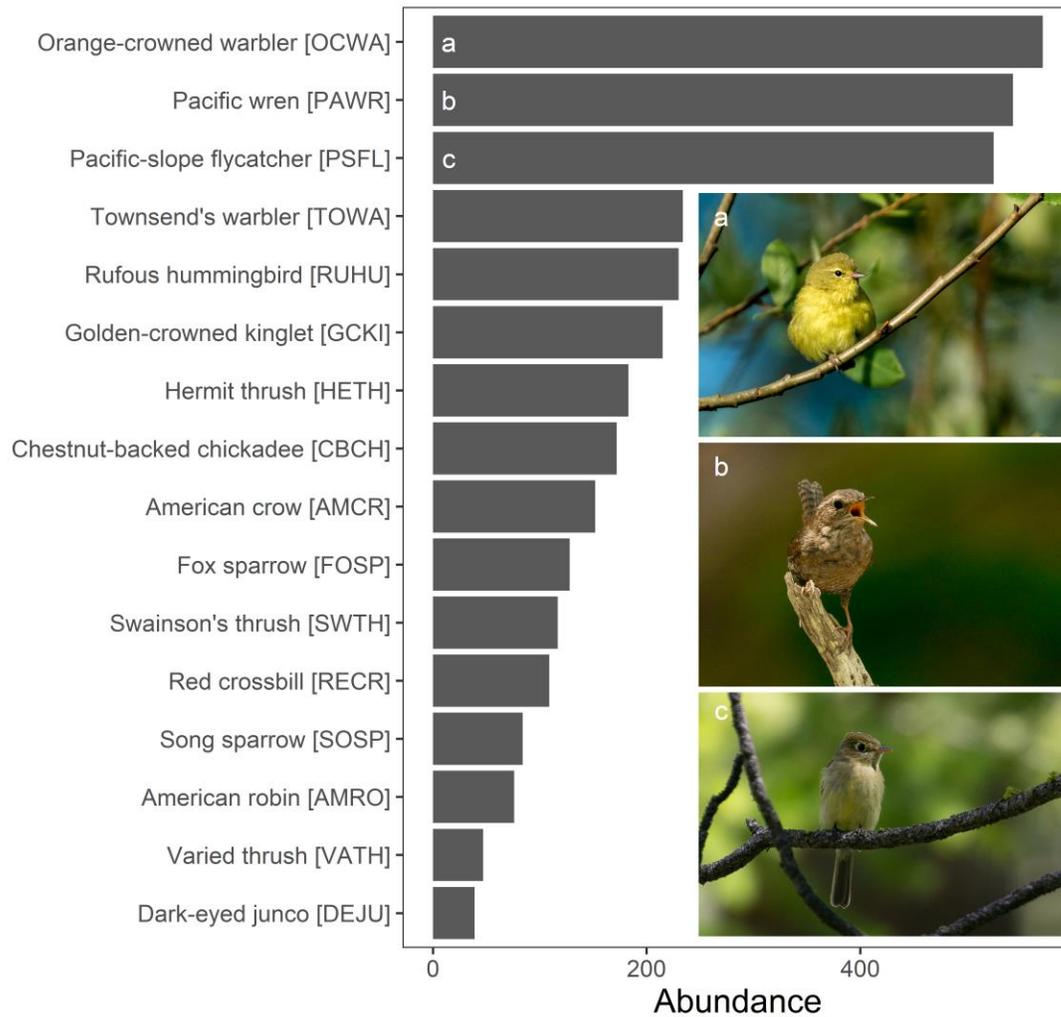


Figure 3.2. Rank abundance of terrestrial breeding bird species detected in at least 20 study plots across 89 islands on the Central Coast of British Columbia, Canada. Inset images represent the three most common species, making up nearly 46% of all observations – (a) Orange-crowned warbler, (b) Pacific wren, and (c) Pacific-slope flycatcher.

Photos taken by John Reynolds.

3.4.1. Variance partitioning

Of the variation in species responses to the environment, the proportion explained by marine influence was approximately equivalent to that of island

characteristics. Specifically, 24.8% of variation in species responses were explained by marine inputs and 23.5% were explained by island characteristics, including habitat heterogeneity (Figure 3.3.). An additional 7.1% was explained by the interaction between island area and forest-edge soil $\delta^{15}\text{N}$ – although this estimate ranged from under 2% for rufous hummingbirds and song sparrows to around 22% for Pacific wrens and hermit thrushes. There was also considerable variation in percent of species' responses explained by island biogeography parameters, with island area, isolation, and habitat heterogeneity collectively explaining 58% of variation in abundance of varied thrushes but only 5% for fox sparrows. Likewise, the influence of marine inputs ranged substantially from species to species, with 44% of the variation explained for song sparrows but only 5% for golden-crowned kinglets.

3.4.2. Environmental filtering

As expected, species showed variable responses to environmental parameters, although we did find some overarching patterns (Figure 3.4.). Overall, we only found positive species abundances at plot level with island area—10 of the 16 species showed preferences for larger islands, and no species preferred smaller islands. Some species, including fox sparrows, song sparrows, Swainson's thrushes, and American crows preferred plots closer to shore, while others, such as dark-eyed juncos and chestnut-backed chickadees preferred inland habitats further from shore. Some species showed preferences for marine inputs. For example, song sparrows and fox sparrows preferred islands with more wrack accumulation, whereas Pacific wrens and Townsend's warblers showed negative responses to such islands. Additionally, islands with higher levels of marine-derived nitrogen in the soil appeared to be preferred by four species but five others displayed negative associations—song sparrows, fox sparrows, American crows, and rufous hummingbirds prefer such islands but Pacific-slope flycatchers, American robins, hermit thrushes, Townsend's warblers, and Pacific wrens showed negative responses.

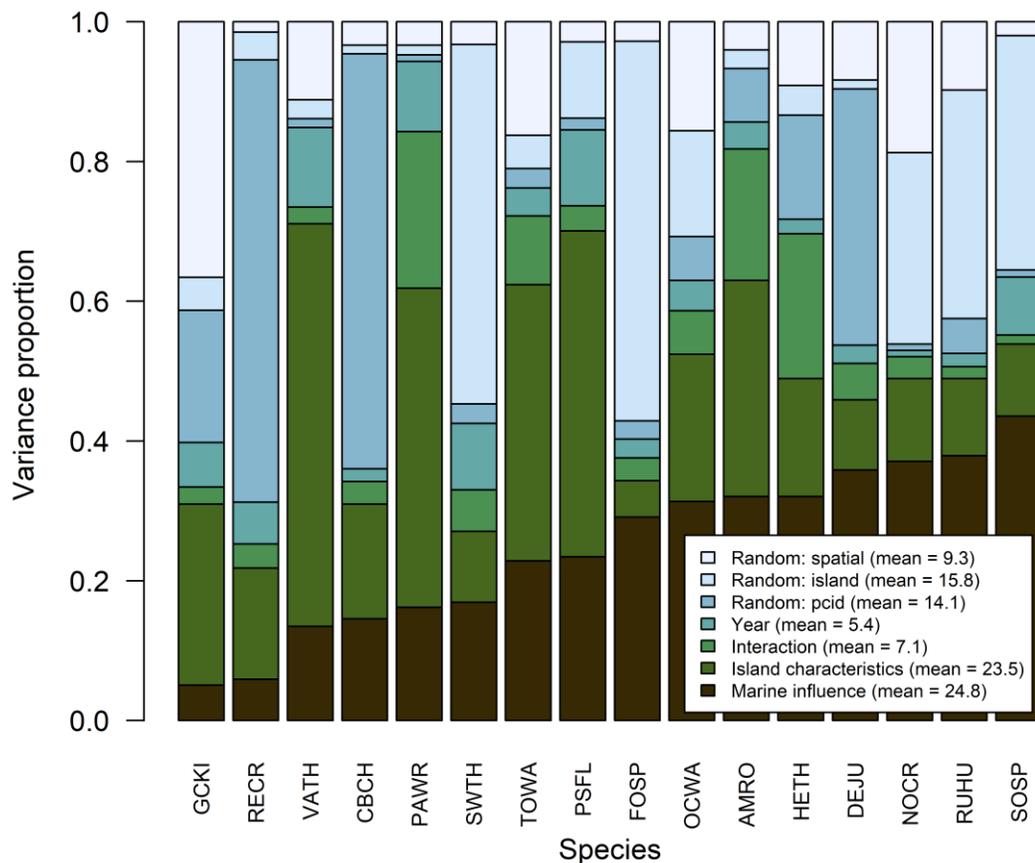


Figure 3.3. Proportions of variance explained by different grouping variables. The “marine influence” grouping includes wrack biomass, $\delta^{15}\text{N}$ of the soil at the edge of the island, distance to shore, and the proportion of shoreline that is rocky, while “island characteristics” includes island area, habitat heterogeneity, and isolation. The “interaction” component is the proportion of variance explained by the interaction between island area and $\delta^{15}\text{N}$ of the soil. The “random: pcid” term is the amount of variance explained by the random effect of point count ID – i.e., the proportion of variance explained in species interactions at the point count level and the unmeasured environmental parameters at the point count level. The “random: island” term represents the variance accounted for by the random effect of island. The “random: spatial” term represents variance explained by the point count’s spatial coordinates – i.e., unexplained additional variance that arises due to certain points being closer together in space than others. Species 4-letter code key is in Figure 2.

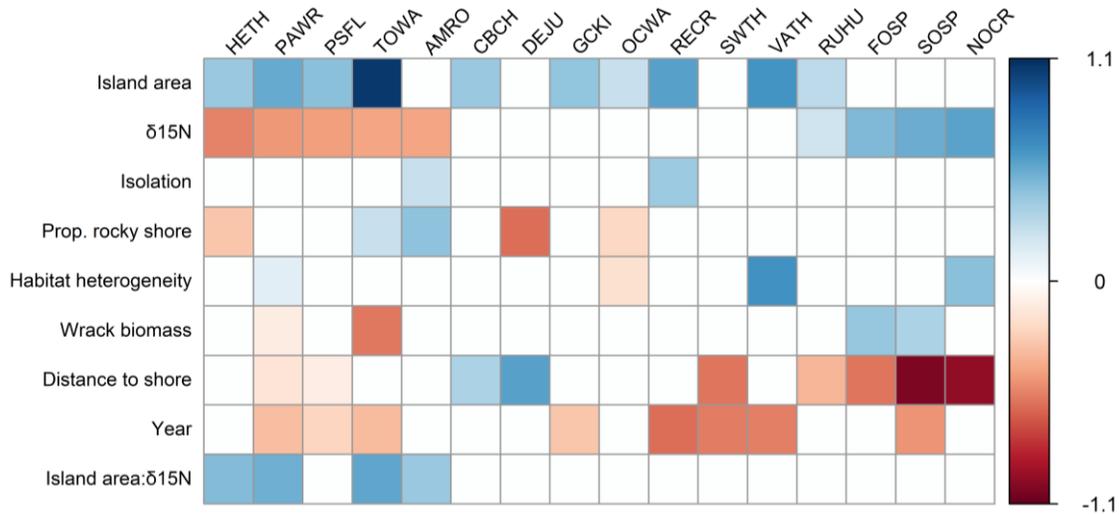


Figure 3.4. Species level responses to environmental parameters (posterior means) in terrestrial breeding birds on the Central Coast of British Columbia, Canada. This plot only shows estimates where the posterior probability of the coefficients > 95%. Species 4-letter code key is in Figure 2.

3.4.3. Species' traits

The traits that we tested explained some of the overall variation in species' responses to environmental parameters, ranging from 21% of variance explained for species' responses to isolation, to 55% of species' responses to soil $\delta^{15}\text{N}$. However, on a trait level, none of the traits we tested were statistically significant at the traditional 95% cut-off—possibly due to the small number of species represented by each trait. Although not statistically significant, it appears that birds with higher body masses (likely driven by American crows), and those which feed on the ground and lower canopy (i.e., song sparrows and Swainson's thrushes), preferred to be closer to shore as seen through a negative association with distance to shore (Figure 3.5.).

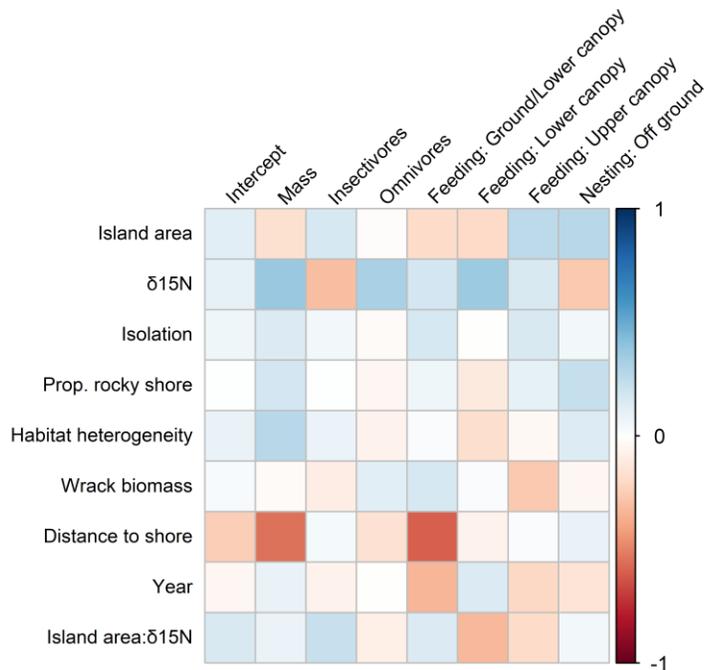


Figure 3.5. Trait level responses to environmental parameters (posterior means) in terrestrial breeding birds on the Central Coast of British Columbia, Canada. This plot shows all estimates: none had a posterior probability of the coefficients > 95%. The intercept (Column 1) represents birds that feed and nest on the ground.

3.4.4. Co-occurrence patterns

Although generally weak, we found evidence of a greater number of negative species associations at the plot level, and stronger, more positive associations at the level of the entire island (Figure 3.6.). Dark-eyed junco was the only species to have negative associations with other species at the coarser, island scale. The median interaction value was 0.06 ± 0.39 (SD) for plot level interactions, 0.42 ± 0.39 for island level interactions and 0.01 ± 0.50 at the coordinate level.

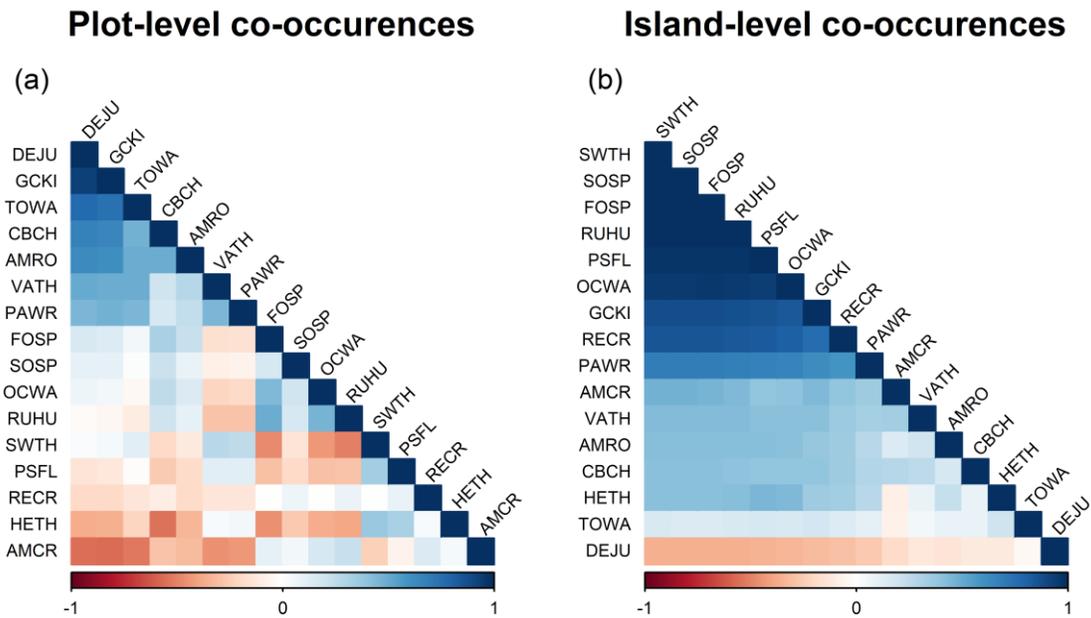


Figure 3.6. Terrestrial breeding bird species co-occurrences on 89 islands on the Central Coast of British Columbia, Canada. These results come from a joint species distribution model, which fits species co-occurrences simultaneously with species responses to environmental parameters. (a) Co-occurrences at a plot (point count location) level, and (b) co-occurrences at the level of the entire island. Species 4-letter code key is in Figure 3.2.

3.5. Discussion

Our field study of 89 islands is the first to explicitly examine the joint effects of island characteristics, marine influence, biological traits, and biotic interactions on species distributions. We found that, on the studied islands, marine influences and island biogeography parameters were equally important in predicting terrestrial breeding bird assemblages. Furthermore, there was evidence of more positive co-occurrences at a coarser, island scale, and more negative co-occurrences on a local, sampling plot scale. To determine whether these plot level negative co-occurrences reflected competition for marine-derived nutrients, we evaluated species-specific responses, and found no evidence of negative co-occurrences (i.e., competitive species interactions) between the species that displayed preferences for marine-derived nutrients. Overall, we reveal environmental filtering as the primary mechanism by which marine subsidies impact

island bird species distributions on the studied islands, rather than through biotic interactions.

Through variance partitioning (Figure 3.3.), we found that marine influence explains just as much variation in island bird species distributions as island characteristics on the islands we examined. On average, we found that marine influences accounted for 24.8% of variation in species distributions, while island characteristics accounted for 23.5%. This finding reveals that flows of nutrients across ecosystems can be particularly important on small islands (Anderson and Wait 2001), which should be evaluated in a meta-ecosystem framework (Loreau et al. 2003). Although studies have evaluated the effects of area and isolation (e.g., Dale, 2019; Harvey & MacDougall, 2014), climate (Ibanez et al. 2018, Sato et al. 2020), environmental heterogeneity (Liu et al. 2018), and *in-situ* evolution (Rosindell and Phillimore 2011) on island species communities, the impacts of cross-ecosystem transfers had not been considered prior to this study. A few studies exist, however, on the effects of marine influences on island alpha diversity (Barrett et al. 2003, Menegotto et al. 2019, Obrist et al. 2020). Results of these studies have been highly variable, likely due to the context-dependent effects of spatial subsidies (Spiller et al. 2010, Piovia-Scott et al. 2019, Subalusky and Post 2019). Our study supports the explanation that although effects on alpha diversity are variable, relatively high beta diversity may be driven by heterogeneity of environmental characteristics on small islands, which are often too small to host multiple habitat types (Liu et al. 2018). In line with the *Subsidized Island Biogeography Hypothesis* (SIB, Anderson & Wait, 2001), this phenomenon may be driven by variability in marine influence in our study.

We were able to provide explanations to some of the broader patterns that we observed by evaluating species level responses to environmental parameters. Overall, the ratios of variance explained by different parameters varied among species according to their natural histories. For example, the occurrence of fox sparrows and song sparrows, two species commonly seen feeding intertidally, was better predicted by marine influence than island biogeography, while the occurrences of forest-specialist birds, including varied thrush, Pacific-slope flycatcher, and Pacific wren, were better predicted by island biogeography characteristics. Similarly, of the 16 species in this analysis, four species showed a preference for islands with higher marine-derived nitrogen content in the soils (fox sparrows, song sparrows, American crows, and rufous

hummingbirds), while another five showed negative associations with such islands (Pacific-slope flycatchers, American robins, hermit thrushes, Townsend's warblers, and Pacific wrens). Since marine-derived nitrogen is likely a good indicator of river otter activity on islands like the ones we studied (Ben-David et al., 1998; C. Ernst, unpublished data), it is possible that the five species with negative associations are either not able to tolerate or do not prefer the edge-type habitats created through disturbances from river otter activity. Meanwhile, song sparrows, fox sparrows, American crows, and rufous hummingbirds prefer earlier successional forest types, such as those on the edges of islands (Billerman et al. 2020). Additionally, we found evidence for strong interannual variability for 7 of the 16 species examined (i.e., an effect of sampling year). Such temporal variability in bird species communities is known to be affected by climatic conditions (Gordo 2007), and to be greater in fragmented habitats (Boulinier et al. 1998). Furthermore, interannual variability is common in irruptive species, such as red crossbills, which showed the strongest response to "sampling year" in our study. These species follow the distribution patterns of highly variable conifer seed crops (Koenig and Knops 2001). Overall, our observed species level responses are in line with our expectations based on the natural histories of species in our study.

Upon evaluation of the relative effects of environmental parameters and biotic interactions between bird species, we found evidence to support the hypothesis that environmental filtering is the dominant mechanism structuring island bird communities on the studied islands. Indeed, biotic interactions accounted for 14.1% of the variance in species distributions at the plot level, and 15.8% at the island level, summing up to less than the total explained by environmental parameters (60.8%). This finding is similar to a study on small islands in the Thousand Island Lake in China, where the environmental filter was found to play a larger role than biotic interactions in avian community assembly (Si et al. 2017). In contrast, in a foundational paper, Diamond (1975) proposed that bird communities on islands in New Guinea were structured through competition, although several studies have questioned this, with some even arguing that species distributions can be just as well explained by randomized null models (e.g., Connor & Simberloff, 1979; Gotelli & Graves, 1996; Hubbell, 2001). A more recent empirical test on Eastern Nearctic islands found that in snake communities neither environmental characteristics nor biotic interactions predicted species' presences as well as random draws from the mainland species pool (Burbrink et al. 2015). In contrast to these studies, the relative

role of the environmental filter in our study was larger than expected, possibly driven by the high per-unit-area influence of marine inputs on relatively small islands (Anderson and Wait 2001), which was experienced by several but not all species.

While accounting for variation explained by environmental parameters, we found more negative species co-occurrences at the plot scale and more positive species co-occurrences at the island scale. This finding is in line with recent studies which have shown that negative interactions (i.e., competition) occur at finer scales, but positive interactions persist across spatial scales (Araújo and Rozenfeld 2014, Mod et al. 2020). Indeed, this pattern suggests that species may be competing for the same resource locally but have shared habitat requirements (Ovaskainen et al. 2016, König et al. 2021). However, the negative co-occurrences we detected at the smaller spatial scale were weak compared to the positive co-occurrences at the island scale, suggesting a potential influence of stochastic processes rather than competition (Triantis et al. 2012). Additionally, there appear to be no negative co-occurrences between species (Figure 6) that show preferences for islands with more marine derived nitrogen in the soil (Figure 4). As such, these species are likely not competing with one another for this resource, but it is possible that although the studied islands are nitrogen-limited (Miller 2019), avian communities are limited by a different resource. It is far more likely that these species are simply able to tolerate environmental changes caused by river otters (e.g., major vegetation disturbances; Ben-David et al., 1998; Roe et al., 2010) rather than competing for the nutrients they provide. Furthermore, an alternative explanation is the possibility that species might be assembled according to a nested pattern, i.e., that species in species-poor areas are simply subsets of those found in species-rich areas (Patterson and Atmar 1986). This pattern is common in land-bridge archipelagos (Wright et al. 1997), but can also arise as a result of island isolation and size (Wang et al. 2010). Although we were able to account for both island size and isolation in the species co-occurrences revealed by our JSDM, it is possible that nestedness could occur due to a missed environmental covariate. Indeed, Zurell et al. (2020) caution that positive co-occurrences tend to be over-represented and more often indicate missed environmental parameters than true facilitation between species.

Finally, it is possible that the importance of environmental parameters that we found (particularly of marine influence) is amplified due to the relatively small size of islands we examined. Indeed, the *Subsidized Island Biogeography Hypothesis* (SIB) is

founded in the idea that marine inputs have higher per-unit-area effects on smaller islands due to their higher perimeter-to-area ratios (Anderson and Wait 2001). Nevertheless, the results from this study are applicable to larger islands and mainland systems as it is known that spatial subsidies, including those from marine inputs, can cause significant shifts in terrestrial species communities across large spatial and temporal scales. Indeed, much of our knowledge of ecological processes in mainland systems is derived from island studies (Santos et al. 2016). For instance, on King George Island, a large island in the Maritime Antarctic, marine inputs provided by seabird colonies result in six very distinct vegetation types in response to marine-derived nutrients and disturbance from the colonies (Zwolicki et al. 2015). Furthermore, in terrestrial ecosystems across their spawning range, Pacific salmon subsidies to nutrient-limited riparian ecosystems cause shifts in plant communities (Hocking and Reynolds 2011), an effect so large it can be detected through satellite imagery (Brown et al. 2020, Kieran et al. 2021). These studies demonstrate the significance of spatial subsidies across large spatial scales, but by leveraging the innate simplicity of small islands, we were able to uncover some more nuanced effects of nutrient subsidies on community composition of island birds. In more complex systems, it is difficult to decipher the effects of multiple resources, arriving at different points across time and space and affecting an unknown multitude of trophic entities (Anderson et al. 2008).

Our study demonstrates the importance of evaluating species communities in a meta-ecosystem framework, which considers flows of nutrients across ecosystem boundaries (Loreau et al. 2003), which are particularly relevant on small islands (Anderson and Wait 2001). Specifically, we found that marine influence was just as important as island characteristics in defining terrestrial breeding bird community assemblages on small temperate islands, and that overall, environmental parameters were more important in predicting species distributions than biotic interactions. Understanding the effects of cross-ecosystem energy flows is fundamental to understanding how species are distributed. Furthermore, there would be value in conducting multitrophic studies to shed light on inter-taxon species interactions that could drive patterns in species distributions on islands. For instance, perhaps birds, as upper level consumers, simply reflect the changes in underlying plant, microbe, and invertebrate communities, which may demonstrate stronger responses to nutrient fluxes (Subalusky and Post 2019).

Chapter 4.

Biogeographic features mediate marine subsidies to island food webs³

4.1. Abstract

Although marine subsidies often enrich terrestrial ecosystems, their influence is known to be context dependent. Additionally, the multitrophic impact of marine subsidies has not been traced through food webs across physically diverse islands. Here, we test predictions about how island characteristics can affect marine enrichment of food web constituents, and how nutrients flow through island food webs. To evaluate enrichment and trace marine nutrients across food webs, we used stable isotopes of soil, flora, and fauna (n = 4752 samples) collected from 97 islands in British Columbia, Canada. Island area was the strongest predictor of enrichment across taxa; we found that samples were more ¹⁵N-rich on smaller islands. Enrichment declined with distance from shore but less so on small islands, implying a higher per-unit-area subsidy effect. These area and distance-to-shore effects were taxon-specific, and nearly twice as strong in basal food web groups. We also found that increases in δ¹⁵N correlated with increases in %N in basal trophic groups, as well as in songbirds, implying biologically relevant uptake of a potentially limiting nutrient. Path analysis demonstrated that subsidies in soil flow through plants, detritivores, and into upper-level consumers. Our results reveal an interplay between island biogeography and marine subsidies in shaping island food webs through bottom-up processes.

4.2. Introduction

MacArthur and Wilson's (1967) *Theory of Island Biogeography* (TIB) provides a framework for predicting equilibrium species richness according to island isolation and size, but marine inputs can impose deviation from these basic predictions (Polis et al.

³ A version of this chapter appears as Obrist, D.S., Hanly, P.J., Brown, N.E.M., Ernst, C.M., Wickham, S.B., Fitzpatrick, O.T., Kennedy, J.C., Nijland, W., Reshitnyk, L.Y., Darimont, C.T., Starzomski, B.M., and Reynolds, J.D. (2022) Biogeographic features mediate marine subsidies to island food webs. *Ecosphere* 13(7):377-99.

1997, Barrett et al. 2003, Obrist et al. 2020). Marine subsidies connect terrestrial and aquatic ecosystems through the movement of materials (i.e., nutrients, detritus, and organisms), and alter dynamics of recipient communities (Polis et al. 1997, Anderson et al. 2008). They can occur through either passive, donor-controlled processes, such as wind and waves depositing macroalgae on shores, or by active, animal-mediated means, including egestion and excretion by consumers, but also carcass deposition (Subalusky and Post 2019). Since such cross-boundary transfers often involve the movement of limiting resources, they have the potential to facilitate increases in recipient habitat productivity. In fact, a meta-analysis across several biomes showed that subsidized ecological communities have 36-57% larger populations (Montagano et al. 2019). This effect is amplified on smaller islands due to higher perimeter-to-area ratios, which facilitate greater per-unit-area effects of marine subsidies than on larger islands (Polis and Hurd 1996). Accordingly, the *Subsidized Island Biogeography Hypothesis* (SIB) suggests more variable consumer responses on subsidized small islands due to trade-offs between increased resource availability and associated competition (Anderson and Wait 2001). As a result, subsidized small islands are ideal model ecosystems to test the potential effects of subsidies on multi-level ecological communities.

Physical, spatial, and temporal characteristics of both subsidies and recipient habitats determine the magnitude and type of effect on recipient communities. Subsidies fluctuate in amount, quality, timing, and duration, eliciting variable effects on ecosystems (Piovia-Scott et al. 2019, Subalusky and Post 2019). In one study, larger amounts of spawning salmon significantly increased riparian per-shrub berry production in Canadian streams (Siemens et al. 2020), which potentially affects avian and mammalian consumers (Traveset and Willson 1998). Another study found that changing the seasonal timing of subsidy addition to plants resulted in a shift from bottom-up effects for herbivores to top-down suppression by predators (Gratton and Denno 2003). Furthermore, physical characteristics of recipient habitats affect rates of delivery and retention of subsidies (Wiens et al. 1985). For instance, island beaches with less rocky substrate (i.e., more sand, gravel, and pebble substrate) have higher rates of wrack retention (Wickham et al. 2020). The degree of isolation between habitats also matters—lizard populations on small, isolated islands responded to artificial seaweed inputs more strongly than more connected populations in plots on large islands (Wright et al. 2020). A recent experiment evaluated effects of both characteristics of the subsidy and the

recipient habitat on very small islands (4-157 m²). This study found varied predator effects on invertebrate prey depending on wrack subsidy amount, pulse frequency, and island size (Piovia-Scott et al. 2017, 2019), suggesting a connection between island characteristics and marine subsidies on island food webs. Overall, both the characteristics of the subsidy and of the recipient habitat determine how a subsidy will influence the biotic components of an ecosystem, but these two components have rarely been studied in unison. Additionally, although much of the seminal work linking trophic ecology with marine subsidies occurred on islands (Polis and Hurd 1996, Polis et al. 1997, Anderson and Polis 1998, Stapp et al. 1999), these studies did not explicitly investigate the role of recipient island characteristics.

In this study, we use a suite of hierarchical models to evaluate how island characteristics (island area, mean slope, and shore-cast macroalgal biomass (i.e., wrack)) and distance from shore affect enrichment of island taxa across six trophic levels. We use stable isotopes of carbon and nitrogen to represent enrichment by marine subsidies on 97 islands on the central coast of British Columbia, Canada, where we collected samples of soil, plants, herbivores (weevils), detritivores (isopods), carnivores (ground-dwelling beetles), and upper-level consumers (songbirds). The main conduits of marine inputs to these islands are wrack accumulation, sea spray, and river otter feces, urine, and discarded prey items. Evidence of enrichment by these sources can be tracked through elevated $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, or both. We predicted island characteristics would have weaker effects on higher trophic levels because these organisms are more mobile (both within and among islands), and feed over larger, more heterogeneous areas. To determine whether subsidy inputs resulted in biologically relevant uptake of nitrogen, we also evaluated the associated increase in %N alongside enrichment of ^{15}N .

We paired this analysis with a structural equation modeling approach to gain insight into the dominant pathways of subsidies through island food webs—specifically, to determine if subsidies move through food webs through plant fertilization, direct consumption of subsidies by consumers, or both. Direct consumption is observable as elevated values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in higher trophic levels but not terrestrial plants, while fertilization is observable as enrichment of ^{15}N without simultaneous ^{13}C enrichment in plants and subsequent consumers. These predictions rely on the reality that plants obtain nitrogen from the soil but carbon from the atmosphere. We predicted that subsidy effects would be primarily bottom-up: subsidies enter the food web through the soil, and

signals of marine influence would flow up the food web through plants, detritivore, herbivore, and carnivore invertebrates, and possibly even into upper-level consumers. We tailor this prediction by considering the types of subsidies considered here (i.e., wrack, feces, urine, and food scraps). Stronger upper-level consumer pathways likely exist in salmon-subsidized ecosystems (e.g., bears in Helfield and Naiman 2006) or in ones with emerging aquatic invertebrates (e.g., birds, bats, and spiders in Recalde et al. 2020), where the subsidy is more attractive to upper-level consumers. Collectively, testing these predictions allowed us to assess how island characteristics can affect both the enrichment of individual components of food webs, as well as the flow of nutrients through island food webs, and as a result, tie together key theories in island biogeography and food web ecology.

4.3. Material and methods

4.3.1. Study area

In the summers of 2015, 2016, and 2017, we collected 4,752 samples from soil and five taxonomic groups of plants and animals on islands (Figure 4.1.), representing links in food chains across 97 islands in the Central Coast region of British Columbia, Canada (51° 26' to 52° 3' N and 127° 41' to 128° 28' W). See Table S1 for species names of samples collected in both local Indigenous languages (Haítzaqv̓l̓a and 'Uik̓ala). The ocean around these islands hosts widespread kelp forests and is one of the most productive marine environments in the world (Steneck et al. 2002). Surveyed islands (0.0001-3 km²) are part of the very wet, hyper maritime subzone of the Coastal Western Hemlock biogeoclimatic zone that receives over 3 m of precipitation annually (Pojar et al. 1987). There are nearly 1,500 islands in this region; the subsample we surveyed was representative of the biogeographical and geomorphological variation of the region and was selected using a two-step clustering method in SPSS statistical software (V23, IBM; results in Appendix C: Table C1). For this cluster analysis, we considered five descriptors per island: distance from mainland, area, wave exposure according to the British Columbia ShoreZone dataset (Howes et al. 1994), normalized (size-independent) perimeter-to-area ratio, and percentage of area occupied by surrounding landmasses within 500 m of each island. Aside from exposure, these metrics were derived using 2 m resolution WorldView-2 satellite imagery.

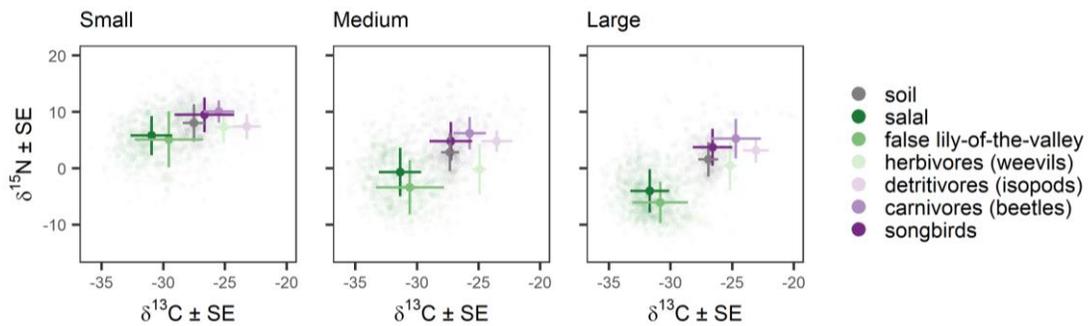


Figure 4.1 Stable isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N} \pm \text{SE}$ in soil, plants, and animals on islands on the central coast of British Columbia, Canada. Plots are separated into tertiles according to island size: small (0.00012-0.016 km^2), medium (0.016-0.22 km^2), and large (0.22-2.88 km^2).

4.3.2. Field collections and measurements

To maximize the number of samples, we collected from a representative species or group of species from each trophic level that is common and abundant rather than species we explicitly know to be consumed by the next trophic level. Many of these samples were originally collected as discrete components of several separate projects under the umbrella of the ‘100 Islands Project’ at the Hakai Institute (see Nijland et al. 2017, Wickham et al. 2019, 2020, Obrist et al. 2020, Davidson et al. 2021). Additionally, due to the nature of small islands, we were unable to collect samples of every trophic level on every island. This variation in availability of organisms across study islands is part of the reason we chose not to fit stable isotope mixing models—instead, our modeling approach is inherently able to account for unequal sampling across islands. See Table S3 for a full list of samples from each island. Additionally, there are different protocols for sample storage, cleaning, and preparation of different tissue types from different organisms. Although varying protocols could lead to biases in stable isotope composition, this is not an issue in our study because, unlike in a mixing model, we compare patterns in responses to environmental covariates and correlations with other taxa rather than raw differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. All samples within taxa were stored and prepared the same way (below).

Soil and plant samples

We collected soil (n = 973), and foliage samples of salal (*Gaultheria shallon*, n = 1485) and false lily-of-the-valley (*Maianthemum dilatatum*, n = 1166) on each study island. These two plant species were selected due to their ubiquity across islands and differences in nutrient regimes—salal is a species that is very tolerant of nitrogen-poor soils, whereas false lily-of-the-valley is a nitrophile (Klinka et al. 1989, Hocking and Reynolds 2011). On each island, we collected samples immediately adjacent to the shoreline at the furthest point in each cardinal direction, and 40 m inland from this point. On islands smaller than 80 m across, we sampled in the approximate middle of the island. We also used soil and vegetation samples collected at each of the 301 random point count locations on the same set of islands, described in Obrist *et al.* (2020). Distance to shore of these samples ranged from shoreline to approximately 400 m inland. We ground dried leaf matter (stored in paper envelopes then dried at 60°C for a minimum of 48 hours) using a Wig-L-Bug (Dentsply Rinn Corp., York, PA, USA) to prepare for stable isotope analysis.

Invertebrate samples

We collected samples of common species of weevils (Coleoptera: Curculionidae, n = 137), isopods (Isopoda: Porcellionidae, Ligidae, n = 142), and ground beetles (Coleoptera: Carabidae, n = 271) to represent invertebrates from the herbivore, decomposer, and carnivore feeding guilds, respectively. We placed networks of pitfall traps at four nearshore and one interior location on each island. Nearshore locations corresponded with the soil and plant sampling sites. Our traps were filled with 1.5 cm of ~30% propylene glycol solution diluted with sea water, to which surfactant was added. Propylene glycol is non-toxic and appropriately preserves specimens for isotope work (Nakamura et al. 2020). We removed invertebrates from the traps after three to four days, rinsed specimens with fresh water, and stored them in a freezer in 95% ethanol until they could be processed. In the lab, we identified, cleaned, dried, and ground specimens into a uniform sample using a Wig-L-Bug to prepare for stable isotope analysis. Specimens were selected for each guild based on availability, in the following descending order of preference: *Steremnius carinatus* was preferred, but if not available, then *S. tuberosus* for weevils; *Porcellio scaber*, then *Ligidium gracile* for isopods; and *Pterostichus algidus*, *P. amethystinus*, *P. crenicollis*, *P. lama*, and then *Scaphinotus angusticollis* for ground beetles. Although individual ground beetles were large enough,

to ensure adequate material for analysis, we had to combine up to five individuals from each trapping location for isopods and weevils.

Bird samples

To represent upper-level consumers, we used conspecific playback to catch live birds of five common species in mist-nets: chestnut-backed chickadees (*Poecile rufescens*), song sparrows (*Melospiza melodia*), fox sparrows (*Passerella iliaca*), Pacific wrens (*Troglodytes pacificus*), and orange-crowned warblers (*Leiothlypis celata*). We took both a fecal (n = 241) and feather sample (2nd right rectrix, n = 337) from each bird. As all five species are primarily insectivorous here on their breeding grounds (Davidson et al. 2015), we considered all of them in combination as representative upper-level consumers in this ecosystem. To prepare for stable isotope analysis, we first soaked feathers for 24 hours in a 2:1 solution of chloroform and methanol, dried them at 60°C for 48 hours, and used scissors to cut them into pieces to pack into capsules. Feces were dried and packed directly into capsules.

4.3.3. Stable isotope analysis

The main pathways by which marine subsidies enter terrestrial food webs—direct consumption and plant fertilization—can be evaluated using stable isotopes of carbon and nitrogen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Elevated $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in samples imply higher ratios of the heavy isotope, ^{15}N to ^{14}N and ^{13}C to ^{12}C . These samples can be said to be enriched in ^{15}N and ^{13}C . These isotopes can also be used to estimate trophic positions of organisms and marine inputs in organisms' diets. Nitrogen enrichment can be tracked through food webs; ^{15}N fractionates by $\sim 3.4\text{‰}$ per trophic level (Post 2002) because metabolic processes favour the lighter isotope of nitrogen, ^{14}N , resulting in ^{15}N -enriched animal tissues. Nitrogen enrichment can also indicate marine input, as marine primary producers typically have higher $\delta^{15}\text{N}$ values than terrestrial primary producers—for example, in our system, the mean $\delta^{15}\text{N}$ value of seaweed wrack was 7.3 ± 1.0 (mean \pm SE, Appendix C: Figure C1), while salal and false lily-of-the-valley had means of -0.3 ± 5.6 and -2.1 ± 6.4 , respectively. Conversely, carbon isotopes do not fractionate much ($\sim 0.4\text{‰}$) when passed up the food chain. Accordingly, they better reflect the $\delta^{13}\text{C}$ values of the basal primary producer (Post 2002). Due to different carbon sources in terrestrial and marine ecosystems, marine photosynthesizers also have higher values of $\delta^{13}\text{C}$ than

terrestrial plants (Fry 2006). In our system, mean $\delta^{13}\text{C}$ of wrack was -15.4 ± 3.0 , salal was -31.4 ± 1.7 , and false lily-of-the-valley was -30.4 ± 2.6 . Consequently, higher $\delta^{13}\text{C}$ values in a consumer's tissues implies a ^{13}C -enriched diet, such as that from a marine origin.

We processed all samples and quantified $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and %N at the Pacific Forestry Centre in Saanich, British Columbia, using a Flash 2000 elemental analyzer coupled to a ConFlo IV interface and DELTA Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific, Waltham, MA).

4.3.4. Island characteristics and wrack biomass

We derived island area using 2 m resolution WorldView-2 satellite imagery. Area was measured as land within the outer vegetation boundary and excluded the tidal and wash (shore) zones. Barren or non-vegetated areas inside the vegetation boundary were included. The mean island slope metric, however, represents the entire island, including the shore zone. Slope was calculated based on lidar where available; where lidar was not available, we flew an unmanned aerial vehicle (UAV) and calculated a ground model with 50 cm resolution. We measured distance to shore as the shortest distance from each sample collection site to the edge of the vegetated land (vegetation boundary) on each island.

We weighed wrack at four locations (one in each cardinal direction) on each island. We placed two 20 m transects parallel to the water—one transect at the most recent high tide line, and one at the most recent storm line, and randomly placed three 1 m² quadrats along each (Wickham et al. 2020). We identified each species in the quadrat to calibrate wet weights to dry weights for total wrack biomass per quadrat (Wickham et al. 2019). We calculated the mean wrack biomass of the 24 quadrats measured (4 sides x 2 transects x 3 quadrats) on each island.

4.3.5. Data analysis

Enrichment analyses: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$

To determine how island characteristics can affect enrichment of island organisms, we first fit separate global linear mixed effects models (LMM) to the heavy

isotopes of carbon and nitrogen, ^{15}N and ^{13}C (measured as $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of samples using the 'glmmTMB' package in R v. 4.0.3 (Brooks et al. 2017, R Core Team 2021). We fit a separate global model for each taxon, each including island area, distance to shore from which a sample was collected, wrack biomass, the mean slope of the island including the shore zone, and an interaction term between area and distance to shore. Each model also included island as a random effect to account for unequal sampling and because some predictors are on the scale of the sample (e.g., distance to shore), while others are island-specific (e.g., area). We \log_{10} -transformed island area, \log_e -transformed distance to shore, and square root-transformed wrack biomass to best linearize their relationships with isotopes prior to scaling and centering all independent variables. Since we had no *a priori* predictions about the relative importance of our independent variables, we model-averaged to calculate coefficient estimates across all possible subsets of our four predictors and the interaction term using the 'MuMIn' package in R (Barton 2020). Our main analyses used fecal samples from songbirds to represent a "snapshot" of what was recently consumed by birds (Appendix C: Table C3 ($\delta^{15}\text{N}$) and S4 ($\delta^{13}\text{C}$)), but we repeated all analyses with feather samples (Appendix C: Table C5 ($\delta^{15}\text{N}$) and C6 ($\delta^{13}\text{C}$)). We checked for multicollinearity between predictors in each model using variance inflation factors, and checked all model diagnostics using the 'DHARMA' package in R (Hartig 2020).

Subsidy analysis: %N

To determine whether the enriched samples were receiving a biologically relevant nutrient subsidy (i.e., that samples with more marine-derived nitrogen also contained more nitrogen overall), we fit a LMM to evaluate the effects of $\delta^{15}\text{N}$ on %N while accounting for island area, distance to shore, wrack biomass, mean island slope, and the random effect of island. We again model-averaged across all possible subsets of our predictors to obtain coefficient estimates. Here, we used bird feather samples in our main analyses rather than fecal samples. Birds excrete and egest waste through a single cloaca, so fecal samples' %N reflects the high variability of excreted nitrogenous wastes in birds, making it less useful for detecting patterns (Vanderklift and Ponsard 2003). The results from the averaged model were comparable to those of the global model. Therefore, to determine if the inclusion of $\delta^{15}\text{N}$ improved the fit of the model, we also used Akaike's Information Criterion corrected for small sample sizes (AICc) to

compete the global model for each taxon with a null model (one without $\delta^{15}\text{N}$ and solely island characteristics) (Appendix C: Table C7).

Path analysis

To determine the mechanism by which subsidies are incorporated into island food webs, we used the '*lavaan*' package in R (Rosseel 2012) to fit a structural equation model (SEM) of pathways through food webs for each stable isotope tracer ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$). This analysis used island-level means of stable isotopes for each taxon. This form of path analysis allowed us to evaluate the strength of pathways among components of island food webs, leading through island ecosystems from the soil to upper-level consumers in a holistic, ecosystem-level framework. SEMs allow for testing of strengths of hypothesized causal relationships among variables, while holding all other variables in the model constant (Pearl 2012). As such, a causal relationship is implied to exist if the coefficient estimate's 95% confidence interval does not overlap with zero. SEMs also allow testing of the strengths of both direct and indirect relationships, where indirect paths are quantified by multiplying direct path coefficients. Since we were unable to collect samples of all organisms on all islands, and the fitting of SEMs requires complete datasets, we used the '*mice*' package (van Buuren and Groothuis-Oudshoorn 2011) in conjunction with '*lavaan*' to impute missing data using predictive mean matching. Due to their potential to have island-level impacts on stable isotope signatures, we included island area and wrack biomass as predictors to impute the missing data. We chose to include 100 imputations as a conservative approach to the rule of thumb that the number of imputations should be at least equal to the percentage of incomplete cases (White et al. 2011). In our case, we were missing at least one sample from 83% of islands (16/94 complete cases), meaning we needed to impute at least 83 iterations. However, even with this approach, some of the estimates of FMI (fraction of missing information), particularly those for upper-level consumers, are higher than 0.5, meaning they should be interpreted with a degree of uncertainty. We used the fecal samples taken from birds (Appendix C: Table C8, C9 for $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ results) but also repeated the analysis using feather samples (Appendix C: Table C10, C11).

We used an iterative decision-making process to build our SEM to trace $\delta^{15}\text{N}$ through the food web. We started with a biologically accurate global model of pathways from marine subsidies into upper-level consumers. At each iteration, if the model did not

meet the conventional cut-offs (below), we used the modification indices to reselect the subset of pathways needed to be included to improve fit but maintain biological accuracy. Specifically, a model was required to meet at least three of the following four criteria: a chi-squared value of at most twice the number of degrees of freedom, a Comparative Fit Index (CFI) of > 0.95 , alongside a standardized root mean-square residual (SRMR) and root mean square error of approximation (RMSEA) of < 0.08 (Hu and Bentler 1999). Because the model initially had difficulty differentiating between the two plant species, we averaged across all plant samples on an island to represent terrestrial primary producers more generally. Detailed documentation of our entire SEM modelling and decision-making process are available online (www.github.com/debobrist/food-web-ibt). Once the biologically accurate path selection met the standard requirements for model fit, we used the same structure to fit the SEM for $\delta^{13}\text{C}$, except the regressions between soil and plants were excluded because we did not expect soil $\delta^{13}\text{C}$ to predict plant $\delta^{13}\text{C}$.

4.4. Results

Enrichment analysis: $\delta^{15}\text{N}$

Island characteristics and marine subsidies tended to affect ^{15}N enrichment across taxa in similar ways, with variation in strength of the effect depending on trophic position of the recipient (Figure 2, Figure 3). Island area was the strongest predictor of $\delta^{15}\text{N}$ across soil, island flora, and fauna (Figure 2a, Figure 3a, RVI = 1.00 for all taxa (Appendix C: Table C6)). As predicted, all groups were more enriched in ^{15}N on smaller islands, an effect that was approximately twice as strong in the two plant species and the herbivorous weevils as in the soil, the detritivores, and in the upper-level consumers (carnivorous ground-dwelling beetles and songbirds). The second strongest effect was the distance from shore at which a sample was collected; $\delta^{15}\text{N}$ decreased with increasing distance from shore (Figure 2a, Figure 3b, RVI = 1.00 for all groups except songbirds). The effect of distance to shore, however, depended on island size in all taxa except for songbirds; enrichment in ^{15}N decreased more quickly with distance to shore on larger islands than smaller ones, particularly for salal (Figure 2a). Although all groups were enriched closer to the land-sea interface, this effect was at least twice as strong in the soil and in the two plant species (particularly in false lily-of-the-valley) than in the invertebrate taxa. Mean island slope and wrack biomass had negligible effects on ^{15}N

enrichment of most taxa, aside from the two plant species, in which $\delta^{15}\text{N}$ was slightly higher on islands with higher wrack biomass (Figure 2a, Appendix C: Figure C2a), and detritivorous isopods and carnivorous beetles, where ^{15}N was less enriched on islands with steeper topographical slopes (Figure 2a, Appendix C: Figure C2b).

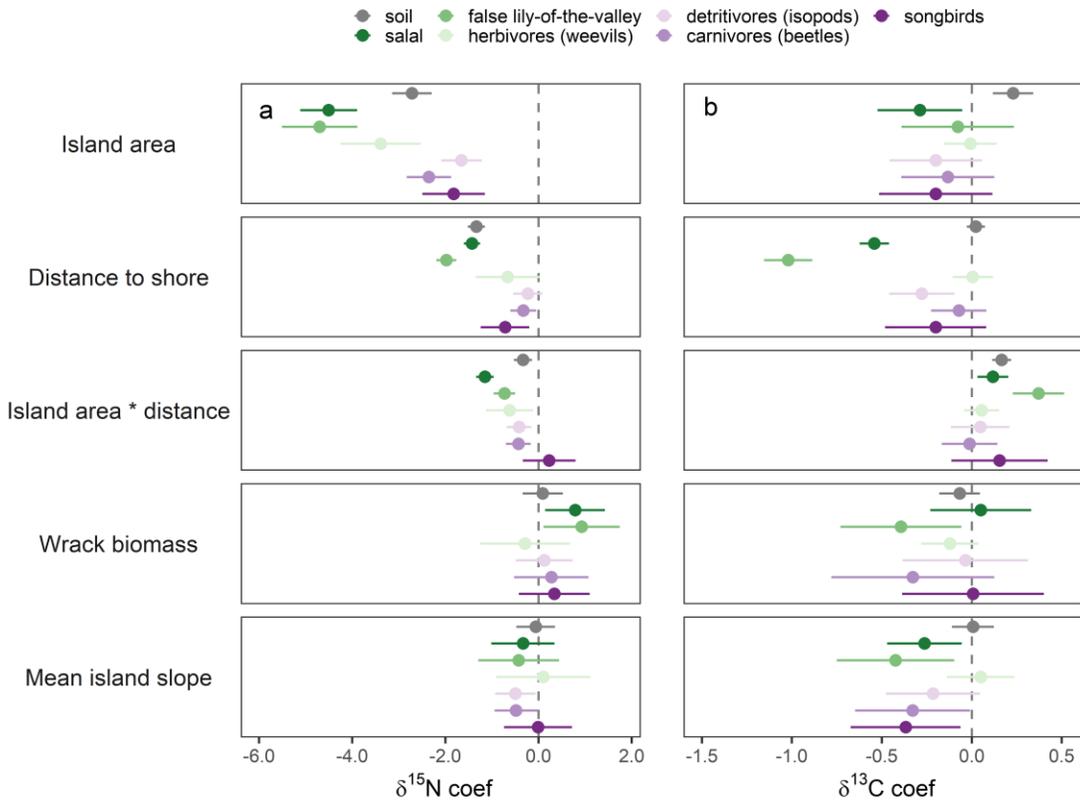


Figure 4.2 Standardized coefficient estimates from taxon-specific model-averaged linear mixed effects models for (a) $\delta^{15}\text{N}$ and (b) $\delta^{13}\text{C}$. Bars represent 95% confidence intervals around estimates.

Enrichment analysis: $\delta^{13}\text{C}$

We detected considerable variability in ^{13}C enrichment across taxa in response to island characteristics and marine subsidies. Interestingly, $\delta^{13}\text{C}$ in the soil was higher on larger islands, while salal had slightly higher $\delta^{13}\text{C}$ on smaller islands (Figure 2b, Figure 3c, Appendix C: Table C7). Both plant species and isopod detritivores collected closer to the shoreline had higher $\delta^{13}\text{C}$ (Figure 2b, Figure 3d). The effect of distance to shore was approximately twice as strong in false lily-of-the-valley as in salal. For soil, $\delta^{13}\text{C}$ increased with distance to shore on smaller islands, but decreased with distance to

shore on larger islands. Contrary to $\delta^{15}\text{N}$, for $\delta^{13}\text{C}$, the effect of distance to shore was stronger in plants on smaller islands. Both plant species, carnivorous beetles, and songbirds also had lower $\delta^{13}\text{C}$ on islands with steeper slopes (Figure 2b).

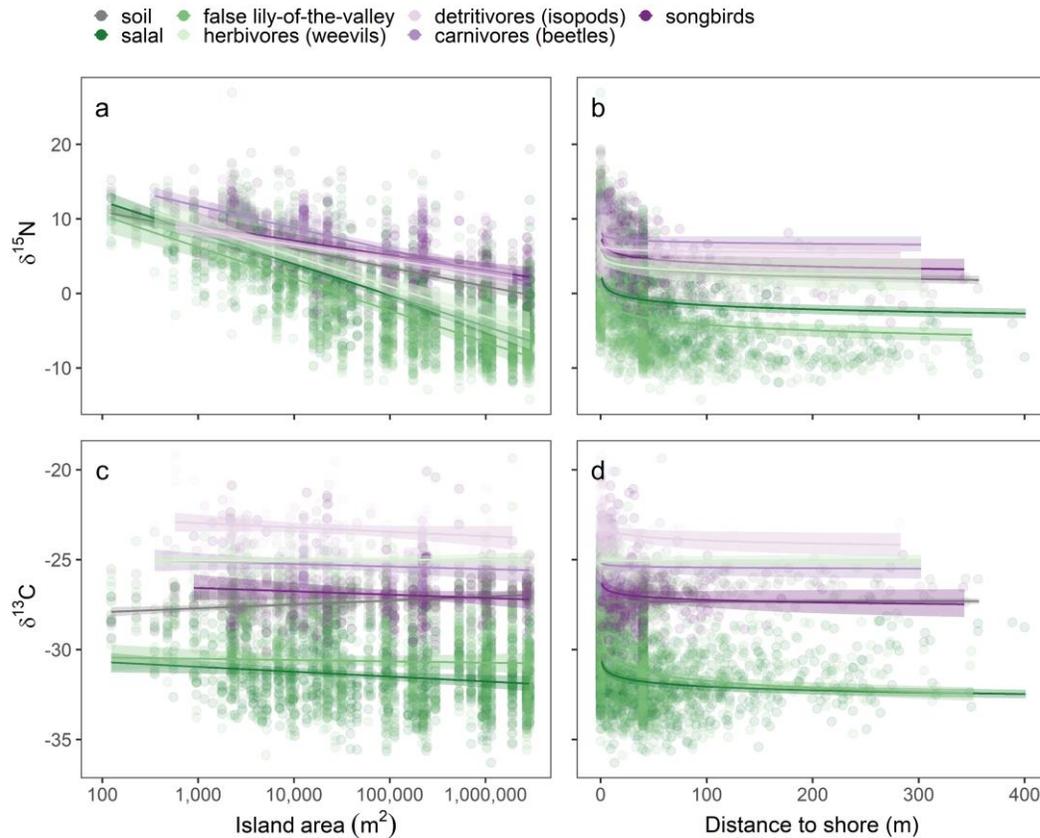


Figure 4.3 Effects of island area (m^2) and distance to shore (m) on $\delta^{15}\text{N}$ (a, b) and $\delta^{13}\text{C}$ (c, d) values of island soil, plants, invertebrates, and songbirds. Shaded areas represent 95% confidence intervals around taxon-specific model-predicted means.

Subsidy analysis: %N

For most taxa, %N was not related to island characteristics, but more basal taxa experienced elevated %N in tandem with higher $\delta^{15}\text{N}$. Specifically, %N was higher in soil and plant samples that had higher $\delta^{15}\text{N}$ (Figure 4a, c). This effect was approximately three times stronger in false lily-of-the-valley than in salal and in the soil. Percent nitrogen in songbird feathers was also slightly higher in samples that had higher $\delta^{15}\text{N}$ (Figure 4a, b). Salal %N was slightly higher on larger islands and further away from the

shoreline, whereas %N in the soil was slightly lower on larger islands and higher closer to shore (Figure 4a, c).

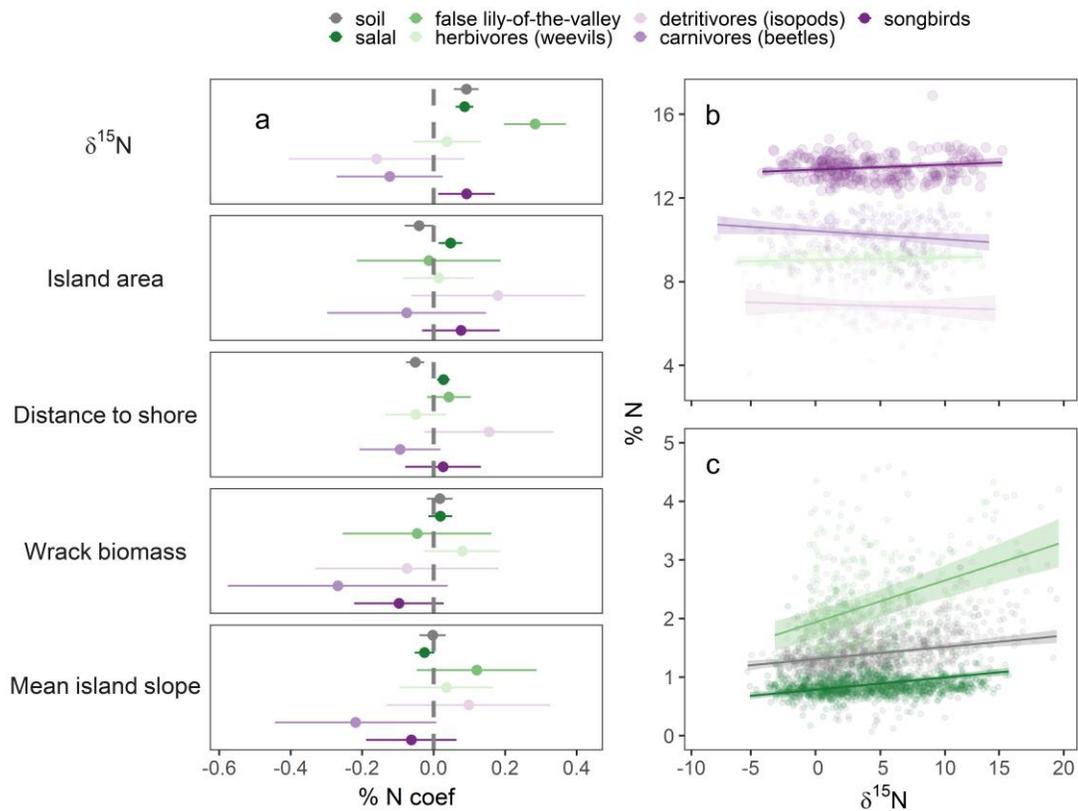


Figure 4.4 (a) Standardized coefficient estimates from taxon-specific model-averaged linear mixed effects models for %N. Bars (a) and shaded areas (b, c) represent 95% confidence intervals around estimates. Modeled relationships between $\delta^{15}\text{N}$ and %N in (b) songbirds, invertebrate beetles, isopods, and weevils, and in false lily-of-the-valley, salal, and soil (c).

Path analysis

Our structural equation model revealed evidence of the plant fertilization pathway as the dominant mechanism of $\delta^{15}\text{N}$ enrichment through island food webs (Figure 5a), while invertebrate detritivore $\delta^{13}\text{C}$ appeared to be driven by plant $\delta^{13}\text{C}$ (Figure 5b). We found evidence that subsidies in the soil in the form of $\delta^{15}\text{N}$ strongly predicted enrichment of ^{15}N in plants (0.93 ± 0.10 (path coefficient estimate \pm 95% confidence interval)). This nutrient subsidy was subsequently reflected in isopod detritivores, whose

$\delta^{15}\text{N}$ signatures were predicted by ^{15}N enrichment in plants (0.38 ± 0.27) and soil (0.50 ± 0.27). Furthermore, the level of $\delta^{15}\text{N}$ in carnivorous beetles was predicted by that of their potential prey source, isopod detritivores (0.95 ± 0.33). We also found strong correlations between the $\delta^{15}\text{N}$ of the soil and that of herbivorous weevils (0.83 ± 0.49), but that $\delta^{15}\text{N}$ of weevils was not predicted by $\delta^{15}\text{N}$ of plants (0.09 ± 0.35). When tracing the stable isotope of carbon, we found evidence that plant $\delta^{13}\text{C}$ predicted $\delta^{13}\text{C}$ in isopod detritivores (0.46 ± 0.25), which subsequently predicted $\delta^{13}\text{C}$ in bird fecal samples (0.62 ± 0.35). We also found a negative correlation between soil $\delta^{13}\text{C}$ and weevil $\delta^{13}\text{C}$ (-0.39 ± 0.33).

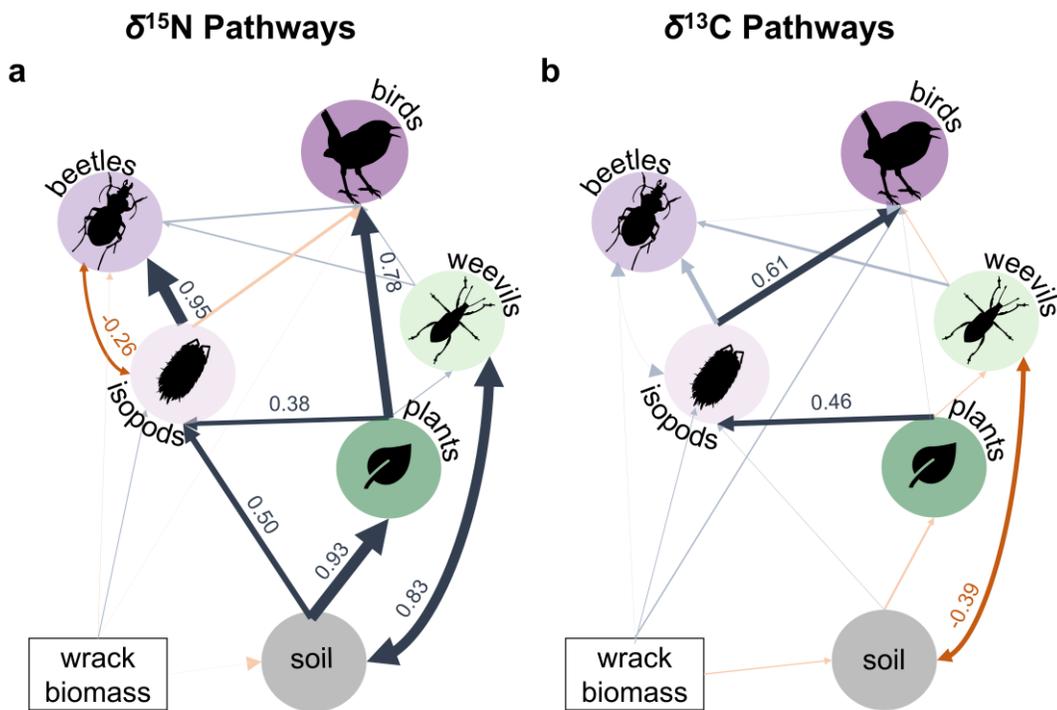


Figure 4.5 Structural equation models showing pathways of (a) $\delta^{15}\text{N}$ and (b) $\delta^{13}\text{C}$ enrichment through soil, and island plants and animals. Highlighted (darker) paths with associated path coefficients are statistically significant at the 95% level.

PhyloPic: Weevil: JCGiron (CC BY 3.0), Isopod: B. Lang (Public Domain Mark 1.0), Beetle: T. M. Keeseey, T. Assmann, J. Buse, C. Drees, A. L. L. Friedman, T. Levanony, A. Matern, A. Timm, and D. W. Wrase (CC BY 3.0), Bird: Troglodytes troglodytes, A. Caravaggi (CC BY-NC-SA 3.0).

4.5. Discussion

Our field study explicitly integrated biogeographical characteristics of islands with food web ecology at a large scale of variation in island size, island slope, and marine subsidy. As predicted, we found that ^{15}N enrichment of soil, primary producers, invertebrate herbivores, detritivores, carnivores, and songbirds was stronger on smaller islands and closer to shore, and that these patterns were stronger in lower trophic levels. We found that distance to shore was less important on smaller islands, suggesting higher per-unit-area effects of subsidies and thereby lending support to SIB. Additionally, we found that increased %N corresponds to increased $\delta^{15}\text{N}$ in lower trophic levels, implying biologically relevant uptake of a potentially limiting nutrient. Finally, using path analysis, we found evidence that marine subsidies predominantly enrich temperate island food webs via fertilization (rather than direct subsidy consumption).

We showed that island characteristics mediate enrichment by marine subsidies across all six trophic levels of island food webs in our analyses. Island area had the largest effect; ^{15}N enrichment was higher on smaller islands across all taxa. The strength of this effect depended on the trophic position of the organism—stronger relationships occurred between ^{15}N enrichment and island area at lower trophic levels. A likely explanation is that lower trophic-level organisms (e.g., plants) uptake nutrients over smaller areas, and are therefore more affected by characteristics of their local environment, while higher trophic-level taxa (e.g., songbirds) forage over larger areas, likely spanning multiple locations both within and among islands. Indeed, a similar study found riparian soil and herbivorous weevils to have higher levels of $\delta^{15}\text{N}$ closer to salmon-bearing streams, but $\delta^{15}\text{N}$ of more mobile, carnivorous beetles was unaffected (Rammell et al. 2021). We also found that ^{15}N enrichment drops off more rapidly with increasing distance to shore on larger islands. This effect is likely explained by larger perimeter-to-area ratios on smaller islands, making them more permeable to marine-derived nutrients further inland. To make sense of this relationship, consider an island that is 10 m in diameter. An organism five meters from shore is five meters from shore in all directions, whereas on an island that is 100 meters in diameter, that organism is 95 meters from shore in the opposing direction. This is a key dimension of SIB, which grounds itself in the foundational prediction that smaller islands experience a higher per-unit-area influence of marine inputs (Anderson and Wait 2001).

By evaluating the relationship between marine-derived nitrogen and percent nitrogen across constituents of a coastal temperate island food web, we were able to confirm that marine inputs provide a biologically relevant nutrient subsidy. Specifically, we found that the soil, foliage from two plant species, and songbird feathers (but not feces) experience higher %N in tandem with higher $\delta^{15}\text{N}$. This finding implies potential for higher subsidy-fueled productivity. Nitrogen is often the most important growth-limiting soil nutrient, and nitrogen limitation is common in these rainforest ecosystems (Klinka et al. 1989). Elemental composition (i.e., ratios of different nutrients) can vary more in plants than in animals due to plant cells' large central vacuoles, which can store excess nutrients not immediately used for metabolic processes (Sterner and Elser 2002). Storage of a nutrient beyond what is required for growth is termed 'luxury consumption', and often indicates limitation by a different nutrient. Indeed, luxury consumption of nitrogen often indicates phosphorus limitation (Greenwood 1976). Since egestion, excretion, and scent-marking by river otters are all processes driving increases in available nitrogen (Ben-David et al. 1998), it is possible that islands subsidized by river otter fertilization experience a shift in nutrient limitation. This hypothesis is supported by our observation that even salal, which is ericaceous and generally not nitrogen-limited (Bennett et al. 2003), experienced an increase in %N alongside $\delta^{15}\text{N}$. Ericaceous plants have specialized mycorrhizae which facilitate acquisition of nutrients from rotting organic matter in nutrient-poor conditions to overcome nitrogen limitation. Similar increases in %N alongside $\delta^{15}\text{N}$ have been seen in ericaceous false-azalea (*Menziesia ferruginea*) on salmon (*Oncorhynchus* sp.) streams in this region of BC (Hocking and Reynolds 2011). Furthermore, the effect of $\delta^{15}\text{N}$ on foliar %N was three times stronger in nitrophilic false lily-of-the-valley, likely because nitrophiles' mycorrhizal associations allow them to more readily capitalize on available nitrogen in the soil's litter layer (Read 1991).

In our study, aside from songbirds, higher trophic levels showed enrichment of ^{15}N without higher levels of %N, likely because the ratios between carbon, nitrogen, and phosphorous are far less flexible in animal tissues than in plant tissues (Sterner and Elser 2002). However, although subsidy effects are not apparent at the tissue-level, subsidies elicit variable consumer responses in individuals that can scale up to community-level consequences (Yang et al. 2010). For instance, herbivorous invertebrates tend to have higher rates of larval survival and development in association

with higher %N content in foliage (Mattson 1980). Such enhanced nutrition can lead to higher prey densities for upper-level consumers, even to the point where subsidized herbivores overgraze plant populations (Leroux and Loreau 2008, Piovia-Scott et al. 2019). Indeed, higher N content in foliage has been associated with multiple pathways of food web change; subsidized plots hosted higher abundances of herbivorous arthropods and predatory lizards in synchrony with higher levels of foliage growth and leaf damage on islands in the Bahamas (Spiller et al. 2010). In addition, food web stability is highly dependent on the trophic position of the subsidy recipient (Polis et al. 1997, Leroux and Loreau 2008). Low amounts of inputs tend to support food web stability, whereas large, variable pulses of inputs can have a destabilizing effect through stronger trophic cascades (Huxel and McCann 1998, Leroux and Loreau 2008, Recalde et al. 2020, McCary et al. 2021). Understanding the pathways by which subsidies enter food webs and knowing who benefits from them can aid our understanding of individual-level to community-level consumer responses.

Finally, we determined that the dominant mechanism of marine nutrient propagation through island food webs was through the plant fertilization pathway. Specifically, our path analysis provided evidence that increased soil $\delta^{15}\text{N}$ leads to higher plant $\delta^{15}\text{N}$, and that this pattern extends up the food web into upper-level consumers. This hypothesis was also supported by our enrichment analyses, where, on smaller islands and closer to shore, we found enrichment of consumer ^{15}N without simultaneous enrichment of ^{13}C . Enrichment of consumer ^{15}N but not ^{13}C implies that the subsidy enriches soil, litter, and vegetation without direct consumption (Hocking and Reimchen 2002). Similar conclusions were reached by a study on mouse diet variation on islands in our study area, where indirect effects of marine subsidies on mouse diets were observed through an increase in $\delta^{15}\text{N}$ of fecal pellets without a simultaneous increase in $\delta^{13}\text{C}$ (Davidson et al. 2021). Due to lack of a consistent pattern, we infer that variability in $\delta^{13}\text{C}$ across taxa is likely driven by variability in plant $\delta^{13}\text{C}$. Plants obtain carbon from the atmosphere, but $\delta^{13}\text{C}$ varies according to soil moisture, salinity, and nitrogen availability (Dawson et al. 2002). Additionally, although we found evidence of bottom-up fertilization effects in this ecosystem, some uncertainty remains about the relative contributions from different subsidy sources. Although $\delta^{15}\text{N}$ in plants was higher on islands receiving more wrack, wrack biomass appeared to have no effect on $\delta^{15}\text{N}$ in the soil nor in any of the consumers. As such, we infer that, moving up the food web, the signal of animal-

mediated nutrient deposits from river otters likely overwhelms effects of wrack fertilization.

Considering how recipient habitat characteristics affect the enrichment of multitrophic island food webs is an important step to improve our understanding of how subsidies affect dynamic island ecosystems more generally. Our finding that organisms are enriched on smaller islands with higher per-unit-area effects of subsidies lends strong support to rarely tested theoretical predictions of SIB (Anderson and Wait 2001). Additionally, we determined that plant fertilization was the dominant pathway by which marine subsidies enter temperate island food webs—an effect that we detected propagating up through soil, plants, invertebrates, and into upper-level consumers. Understanding the pathways by which subsidies enter food webs and knowing who benefits from them is fundamental to our understanding of individual, population, and community-level consumer responses.

Chapter 5.

General discussion

Although islands are often studied as isolated entities, my thesis incorporates the ecological effects of marine nutrients, detritus, and organisms that cross the land-sea interface into terrestrial habitats on islands. Specifically, I evaluated how marine subsidies mediate patterns in terrestrial avian species richness and total density (Chapter 2), and species distributions (Chapter 3). I then highlighted the pathways of nutrients from the sea into upper-level consumers and determined which components of island food webs experienced enrichment through marine subsidization (Chapter 4). As such, my thesis contributes to a growing body of work combining key ecological theories in a meta-ecosystem framework (Loreau et al. 2003).

In Chapter 2, I used a combination of field-collected and remote sensing data to answer questions about how terrestrial breeding bird communities respond to classical island biogeography parameters and to three metrics of marine subsidy: the amount of wrack that washed up on island shores, shoreline substrate, and marine-derived nitrogen in the soil, an approximation of animal-mediated nutrient deposits and sea spray. I found that species richness of birds was higher on larger islands, and on those with less marine-derived nitrogen in the soil. In contrast, I found higher densities of birds on smaller islands, and on those with more marine-derived nitrogen in the soil. The effect of marine-derived nitrogen was stronger on smaller islands, implying a higher per-unit-area effect of subsidies, and lending some support to the *Subsidized Island Biogeography Hypothesis* (SIB). This result led me to conduct a follow-up analysis (Chapter 3) to determine whether the concurrent decrease in species richness with an increase in density on small, subsidized islands was due to competitive exclusion of certain species, as expected through SIB.

In Chapter 3, I used a joint species distribution model to evaluate multiple mechanisms driving bird species assemblages. Specifically, I investigated the relative effects of the habitat filter and biotic interactions on island bird species distributions. I found that the habitat filter explained roughly twice as much variation in species distributions as biotic interactions, suggesting that competition was likely not the primary

driver in shaping these species communities. Additionally, I found no evidence of competition between species that exhibited preferences for marine-derived nutrients, suggesting that these species may simply tolerate similar environmental conditions. Furthermore, when I dug deeper into the parameters behind the habitat filter, I found that marine influences (marine-derived nitrogen in the soil, wrack biomass, proportion rocky shoreline, and distance to shore) explained just as much variation in species distributions as the classical *Theory of Island Biogeography* (TIB) predictors of island area, isolation, and habitat heterogeneity. This finding supports the value of examining communities as parts of meta-ecosystems because studies which examine just the classical island biogeography parameters are missing important information about species whose distributions are better explained by parameters relating to the surrounding marine matrix.

Finally, in Chapter 4, I used stable isotope signatures from samples of soil, two species of plants, three guilds of invertebrates (herbivores, detritivores, and carnivores), and songbirds, to examine patterns in enrichment and pathways of nutrient subsidies through island food webs. I found that samples from across the food web were ubiquitously enriched in $\delta^{15}\text{N}$ on smaller islands and closer to shore. I also found evidence that the relationship with distance to shore matters more on larger islands—likely due to more rapid attenuation of the subsidy where marine influence is not as strong. Finally, I determined that nutrients primarily enter the food web through bottom-up processes. Specifically, I found that $\delta^{15}\text{N}$ in the soil predicted $\delta^{15}\text{N}$ in plants, which predicted $\delta^{15}\text{N}$ in higher trophic level taxa, suggesting that sources of $\delta^{15}\text{N}$ that enter the soil have a fertilizing effect on island plants and their subsequent consumers. Determining the recipients of marine subsidies is an important step in understanding individual-, population-, and community-level consumer responses due to effects related to ecosystem stability and function.

5.1. “Wrack myopia” and the river otter realization

In evaluating the effects of marine subsidies to coastal terrestrial systems, most studies have focused either on spawning Pacific salmon (reviewed in Walsh et al. 2020) or on deposits of seaweed (wrack) and carrion detritus (reviewed in Hyndes et al. 2022). Since the islands studied in this thesis were specifically selected to not have freshwater streams that salmon could use for spawning, my collaborators and I initially gave our

undivided attention to studying wrack deposits. Wrack can have important ecological impacts (Hyndes et al. 2022), and given the vast expanse of kelp forests in the region, it seemed like a logical focal point. Indeed, the eastern Pacific Ocean is one of the most productive marine habitats in the world (Steneck et al. 2002), and hosts several potential wrack subsidy donor habitats: intertidal macroalgal beds, subtidal kelp forests, and seagrass meadows. Off the Canadian coast, kelp forests can produce up to 900 grams of carbon per m² on an annual basis (Wilmers et al. 2012). Dislodgement rates are high, and an estimated 650 grams of carbon per m² ends up as detritus every year (Druehl and Wheeler 1986). In addition, seagrass meadows extend across over 400 km² of coastline on the Central Coast of BC (Reshitnyk et al. 2016). As such, I anticipated that shoreline depositions of wrack would have a fairly large influence on islands' terrestrial communities.

Despite the extent of seaweed in the donor habitat, I was surprised to find no effect of wrack on species richness in island plants (Obrist et al. 2022) or terrestrial breeding birds (Chapter 2). In Chapter 3, I found that song sparrows and fox sparrows preferred islands that received more wrack. This was expected since these species are commonly seen feeding on semi-terrestrial invertebrates amongst the wrack on shorelines. Townsend's warblers and Pacific wrens showed a negative association with more wrack-laden islands, but this is likely due to a correlation with a habitat parameter I was unable to control for. Furthermore, in Chapter 4, I found slightly elevated levels of $\delta^{15}\text{N}$ in plants (but no other taxa) on islands receiving more wrack. This finding suggests that wrack does contribute to the fertilization of coastal plant communities. However, due to the steep, rocky nature of shorelines in this study (Figure 5.1A, B), wrack penetrance into island ecosystems was likely relatively low, which likely minimizes the overall ecological effects of wrack deposition. Indeed, 75% of shorelines in this study consisted of rock substrate (Wickham et al. 2020), and 40 islands had no wrack in any of the quadrats surveyed.



Figure 5.1 A) and B) show two of the studied islands on the Central Coast of British Columbia, Canada. The steep, rocky shorelines seen here are characteristic of many of the islands in this study. C) and D) show examples of North American river otter (*Lontra canadensis*) latrines. Island photos by Kate Prince (2015, 2016); river otter latrine photos by Christopher Ernst (2016).

It is likely that the effects of marine matrix productivity on island terrestrial communities are just less direct than we had originally anticipated. In addition to their potential for direct subsidy deposition, kelp forests are home to the prey of terrestrial and semi-terrestrial upper-level consumers that cross the land-sea interface to feed. For example, an adult male North American river otter (*Lontra canadensis*) eats up to 1/10th of its body weight in marine fish and invertebrates daily, and may excrete up to 40 grams of nitrogen at terrestrial latrine sites each day (Ben-David et al. 2005). In addition to depositing nutrients, non-herbivorous animals can cause disturbances to plant communities through digging and trampling behaviours (Jones et al. 1997, Figure 5.1B,C). As such, plant production and community composition tend to vary between latrine and non-latrine sites (Ben-David et al. 1998, Crait and Ben-David 2007, Roe et al.

2010). River otters are ubiquitous on the islands considered in this thesis, and in hindsight, it would have been incredibly valuable to designate a field crew to quantify their abundances as part of the 100 Islands Project. Although the number of river otters is unknown, my collaborators and I found anecdotal evidence of their presence on over 90% of the islands through documentation in our field notebooks and datasheets. Additionally, it has been estimated that river otters on Alaskan islands have approximately 160 latrines on every 100 km of shoreline (Ben-David et al. 2005). If river otter density is similar, we could expect up to 424 river otter latrines across 265 km of shoreline on our studied islands. The number of river otters that use each latrine is variable, but Ben-David et al. (2005) suggested that the number ranges from one solitary individual to 11 social river otters. Since animal vectors can facilitate nutrient transports against energy gradients, including moving marine-derived nutrients up steep shorelines (McInturf et al. 2019), their impact can be substantial.

In this thesis, I have attempted to capture the influence various sources of marine subsidies, including river otter activity, through signatures of marine-derived nitrogen ($\delta^{15}\text{N}$). Soil $\delta^{15}\text{N}$ appeared to be an important predictor of terrestrial bird species richness, density, and community composition, and could be traced up the food web through plants and into upper-level consumers. Although other factors (e.g., denitrification; Pinay et al. 2003) can influence $\delta^{15}\text{N}$ in the soil, unpublished work on soil, plants, and bugs on, near, and away from otter latrines on the studied islands shows a tight relationship between $\delta^{15}\text{N}$ and river otter activity. River otters as a subsidy source further complicate the story because in addition to fertilizing effects, they also cause habitat disturbances (Ben-David et al. 1998, Roe et al. 2010). Indeed, with the current data set, it is difficult to discern whether observed patterns are due to fertilization or species responses to habitat disturbances. A true understanding of the mechanisms behind the patterns observed in this thesis could be gained through an experimental approach that controls for the fertilization and disturbance factors independently.

5.2. The context-dependent nature of marine subsidies

One of the key lessons that I learned while conducting the research for this thesis is that a lot of (if not most) results are incredibly nuanced, context-specific, and highly uncertain. This is particularly true when studying spatial subsidies, where several reviews and meta-analyses have deduced that they elicit highly context-dependent

effects in recipient communities, particularly when vectored by animals (Marczak et al. 2007, McInturf et al. 2019, Subalusky and Post 2019). Characteristics of the donor habitat, the transfer mechanism, and the recipient habitat determine the rates and amounts of cross-boundary delivery and retention. The identity of the direct subsidy recipient may result in variable trophic responses (Leroux and Loreau 2008), which can also vary depending on the size and timing of the delivery of the subsidy (Piovia-Scott et al. 2019, Wright et al. 2020). Although we ecologists tend to love generalizations, these context-specific responses make it very difficult to come up with a framework or a generalization for understanding or predicting the effects of spatial subsidies.

Although the results presented in this thesis appear to be most influenced by animal-mediated nutrient transfers, they represent just a snapshot in time. It is possible that I might have arrived at different results had I conducted this research in a different season. For instance, I am confident in our finding that wrack input did not play a huge role on island communities overall during the surveyed summer months. However, both the amount and the species composition of wrack deposition on shorelines in this region are significantly different in the summer and winter months (Wickham et al. 2020). A different set of environmental drivers of species communities on these islands may be important during the winter months, where species communities may consist of entirely different components. Winter surveys would need to be done to verify these hypotheses, albeit difficult in this region. The seas can be rough in the winter and working on both land and water is riskier than during summer months. Both spatial and temporal biases are pervasive in ecological research (Boakes et al. 2010, Hughes et al. 2021), and assessing seasonal sampling bias could be one way to address context-dependent results.

5.3. Does the unimodal productivity-diversity relationship even exist?

The shape of the productivity-diversity relationship must be one of the most debated topics in ecology in the last 50 years. As such, the fact that SIB relies on the relationship being unimodal (hump-shaped) means it has somewhat of a shaky foundation. First observed in herbaceous plants by Whittaker and Niering (1975), the unimodal productivity-diversity relationship was also found in desert rodents in Texas (Abramsky and Rosenzweig 1984), plants in oak savannahs in Minnesota (Tilman 1987),

and even fossilized invertebrates (Mikulic and Watkins 1981). By the early 1990s, unimodality was the textbook explanation of the productivity-diversity relationship (Begon et al. 1990). In 1993, Rosenzweig and Abramsky summarized support and proposed several possible mechanisms behind the downward-sloping side of the curve. Despite eventually debunking all 9 suggested mechanisms, they stood firmly by the unimodal curve.

Starting in 1999, the relationship became contentious, as an avalanche of reviews, summaries, meta-analyses, and further original works investigating the productivity-diversity relationship was published. Waide et al. (1999) conducted an extensive literature review and found inconclusive support for unimodality, but in 2001, Mittelbach et al. found slightly more support through a meta-analysis. In 2006, Gillman and Wright applied more stringent restrictions on studies included in a follow-up meta-analysis, and again found less support for the unimodal relationship. Adler et al. (2011) conducted a systematic survey of herbaceous plants across five continents. In an extremely convincing *Science* paper, this study demonstrated no reliable relationship between productivity and diversity. The authors concluded that it was in the best interest of researchers' time, money, and resources to stop looking for a relationship between productivity and diversity as it did not exist. Not surprisingly, a passionate debate ensued. Arguments critiqued the statistical framework, the amount and type of data collected, the metrics and levels of productivity considered, and the inclusion of too much and/or not enough anthropogenic data (Fridley et al. 2012, Pan et al. 2012, Pierce 2014). Contrasting critiques argued that Adler et al.'s data actually showed a strong positive relationship (Pan et al. 2012) or a strong unimodal pattern (Fridley et al. 2012, Pierce 2014). Pierce (2014) even claimed that Adler et al.'s paper supported a "*worldview that human impacts on biodiversity can be ignored*", and that by abandoning the idea of the unimodal relationship, ecologists would be "*endorsing the message that management regimes and human impacts are not important for habitat conservation*". However, in support of Adler et al. (2011), Cusens et al. (2012) conducted yet another meta-analysis and determined that unimodal and negative relationships between diversity and productivity are extremely rare in both plants and animals, at all spatial scales. It seemed like the hump-shaped curve had (finally) been debunked, until 2015, when Fraser et al. (2015) conducted the largest test of the productivity-diversity curve yet and found strong evidence of a hump-shaped global productivity-diversity

relationship. This study focused on herbaceous grassland plant communities specifically and examined a wide range in levels of productivity.

Evidently, the productivity-diversity relationship is highly sensitive to metrics of productivity, spatial scale, habitat type, and statistical analyses used. While Fraser et al. (2015) provide a convincing argument that the relationship exists on a global scale, I am not sure what it means for processes happening at the scale at which marine inputs subsidize terrestrial island ecosystems. Marine inputs can be very heterogeneous in distribution, yielding highly variable patches of productivity on small spatial scales. Furthermore, although early evidence implied the existence of a unimodal productivity-diversity relationship for large carnivores in Texas (Rosenzweig and Abramsky 1993), I am not convinced that the relationship translates in a meaningful way for upper-level consumers, like the birds I studied in my thesis work. Indeed, while in Chapter 2 I found evidence of a decrease in species richness with an increase in productivity, which would have implied that the community laid on the downward-sloping side of the hump-shaped productivity-diversity curve. However, in Chapter 3, I found no evidence of competition between species. It is possible that marine-derived nitrogen in the soil is too variable to be a good representative metric of productivity. However, in Chapter 4, I found concurrent increases in %N with increases in $\delta^{15}\text{N}$ in both soil and plants, implying that where the subsidy was being received, the soil and plants were overcoming nitrogen limitation (Sterner and Elser 2002). This finding supports my use of soil $\delta^{15}\text{N}$ as an adequate measure of productivity in my thesis work.

Overall, I agree with Adler et al. (2010) and Fraser et al. (2015) that there may be more value in evaluating multivariate drivers of species communities, and that there are limitations to the utility of overly broad generalizations. As such, in my thesis, I focused more on evaluating multiple drivers of species richness and considered species level responses to biotic parameters.

5.4. The meta-ecosystem in conservation

Human activities are changing patterns in subsidy distributions through impacts on donor systems, transfer pathways, and recipient habitats (Buckner et al. 2018). In each case, human influence can elicit top-down or bottom-up trophic responses in the afflicted ecological community. For instance, in the donor habitat, overfishing and

exploitation of marine fishes can yield top-down trophic effects (Layman et al. 2011), and pollution and introduced species may result in bottom-up effects (Buckner et al. 2018). Beach grooming (Hyndes et al. 2022) and habitat fragmentation resulting in decreased animal movement (Tucker et al. 2018) can elicit top-down and bottom-up trophic responses, respectively, due to disruptions of nutrient transfer pathways. Less directly, extreme climate events due to human-induced climate change can also impact subsidy availability and potential for transfer. For instance, in Northern California, climate change-driven extreme climate events resulted in depletions of over 90% of once prolific kelp forests (Rogers-Bennett and Catton 2019). Furthermore, the amount of nutrients transferred from sea to land by seabirds and anadromous fish is estimated to have decreased of 96% since the Pleistocene due to losses of these animals (Doughty et al. 2016). Due to nutrient legacy effects and recent changes in the capacity of animals to facilitate nutrient diffusion through meta-ecosystems (Frauendorf et al. 2021), it is more important than ever to understand the connections between complexly linked ecosystems.

Cross-ecosystem movements of nutrients can have substantial ecological effects on recipient ecosystems. I found evidence of this in all three chapters of my thesis. My results from Chapter 3 especially demonstrate the importance of evaluating species communities as parts of meta-ecosystems. I showed how key information can be missed when the effects of marine influences are ignored. For example, if I were to design a conservation reserve to protect bird species on islands, but I only considered TIB as a framework, I may unintentionally select only the subset of species for which marine influence is less important. According to Chapter 3, I might select against song sparrows, fox sparrows, dark-eyed juncos, rufous hummingbirds, and American crows. By using modern techniques, such as joint species distribution models, and evaluating island communities in a meta-ecosystem framework, it is possible to facilitate a better sense of what is important for the various components of species communities.

5.5. Concluding remarks

Coastal regions (including islands) experience disproportionately high degrees of human impacts (Williams et al. 2021). Yet, our understanding of cross-boundary processes at various scales at the land-sea interface remains limited (Fang et al. 2018). In this thesis, I uncovered links between marine and terrestrial ecosystems by examining

of the effects of marine subsidies on terrestrial breeding bird diversity, density, and community composition. I also revealed some of the pathways by which marine nutrients enrich temperate ecosystems. Overall, this thesis demonstrates the necessity of a multi-faceted, interdisciplinary approach to understand the ecological effects of behavioural, biochemical, and biogeographic patterns in island biota, as well as their intricate connections to the marine realm.

References

- Abramsky, Z., and M. L. Rosenzweig. 1984. Tilman' s predicted productivity-diversity relationship shown by desert rodents. *Nature* 309:150–151.
- Adler, P. B., E. W. Seabloom, E. T. Borer, H. Hillebrand, Y. Hautier, A. Hector, W. S. Harpole, L. R. O. Halloran, J. B. Grace, T. M. Anderson, J. D. Bakker, L. a Biederman, C. S. Brown, Y. M. Buckley, L. B. Calabrese, C. Chu, E. E. Cleland, and S. L. Collins. 2011. Productivity is a poor predictor of plant species richness. *Science* 333:1750–1754.
- Anderson, W. B., and G. A. Polis. 1998. Marine subsidies of island communities in the Gulf of California: evidence from stable carbon and nitrogen isotopes. *Oikos* 81:75–80.
- Anderson, W. B., and D. A. Wait. 2001. Subsidized Island Biogeography Hypothesis: another new twist on an old theory. *Ecology Letters* 4:289–291.
- Anderson, W. B., D. A. Wait, and P. Stapp. 2008. Resources from another place and time: responses to pulses in a spatially subsidized system. *Ecology* 89:660–670.
- Araújo, M. B., and A. Rozenfeld. 2014. The geographic scaling of biotic interactions. *Ecography* 37:406–415.
- Art, H. W., F. H. Bormann, G. K. Voigt, and G. M. Woodwell. 1974. Barrier island forest ecosystem: role of meteorologic nutrient inputs. *Science* 184:60–62.
- Banner, A., W. MacKenzie, S. Haeussler, S. Thomson, J. Pojar, and R. Trowbridge. 1993. A field guide to site identification and interpretation for the Prince Rupert Forest Region Part 2. Research Branch, Ministry of Forests, Victoria, British Columbia.
- Barreiro, F., M. Gómez, M. Lastra, J. López, and R. De La Huz. 2011. Annual cycle of wrack supply to sandy beaches: Effect of the physical environment. *Marine Ecology Progress Series* 433:65–74.
- Barrett, K., D. A. Wait, and W. B. Anderson. 2003. Small island biogeography in the Gulf

of California: lizards, the subsidized island biogeography hypothesis, and the small island effect. *Journal of Biogeography* 30:1575–1581.

Barton, K. 2020. MuMIn: Multi-model inference. R package version 1.43.17 1:18.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. R package version 1.1–7. 2014. *Journal of Statistical Software* 67:1–48.

Begon, M., J. Harper, and C. Townsend. 1990. *Ecology: Individuals, Populations and Communities*. 2nd ed. Blackwell Science, Boston, Massachusetts.

Ben-David, M., G. M. Blundell, J. W. Kern, J. A. K. Maier, E. D. Brown, and S. C. Jewett. 2005. Communication in river otters: Creation of variable resource sheds for terrestrial communities. *Ecology* 86:1331–1345.

Ben-David, M., R. T. Bowyer, L. K. Duffy, D. D. Roby, and D. M. Schell. 1998. Social behavior and ecosystem processes: river otter latrines and nutrient dynamics of terrestrial vegetation. *Ecology* 79:2567.

Bennett, J. N., L. L. Blevins, J. E. Barker, D. P. Blevins, and C. E. Prescott. 2003. Increases in tree growth and nutrient supply still apparent 10 to 13 years following fertilization and vegetation control of salal-dominated cedar-hemlock stands on Vancouver Island. *Canadian Journal of Forest Research* 33:1516–1524.

Billerman, S. M., B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg, editors. 2020. *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, New York.

Blackburn, T. M., S. Delean, P. Pysek, and P. Cassey. 2016. On the island biogeography of aliens: a global analysis of the richness of plant and bird species on oceanic islands. *Global Ecology and Biogeography* 25:859–868.

Boakes, E. H., P. J. K. McGowan, R. A. Fuller, D. Chang-qing, N. E. Clark, K. O'Connor, and G. M. Mace. 2010. Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data. *PLoS Biology* 8:e1000385.

Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 1998. Higher temporal variability of forest breeding bird communities in fragmented

landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 95:7497–7501.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9:379–400.

Brooks, S. P., and A. Gelman. 1998. General Methods for Monitoring Convergence of Iterative Simulations. *Journal of Computational and Graphical Statistics* 7:434–455.

Brown, C. J., B. Parker, M. D. Hocking, and J. D. Reynolds. 2020. Salmon abundance and patterns of forest greenness as measured by satellite imagery. *Science of The Total Environment* 725:138448.

Brown, J. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. *Great Basin Naturalist Memoirs* 2:209–227.

Browne, J. 1983. *The Secular Ark: Studies in the History of Biogeography*. Yale University Press, New Haven, Connecticut.

Browne, R. A. 1981. Lakes as Islands: Biogeographic Distribution, Turnover Rates, and Species Composition in the Lakes of Central New York. *Journal of Biogeography* 8:75.

Buckner, E. V., D. L. Hernández, and J. F. Samhour. 2018. Conserving connectivity: Human influence on subsidy transfer and relevant restoration efforts. *Ambio* 47:493–503.

Burbrink, F. T., A. D. McKelvy, R. A. Pyron, and E. A. Myers. 2015. Predicting community structure in snakes on Eastern Nearctic islands using ecological neutral theory and phylogenetic methods. *Proceedings of the Royal Society B: Biological Sciences* 282:1–10.

van Buuren, S., and K. Groothuis-Oudshoorn. 2011. mice: Multivariate Imputation by Chained Equations in R. *Journal of Statistical Software* 45:1–67.

Carnicer, J., L. Brotons, C. Stefanescu, and J. Peñuelas. 2012. Biogeography of species

richness gradients: Linking adaptive traits, demography and diversification. *Biological Reviews* 87:457–479.

- Cazelles, K., M. B. Araújo, N. Mouquet, and D. Gravel. 2016. A theory for species co-occurrence in interaction networks. *Theoretical Ecology* 9:39–48.
- Chang, S. X., and C. M. Preston. 2000. Understorey competition affects tree growth and fate of fertilizer-applied ¹⁵N in a Coastal British Columbia plantation forest: 6-year results. *Canadian Journal of Forest Research* 30:1379–1388.
- Chang, S. X., G. F. Weetman, C. M. Preston, K. McCullough, and J. Barker. 1996. Effect of understory competition on distribution and recovery of ¹⁵N applied to a western red cedar–western hemlock clear-cut site. *Canadian Journal of Forest Research* 26:313–321.
- Chib, S., and E. Greenberg. 1998. Analysis of multivariate probit models. *Biometrika* 85:347–361.
- Christie, K. S., and T. E. Reimchen. 2008. Presence of salmon increases passerine density on Pacific Northwest streams. *The Auk* 125:51–59.
- Connor, E. F., and D. Simberloff. 1979. The assembly of species communities: chance or competition? *Ecology* 60:1132–1140.
- Crait, J. R., and M. Ben-David. 2007. Effects of river otter activity on terrestrial plants in a trophically altered Yellowstone lake. *Ecology* 88:1040–1052.
- Crowley, S., C. J. Johnson, and D. Hodder. 2012. Spatial and behavioral scales of habitat selection and activity by river otters at latrine sites. *Journal of Mammalogy* 93:170–182.
- Cusens, J., S. D. Wright, P. D. McBride, and L. N. Gillman. 2012. What is the form of the productivity–animal-species-richness relationship? A critical review and meta-analysis. *Ecology* 93:2241–2252.
- Dale, S. 2019. Islands in the forest : effects of patch size and isolation on farmland bird species richness and community composition of farmland patches in forest landscapes. *Landscape Ecology* 34:2823–2836.

- Darcy, J. L., E. M. S. Gendron, P. Sommers, D. L. Porazinska, and S. K. Schmidt. 2018. Island biogeography of cryoconite hole bacteria in Antarctica's Taylor Valley and around the world. *Frontiers in Ecology and Evolution* 6:1–9.
- Davidson, K. H., B. M. Starzomski, R. El-Sabaawi, M. D. Hocking, J. D. Reynolds, S. B. Wickham, and C. T. Darimont. 2021. Marine subsidy promotes spatial and dietary niche variation in an omnivore, the Keen's mouse (*Peromyscus keeni*). *Ecology and Evolution*:1–23.
- Davidson, P. J. A., R. J. Cannings, A. R. Couturier, D. Lepage, and C. M. Di Corrado. 2015. *The Atlas of Breeding Birds of British Columbia, 2008-2012*. Delta, B.C.
- Dawson, T. E., S. Mambelli, A. H. Plamboeck, P. H. Templer, and K. P. Tu. 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* 33:507–559.
- Dembicz, I., I. I. Moysiyanenko, Ł. Kozub, J. Dengler, M. Zakharova, and B. Sudnik-Wójcikowska. 2021. Steppe islands in a sea of fields: Where island biogeography meets the reality of a severely transformed landscape. *Journal of Vegetation Science* 32.
- Diamond, J. M. 1975. Assembly of species communities. Page *in* M. L. Cody and D. J. M, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- Diamond, J. M. 1976. Island biogeography and conservation: Strategy and limitations. *Science* 193:1027–1032.
- Diamond, J. M., M. E. Gilpin, and E. Mayr. 1976. Species-distance relation for birds of the Solomon Archipelago, and the paradox of the great speciators. *Proceedings of the National Academy of Sciences of the United States of America* 73:2160–2164.
- Diamond, J. M., and E. Mayr. 1976. Species-area relation for birds of the Solomon Archipelago. *Proceedings of the National Academy of Sciences of the United States of America* 73:262–266.
- Doughty, C. E., J. Roman, S. Faurby, A. Wolf, A. Haque, E. S. Bakker, Y. Malhi, J. B. Dunning, and J. C. Svenning. 2016. Global nutrient transport in a world of giants.

Proceedings of the National Academy of Sciences of the United States of America
113:868–873.

Druehl, L. D., and W. N. Wheeler. 1986. Population biology of *Macrocystis integrifolia* from British Columbia, Canada. *Marine Biology* 90:173–179.

Dunning Jr., J. B. 2007. *CRC Handbook of Avian Body Masses*. Page (J. B. Dunning Jr, Ed.). Second Edi. CRC Press, Boca Raton.

Fahrig, L. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography* 40:1649–1663.

Fang, X., X. Hou, X. Li, W. Hou, M. Nakaoka, and X. Yu. 2018. Ecological connectivity between land and sea : a review. *Ecological Research* 33:51–61.

Field, R. D., and J. D. Reynolds. 2011. Sea to sky: impacts of residual salmon-derived nutrients on estuarine breeding bird communities. *Proceedings of the Royal Society B: Biological Sciences* 278:3081–3088.

Forman, R. T. T., A. E. Galli, and C. F. Leck. 1976. Forest size and avian diversity in New Jersey woodlots with some land use implications. *Oecologia* 26:1–8.

Forster, J. R. 1778. *Observations made during a voyage round the world, on physical geography, natural history, and ethic philosophy*. G. Robinson, 1778, London.

Fox, B. J., and M. D. Fox. 2000. Factors determining mammal species richness on habitat islands and isolates: Habitat diversity, disturbance, species interactions and guild assembly rules. *Global Ecology and Biogeography* 9:19–37.

Fraser, L. H., J. Pither, A. Jentsch, M. Sternberg, M. Zobel, D. Askarizadeh, S. Bartha, C. Beierkuhnlein, J. A. Bennett, A. Bittel, B. Boldgiv, I. I. Boldrini, E. Bork, L. Brown, M. Cabido, J. Cahill, C. N. Carlyle, G. Campetella, S. Chelli, O. Cohen, A.-M. Csergo, S. Díaz, L. Enrico, D. Ensing, A. Fidelis, J. D. Fridley, B. Foster, H. Garris, J. R. Goheen, H. A. L. Henry, M. Hohn, M. H. Jouri, J. Klironomos, K. Koorem, R. Lawrence-Lodge, R. Long, P. Manning, R. Mitchell, M. Moora, S. C. Müller, C. Nabinger, K. Naseri, G. E. Overbeck, T. M. Palmer, S. Parsons, M. Pesek, V. D. Pillar, R. M. Pringle, K. Roccaforte, A. Schmidt, Z. Shang, R. Stahlmann, G. C.

- Stotz, S. Sugiyama, S. Szentes, D. Thompson, R. Tungalag, S. Undrakhbold, M. van Rooyen, C. Wellstein, J. B. Wilson, and T. Zupo. 2015. Worldwide evidence of a unimodal relationship between productivity and plant species richness. *Science* 349:302–305.
- Frauendorf, T. C., A. L. Subalusky, C. L. Dutton, S. K. Hamilton, F. O. Masese, E. J. Rosi, G. A. Singer, and D. M. Post. 2021. Animal legacies lost and found in river ecosystems. *Environmental Research Letters* 16:115011.
- Fridley, J. D., J. P. Grime, M. A. Huston, S. Pierce, S. M. Smart, K. Thompson, L. Börger, R. W. Brooker, B. E. L. Cerabolini, N. Gross, P. Liancourt, R. Michalet, and Y. Le Bagousse-Pinguet. 2012. Comment on “productivity is a poor predictor of plant species richness.” *Science* 335.
- Gende, S. M., and M. F. Willson. 2001. Passerine densities in riparian forests of southeast Alaska: Potential effects of anadromous spawning salmon. *The Condor* 103:624–629.
- Gentile, G., and R. Argano. 2005. Island biogeography of the Mediterranean sea: the species-area relationship for terrestrial isopods. *Journal of Biogeography* 32:1715–1726.
- Gillespie, R. G., and B. G. Baldwin. 2010. Island biogeography of remote archipelagoes. Pages 358–387 *The theory of island biogeography revisited*.
- Gillman, L. N., and S. D. Wright. 2006. The influence of productivity on the species richness of plants: A critical assessment. *Ecology* 87:1234–1243.
- Gilpin, M. E., and J. M. Diamond. 1976. Calculation of immigration and extinction curves from the species-area-distance relation. *Proceedings of the National Academy of Sciences of the United States of America* 73:4130–4134.
- Gordo, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research* 35:37–58.
- Gotelli, N. J., and R. K. Colwell. 2011. Estimating species richness. Pages 39–54 *Biological Diversity: Frontiers in Measurement and Assessment*. Oxford University

Press, United Kingdom.

- Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, DC.
- Grace, J. B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. *Perspectives in Plant Ecology, Evolution and Systematics* 2:1–28.
- Grace, J. B., T. M. Anderson, E. W. Seabloom, E. T. Borer, P. B. Adler, W. S. Harpole, Y. Hautier, H. Hillebrand, E. M. Lind, M. Pärtel, J. D. Bakker, Y. M. Buckley, M. J. Crawley, E. I. Damschen, K. F. Davies, P. A. Fay, J. Firn, D. S. Gruner, A. Hector, J. M. H. Knops, A. S. MacDougall, B. A. Melbourne, J. W. Morgan, J. L. Orrock, S. M. Prober, and M. D. Smith. 2016. Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* 529:390–393.
- Graham, N. A. J., S. K. Wilson, P. Carr, A. S. Hoey, S. Jennings, and M. A. MacNeil. 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature* 559:250–253.
- Gratton, C., and R. F. Denno. 2003. Seasonal shift from bottom-up to top-down impact in phytophagous insect populations. *Oecologia* 134:487–495.
- Greenwood, E. A. N. 1976. Nitrogen Stress in Plants. *Advances in Agronomy* 28:1–35.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347.
- Haila, Y., O. Jarvinen, and S. Kuusela. 1983. Colonization of islands by land birds: prevalence functions in a Finnish archipelago. *Journal of Biogeography* 10:499–531.
- Hartig, F. J. 2020. DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3.3.0.
- Harvey, E., and A. S. MacDougall. 2014. Trophic island biogeography drives spatial divergence of community establishment. *Ecology* 95:2870–2878.

- Heatwole, H., and R. Levins. 1973. Biogeography of the Puerto Rican Bank: Species-Turnover on a Small Cay, Cayo Ahogado. *Ecology* 54:1042–1055.
- Helfield, J. M., and R. J. Naiman. 2006. Keystone Interactions: Salmon and Bear in Riparian Forests of Alaska. *Ecosystems* 9:167–180.
- Hocking, M. D., and T. E. Reimchen. 2002. Salmon-derived nitrogen in terrestrial invertebrates from coniferous forests of the Pacific Northwest. *BMC Ecology* 2:1–14.
- Hocking, M. D., and J. D. Reynolds. 2011. Impacts of salmon on riparian plant diversity. *Science* 331:1609–1612.
- Howes, D., J. Harper, and E. Owens. 1994. Physical Shore-Zone Mapping System for British Columbia. Technical report by the Coastal Task Force of the Resource Inventory Committee (RIC), R. I. C. Secretariat.:97.
- Hu, L. T., and P. M. Bentler. 1999. Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives. *Structural Equation Modeling* 6:1–55.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey.
- Hughes, A. C., M. C. Orr, K. Ma, M. J. Costello, J. Waller, P. Provoost, Q. Yang, C. Zhu, and H. Qiao. 2021. Sampling biases shape our view of the natural world. *Ecography* 44:1259–1269.
- Hutchinson, G. 1957. Concluding remarks. *Cold Springs Harbor Symp. Quant. Biol.* 22:415–427.
- Huxel, G. R., and K. McCann. 1998. Food web stability: The influence of trophic flows across habitats. *American Naturalist* 152:460–469.
- Hyndes, G. A., E. L. Berdan, C. Duarte, J. E. Dugan, K. A. Emery, P. A. Hambäck, C. J. Henderson, D. M. Hubbard, M. Lastra, A. Mateo, A. Olds, and T. A. Schlacher. 2022. Flotsam and jetsam : a global review of the role of inputs of marine organic matter in sandy beach ecosystems.

- Ibanez, T., G. Keppel, C. Baider, C. Birkinshaw, H. Culmsee, S. Cordell, F. B. V. Florens, J. Franklin, C. P. Giardina, T. W. Gillespie, M. Laidlaw, C. M. Litton, T. G. Martin, R. Ostertag, N. Parthasarathy, R. Randrianaivo, M. Randrianjanahary, M. Rajkumar, L. Rasingam, F. Ratovoson, L. Reza, L. Sack, S. I. Aiba, E. Webb, T. J. S. Whitfeld, R. Zang, and P. Birnbaum. 2018. Regional forcing explains local species diversity and turnover on tropical islands. *Global Ecology and Biogeography* 27:474–486.
- Jones, C. G., J. H. Lawron, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946–1957.
- Kalmar, A., and D. J. Currie. 2006. A global model of island biogeography. *Global Ecology and Biogeography* 15:72–81.
- Kieran, C. N., D. S. Obrist, N. J. Muñoz, P. J. Hanly, and J. D. Reynolds. 2021. Links between fluctuations in sockeye salmon abundance and riparian forest productivity identified by remote sensing. *Ecosphere* 12:e03699.
- Kissling, W. D., Ç. H. Şekercioğlu, and W. Jetz. 2012. Bird dietary guild richness across latitudes, environments and biogeographic regions. *Global Ecology and Biogeography* 21:328–340.
- Kitahara, M., and K. Fuji. 1997. An Island Biogeographical Approach to the Analysis of Butterfly Community Patterns in Newly Designed Parks. *Researches on Population Ecology* 39:23–35.
- Klinka, K., V. J. Krajina, A. Ceska, and A. M. Scagel. 1989. Indicator plants of coastal British Columbia. UBC Press, Vancouver, BC.
- Koenig, W. D., and J. M. H. Knops. 2001. Seed-crop size and eruptions of North American boreal seed-eating birds. *Journal of Animal Ecology* 70:609–620.
- König, C., R. O. Wüest, C. H. Graham, D. N. Karger, T. Sattler, N. E. Zimmermann, and D. Zurell. 2021. Scale dependency of joint species distribution models challenges interpretation of biotic interactions. *Journal of Biogeography* 48:1541–1551.
- Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015.

Community assembly, coexistence and the environmental filtering metaphor.
Functional Ecology 29:592–599.

Lack, D. 1969. The numbers of bird species on islands. *Bird Study* 16:193–209.

Lassen, H. H. 1975. The diversity of freshwater snails in view of the equilibrium theory of island biogeography. *Oecologia* 19:1–8.

Laurance, W. F. 2008. Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation* 141:1731–1744.

Laurance, W. F. 2009. Beyond island biogeography theory: understanding habitat fragmentation in the real world. Pages 215–236 *in* J. B. Losos and R. E. Ricklefs, editors. *The theory of island biogeography revisited*. Princeton University Press, Princeton, New Jersey, USA.

Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology* 16:605–618.

Layman, C. A., J. E. Allgeier, A. D. Rosemond, C. P. Dahlgren, and L. A. Yeager. 2011. Marine fisheries declines viewed upside down: human impacts on consumer-driven nutrient recycling. *Ecological Applications* 21:343–349.

Leroux, S. J., and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters* 11:1147–1156.

Liebowitz, D. M., K. J. Nielsen, J. E. Dugan, S. G. Morgan, D. P. Malone, J. L. Largier, D. M. Hubbard, and M. H. Carr. 2016. Ecosystem connectivity and trophic subsidies of sandy beaches 7:e01503.

Liu, J., M. Vellend, Z. Wang, and M. Yu. 2018. High beta diversity among small islands is due to environmental heterogeneity rather than ecological drift. *Journal of Biogeography* 45:2252–2261.

Lomolino, M. V., J. H. Brown, and D. F. Sax. 2009. Island Biogeography Theory: Reticulations and reintegration of “A Biogeography of the Species.” Pages 13–51 *in*

- J. B. Losos and R. E. Ricklefs, editors. *The theory of island biogeography revisited*. Princeton University Press, Princeton, New Jersey, USA.
- Lomolino, M. V, and M. D. Weiser. 2001. Towards a more general species-area relationship: diversity on all islands, great and small. *Journal of Biogeography* 28:431–445.
- Loreau, M., N. Mouquet, and R. D. Holt. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters* 6:673–679.
- Losos, J. B., T. R. Jackman, A. Larson, K. De Queiroz, and L. Rodríguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279:2115–2118.
- Losos, J. B., and R. E. Ricklefs. 2009. *The Theory of Island Biogeography Revisited*. Page (J. B. Losos and R. E. Ricklefs, Eds.). Princeton University Press, Princeton, New Jersey, USA.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- MacArthur, R., and J. W. MacArthur. 1961. On bird species-diversity. *Ecology* 42:594–598.
- Marczak, L. B., R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: Trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* 88:140–148.
- Maron, J. L., J. A. Estes, D. A. Croll, E. M. Danner, S. C. Elmendorf, and S. L. Buckelew. 2006. An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. *Ecological Monographs* 76:3–24.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11:119–161.
- McCary, M. A., J. S. Phillips, T. Ramiadantsoa, L. A. Nell, A. R. McCormick, and J. C. Botsch. 2021. Transient top-down and bottom-up effects of resources pulsed to multiple trophic levels. *Ecology* 102:1–13.

- McInturf, A. G., L. Pollack, L. H. Yang, and O. Spiegel. 2019. Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors? *Biological Reviews* 94:1761–1773.
- McNeill, S. E., and P. G. Fairweather. 1993. Single Large or Several Small Marine Reserves? An Experimental Approach with Seagrass Fauna. *Journal of Biogeography* 20:429.
- Mendenhall, C. D., D. S. Karp, C. F. J. Meyer, E. A. Hadly, and G. C. Daily. 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature* 509:213–217.
- Menegotto, A., T. F. Rangel, J. Schrader, P. Weigelt, and H. Kreft. 2019. A global test of the subsidized island biogeography hypothesis. *Global Ecology and Biogeography*:1–11.
- Mews, M., M. Zimmer, and D. E. Jelinski. 2006. Species-specific decomposition rates of beach-cast wrack in Barkley Sound, British Columbia, Canada. *Marine Ecology Progress Series* 328:155–160.
- Mikulic, D., and R. Watkins. 1981. Trilobite ecology in the Ludlow Series of the Welsh Borderland. Pages 101–117 in J. Gray, A. Boucot, and W. Berry, editors. *Communities of the past*. Stroudsburg, Pennsylvania.
- Miller, R. 2019. *Nutrient Subsidies in the Coastal Margin: Implications for Tree Species Richness and Understory Composition*. University of Victoria, Victoria, BC.
- Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82:2381–2396.
- Mod, H. K., M. Chevalier, M. Luoto, and A. Guisan. 2020. Scale dependence of ecological assembly rules: Insights from empirical datasets and joint species distribution modelling. *Journal of Ecology* 108:1967–1977.
- Montagano, L., S. J. Leroux, M. A. Giroux, and N. Lecomte. 2019. The strength of ecological subsidies across ecosystems: a latitudinal gradient of direct and indirect

impacts on food webs. *Ecology Letters* 22:265–274.

Morrison, L. W. 2014. The small-island effect: empty islands, temporal variability and the importance of species composition. *Journal of Biogeography* 41:1007–1017.

Nakamura, S., S. Tamura, H. Taki, and E. Shoda-Kagaya. 2020. Propylene glycol: a promising preservative for insects, comparable to ethanol, from trapping to DNA analysis. *Entomologia Experimentalis et Applicata* 168:158–165.

Niering, W. A. 1963. Terrestrial Ecology of Kapingamarangi Atoll, Caroline Islands. *Ecological Monographs* 33:131–160.

Nijland, W., L. Y. Reshitnyk, B. M. Starzomski, J. D. Reynolds, C. T. Darimont, and T. A. Nelson. 2017. Deriving Rich Coastal Morphology and Shore Zone Classification from LIDAR Terrain Models. *Journal of Coastal Research* 33:949–958.

Obrist, D. S., O. T. Fitzpatrick, N. E. M. Brown, P. J. Hanly, W. Nijland, L. Y. Reshitnyk, S. B. Wickham, C. T. Darimont, J. D. Reynolds, and B. M. Starzomski. 2022. Scale dependent effects of marine subsidies on the island biogeographic patterns of plants. *Ecology and Evolution*.

Obrist, D. S., P. J. Hanly, J. C. Kennedy, O. T. Fitzpatrick, S. B. Wickham, C. M. Ernst, W. Nijland, L. Y. Reshitnyk, C. T. Darimont, B. M. Starzomski, and J. D. Reynolds. 2020. Marine subsidies mediate patterns in avian island biogeography. *Proceedings of the Royal Society B: Biological Sciences* 287:20200108.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2019. *vegan: Community Ecology Package*.

Olson, Z. H., T. L. Serfass, and O. E. Rhodes. 2008. Seasonal variation in latrine site visitation and scent marking by Nearctic river otters (*Lontra canadensis*). *IUCN Otter Specialist Group Bulletin* 25:108–120.

Orr, M., M. Zimmer, D. E. Jelinski, and M. Mews. 2005. Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. *Ecology* 86:1496–1507.

- Ovaskainen, O., D. B. Roy, R. Fox, and B. J. Anderson. 2016. Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. *Methods in Ecology and Evolution* 7:428–436.
- Ovaskainen, O., G. Tikhonov, A. Norberg, F. Guillaume Blanchet, L. Duan, D. Dunson, T. Roslin, and N. Abrego. 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters* 20:561–576.
- Pan, X., F. Liu, and M. Zhang. 2012. Comment on “productivity is a poor predictor of plant species richness.” *Science* 335:2011–2012.
- Patiño, J., R. J. Whittaker, P. A. V Borges, J. M. Fernández-Palacios, C. Ah-Peng, M. B. Araújo, S. P. Ávila, P. Cardoso, J. Cornuault, E. J. de Boer, L. de Nascimento, A. Gil, A. González-Castro, D. S. Gruner, R. Heleno, J. Hortal, J. C. Illera, C. N. Kaiser-Bunbury, T. J. Matthews, A. Papadopoulou, N. Pettorelli, J. P. Price, A. M. C. Santos, M. J. Steinbauer, K. A. Triantis, L. Valente, P. Vargas, P. Weigelt, and B. C. Emerson. 2017. A roadmap for island biology: 50 fundamental questions after 50 years of *The Theory of Island Biogeography*. *Journal of Biogeography* 44:963–983.
- Patterson, B. D., and W. Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society* 28:65–82.
- Pedersen, M. F., K. Filbee-Dexter, K. M. Norderhaug, S. Fredriksen, N. L. Frisk, C. W. Fagerli, and T. Wernberg. 2020. Detrital carbon production and export in high latitude kelp forests. *Oecologia* 192:227–239.
- Pierce, S. 2014. Implications for biodiversity conservation of the lack of consensus regarding the humped-back model of species richness and biomass production. *Functional Ecology* 28:253–257.
- Pinay, G., T. O’Keefe, R. Edwards, and R. J. Naiman. 2003. Potential denitrification activity in the landscape of a western Alaska drainage basin. *Ecosystems* 6:336–343.

- Piovia-Scott, J., L. H. Yang, A. N. Wright, D. A. Spiller, and T. W. Schoener. 2017. The effect of lizards on spiders and wasps: variation with island size and marine subsidy. *Ecosphere* 8:e01909.
- Piovia-Scott, J., L. H. Yang, A. N. Wright, D. A. Spiller, and T. W. Schoener. 2019. Pulsed seaweed subsidies drive sequential shifts in the effects of lizard predators on island food webs. *Ecology Letters* 22:1850–1859.
- Pojar, J., K. Klinka, and D. V Meidinger. 1987. Biogeoclimatic ecosystem classification in British Columbia. *Forest Ecology and Management* 22:119–154.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Polis, G. A., and S. D. Hurd. 1995. Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences of the United States of America* 92:4382–4386.
- Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist* 147:396–423.
- Pollock, L. J., R. Tingley, W. K. Morris, N. Golding, R. B. O’Hara, K. M. Parris, P. A. Vesk, and M. A. McCarthy. 2014. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution* 5:397–406.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718.
- Prescott, C. E., M. A. McDonald, and G. F. Weetman. 1993. Availability of N and P in the forest floors of adjacent stands of western red cedar–western hemlock and western hemlock–amabilis fir on northern Vancouver Island. *Canadian Journal of Forest Research* 23:605–610.

- Prescott, C. E., L. Vesterdal, J. Pratt, K. H. Venner, L. M. de Montigny, and J. A. Trofymow. 2000. Nutrient concentrations and nitrogen mineralization in forest floors of single species conifer plantations in coastal British Columbia. *Canadian Journal of Forest Research* 30:1341–1352.
- Preston, F. W. 1962. The canonical distribution of commonness and rarity: Part II. *Ecology* 43:410–432.
- Pyron, R. A., and F. T. Burbrink. 2014. Ecological and evolutionary determinants of species richness and phylogenetic diversity for island snakes. *Global Ecology and Biogeography* 23:848–856.
- Quesnel, H. J., and L. M. Lavkulich. 1980. Nutrient variability of forest floors near Port Hardy, British Columbia, Canada. *Canadian Journal of Soil Science* 60:565–573.
- R Core Team. 2021. R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria.
- Ralph, C. J., J. R. Sauer, and S. Droege. 1995. Monitoring bird populations by point counts. Albany, CA.
- Rammell, N. F., A. M. Dennert, C. M. Ernst, and J. D. Reynolds. 2021. Effects of spawning Pacific salmon on terrestrial invertebrates: Insects near spawning habitat are isotopically enriched with nitrogen-15 but display no differences in body size. *Ecology and Evolution* 11:12728–12738.
- Read, D. J. 1991. Mycorrhizas in ecosystems. *Experientia* 47:376–391.
- Recalde, F. C., C. P. B. Breviglieri, and G. Q. Romero. 2020. Allochthonous aquatic subsidies alleviate predation pressure in terrestrial ecosystems. *Ecology* 101:1–11.
- Reshitnyk, L., T. Denouden, W. McInnes, M. Hessing-Lewis, C. Prentice, and F. Short. 2016. Estimating seagrass extent in coastal British Columbia. Victoria, British Columbia.
- Richardson, J. S., Y. Zhang, and L. B. Marczak. 2010. Resource subsidies across the land–freshwater interface and responses in recipient communities. *River Research and Applications* 26:55–66.

- Ricklefs, R. E., and I. J. Lovette. 1999. The roles of island area per se and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology* 68:1142–1160.
- Roe, A. M., C. B. Meyer, N. P. Nibbelink, and M. Ben-David. 2010. Differential tree and shrub production in response to fertilization and disturbance by coastal river otters in Alaska. *Ecology* 91:3177–3188.
- Rogers-Bennett, L., and C. A. Catton. 2019. Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. *Scientific Reports* 9:1–9.
- Rosenzweig, M. L., and Z. Abramsky. 1993. How are diversity and productivity related? Pages 52–65 *Species Diversity in Ecological Communities*. University of Chicago Press.
- Rosindell, J., and A. B. Phillimore. 2011. A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters* 14:552–560.
- Rosseel, Y. 2012. lavaan: An R Package for Structural Equation Modeling. *Journal of Statistical Software* 48:1–36.
- Rydin, H., and S. O. Borgegård. 1988. Plant species richness on islands over a century of primary succession: Lake Hjälmaren. *Ecology* 69:916–927.
- Santos, A. M. C., R. Field, and R. E. Ricklefs. 2016. New directions in island biogeography. *Global Ecology and Biogeography* 25:751–768.
- Sato, E., B. Kusumoto, Ç. H. Şekercioğlu, Y. Kubota, and M. Murakami. 2020. The influence of ecological traits and environmental factors on the co-occurrence patterns of birds on islands worldwide. *Ecological Research* 35:394–404.
- Schoener, T. W. 2009. The MacArthur-Wilson Equilibrium Model. Pages 52–87 *The Theory of Island Biogeography Revisited*.
- Schrader, J., C. König, K. A. Triantis, P. Trigas, H. Kreft, and P. Weigelt. 2020. Species–area relationships on small islands differ among plant growth forms. *Global Ecology and Biogeography* 29:814–829.

- Shannon, C. E. 1948. A mathematical theory of communication. *Bell System Technical Journal* 27:379–423.
- Sheard, C., M. H. C. Neate-Clegg, N. Alioravainen, S. E. I. Jones, C. Vincent, H. E. A. MacGregor, T. P. Bregman, S. Claramunt, and J. A. Tobias. 2020. Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications* 11.
- Si, X., M. W. Cadotte, D. Zeng, A. Baselga, Y. Zhao, J. Li, Y. Wu, S. Wang, and P. Ding. 2017. Functional and phylogenetic structure of island bird communities. *Journal of Animal Ecology* 86:532–542.
- Siemens, L. D., A. M. Dennert, D. S. Obrist, and J. D. Reynolds. 2020. Spawning salmon density influences fruit production of salmonberry (*Rubus spectabilis*). *Ecosphere* 11:e03282.
- Simberloff, D. 1976. Experimental zoogeography of islands: effects of island size. *Ecology* 57:629–648.
- Simberloff, D. S., and L. G. Abele. 1976. Island Biogeography Theory and Conservation Practice. *Science* 191:285–286.
- Spiller, D. A., J. Piovra-Scott, A. N. Wright, L. H. Yang, G. Takimoto, T. W. Schoener, and T. Iwata. 2010. Marine subsidies have multiple effects on coastal food webs. *Ecology* 91:1424–1434.
- Stapp, P., G. A. Polis, and F. Sánchez Piñero. 1999. Stable isotopes reveal strong marine and El Niño effects on island food webs. *Nature* 401:467–469.
- Stark, K. A., P. L. Thompson, J. Yakimishyn, L. Lee, E. M. Adamczyk, M. Helsing-Lewis, and M. I. O'Connor. 2020. Beyond a single patch: Local and regional processes explain diversity patterns in a seagrass epifaunal metacommunity. *Marine Ecology Progress Series* 655:91–106.
- Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters* 17:866–880.

- Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* 29:436–459.
- Sterner, R. W., and J. J. Elser. 2002. *Ecological Stoichiometry: The biology of elements from molecules to the biosphere*. Princeton University Press, Princeton, New Jersey.
- Subalusky, A. L., and D. M. Post. 2019. Context dependency of animal resource subsidies. *Biological Reviews* 94:517–538.
- Tikhonov, G., Ø. H. Opedal, N. Abrego, A. Lehikoinen, M. M. J. Jonge, J. Oksanen, and O. Ovaskainen. 2020. Joint species distribution modelling with the R-package HMSC. *Methods in Ecology and Evolution* 11:442–447.
- Tilman, D. 1987. Secondary Succession and the Pattern of Plant Dominance Along Experimental Nitrogen Gradients. *Ecological Monographs* 57:189–214.
- Traveset, A., and M. F. Willson. 1998. Ecology of the fruit-colour polymorphism in *Rubus spectabilis*. *Evolutionary Ecology* 12:331–345.
- Triantis, K. A., F. Guilhaumon, and R. J. Whittaker. 2012. The island species-area relationship: Biology and statistics. *Journal of Biogeography* 39:215–231.
- Triantis, K. A., M. Mylonas, K. Lika, K. V. Natural, and H. Museum. 2003. A model for the species – area – habitat relationship:19–27.
- Triantis, K. A., K. Vardinoyannis, E. P. Tsolaki, I. Botsaris, K. Lika, and M. Mylonas. 2006. Re-approaching the small island effect. *Journal of Biogeography* 33:914–923.
- Tucker, M. A., K. Böhning-Gaese, W. F. Fagan, J. M. Fryxell, B. Van Moorter, S. C. Alberts, A. H. Ali, A. M. Allen, N. Attias, T. Avgar, H. Bartlam-Brooks, B. Bayarbaatar, J. L. Belant, A. Bertassoni, D. Beyer, L. Bidner, F. M. van Beest, S. Blake, N. Blaum, C. Bracis, D. Brown, P. J. N. de Bruyn, F. Cagnacci, J. M. Calabrese, C. Camilo-Alves, S. Chamillé-Jammes, A. Chiaradia, S. C. Davidson, T. Dennis, S. DeStefano, D. Diefenbach, I. Douglas-Hamilton, J. Fennessy, C. Fichtel, W. Fiedler, C. Fischer, I. Fischhoff, C. H. Fleming, A. T. Ford, S. A. Fritz, B.

Gehr, J. R. Goheen, E. Gurarie, M. Hebblewhite, M. Heurich, A. J. M. Hewison, C. Hof, E. Hurme, L. A. Isbell, R. Janssen, F. Jeltsch, P. Kaczensky, A. Kane, P. M. Kappeler, M. Kauffman, R. Kays, D. Kimuyu, F. Koch, B. Kranstauber, S. LaPoint, P. Leimgruber, J. D. C. Linnell, P. López-López, A. C. Markham, J. Mattisson, E. P. Medici, U. Mellone, E. Merrill, G. de Miranda Mourão, R. G. Morato, N. Morellet, T. A. Morrison, S. L. Díaz-Muñoz, A. Mysterud, D. Nandintsetseg, R. Nathan, A. Niamir, J. Odden, R. B. O'Hara, L. G. R. Oliveira-Santos, K. A. Olson, B. D. Patterson, R. Cunha de Paula, L. Pedrotti, B. Reineking, M. Rimmler, T. L. Rogers, C. M. Rolandsen, C. S. Rosenberry, D. I. Rubenstein, K. Safi, S. Saïd, N. Sapir, H. Sawyer, N. M. Schmidt, N. Selva, A. Sergiel, E. Shiilegdamba, J. P. Silva, N. Singh, E. J. Solberg, O. Spiegel, O. Strand, S. Sundaresan, W. Ullmann, U. Voigt, J. Wall, D. Wattles, M. Wikelski, C. C. Wilmers, J. W. Wilson, G. Wittemyer, F. Zięba, T. Zwijacz-Kozica, and T. Mueller. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* 359:466–469.

van der Valk, A. G. 1981. Succession in wetlands: a gleasonian approach. *Ecology* 62:688–696.

Vanderklift, M. A., and S. Ponsard. 2003. Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: A meta-analysis. *Oecologia* 136:169–182.

Del Vecchio, S., T. Jucker, M. Carboni, and A. T. R. Acosta. 2017. Linking plant communities on land and at sea: The effects of *Posidonia oceanica* wrack on the structure of dune vegetation. *Estuarine, Coastal and Shelf Science* 184:30–36.

Wagner, M. A., and J. D. Reynolds. 2019. Salmon increase forest bird abundance and diversity. *PLoS ONE* 14:1–16.

Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The Relationship Between Productivity and Species Richness. *Annual Review of Ecology and Systematics* 30:257–300.

Walsh, J. C., J. E. Pendray, S. C. Godwin, K. A. Artelle, H. K. Kindsvater, R. D. Field, J. N. Harding, N. R. Swain, and J. D. Reynolds. 2020. Relationships between Pacific salmon and aquatic and terrestrial ecosystems: implications for ecosystem-based management. *Ecology* 101:1–16.

- Wang, Y., Y. Bao, M. Yu, G. Xu, and P. Ding. 2010. Nestedness for different reasons: The distributions of birds, lizards and small mammals on islands of an inundated lake. *Diversity and Distributions* 16:862–873.
- Wang, Y., C. Chen, and V. Millien. 2018. A global synthesis of the small-island effect in habitat islands. *Proceedings of the Royal Society B: Biological Sciences* 285:20181868.
- Warton, D. I., F. G. Blanchet, R. B. O'Hara, O. Ovaskainen, S. Taskinen, S. C. Walker, and F. K. C. Hui. 2015. So many variables: joint modeling in community ecology. *Trends in Ecology & Evolution* 30:766–779.
- Weathers, K. C., and G. E. Likens. 1997. Clouds in Southern Chile: An Important Source of Nitrogen to Nitrogen-Limited Ecosystems? *Environmental Science & Technology* 31:210–213.
- Weigelt, P., and H. Kreft. 2013. Quantifying island isolation - insights from global patterns of insular plant species richness. *Ecography* 36:417–429.
- White, I. R., P. Royston, and A. M. Wood. 2011. Multiple imputation using chained equations: Issues and guidance for practice. *Statistics in Medicine* 30:377–399.
- Whittaker, R. H., and W. A. Niering. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. *Ecology* 56:771–790.
- Whittaker, R. J., J. M. Fernández-Palacios, T. J. Matthews, M. K. Borregaard, and K. A. Triantis. 2017. Island biogeography: Taking the long view of nature's laboratories. *Science* 357.
- Wickham, S. B., C. T. Darimont, J. D. Reynolds, and B. M. Starzomski. 2019. Species-specific wet-dry mass calibrations for dominant Northeastern Pacific Ocean macroalgae and seagrass. *Aquatic Botany* 152:27–31.
- Wickham, S., N. Shackelford, C. Darimont, W. Nijland, L. Reshitnyk, J. Reynolds, and B. Starzomski. 2020. Sea wrack delivery and accumulation on islands: factors that mediate marine nutrient permeability. *Marine Ecology Progress Series* 635:37–54.

- Wiens, J. A., C. S. Crawford, and J. R. Gosz. 1985. Boundary Dynamics: A Conceptual Framework for Studying Landscape Ecosystems. *Oikos* 45:421.
- Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *The American Naturalist* 125:879–887.
- Wilcox, K. A., M. A. Wagner, and J. D. Reynolds. 2021. Salmon subsidies predict territory size and habitat selection of an avian insectivore. *PLOS ONE* 16:e0254314.
- Williams, B. A., J. E. M. Watson, H. L. Beyer, C. J. Klein, J. Montgomery, R. K. Runting, L. A. Roberson, B. S. Halpern, H. S. Grantham, C. D. Kuempel, M. Frazier, O. Venter, and A. Wenger. 2021. Global rarity of intact coastal regions. *Conservation Biology*:1–12.
- Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W. Jetz. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* 95:2027.
- Wilmers, C. C., J. A. Estes, M. Edwards, K. L. Laidre, and B. Konar. 2012. Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Frontiers in Ecology and the Environment* 10:409–415.
- Wright, A. N., L. H. Yang, J. Piovita-Scott, D. A. Spiller, and T. W. Schoener. 2020. Consumer responses to experimental pulsed subsidies in isolated versus connected habitats. *American Naturalist* 196:369–381.
- Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. *Oikos* 41:496–506.
- Wright, D. H., B. D. Patterson, G. M. Mikkelsen, A. Cutler, and W. Atmar. 1997. A comparative analysis of nested subset patterns of species composition. *Oecologia* 113:1–20.
- Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse–consumer interactions. *Ecological Monographs* 80:125–151.

- Zurell, D. 2017. Integrating demography, dispersal and interspecific interactions into bird distribution models. *Journal of avian biology* 48:1505–1516.
- Zurell, D., N. E. Zimmermann, H. Gross, A. Baltensweiler, T. Sattler, and R. O. Wüest. 2020. Testing species assemblage predictions from stacked and joint species distribution models. *Journal of Biogeography* 47:101–113.
- Zwolicki, A., M. Barcikowski, A. Barcikowski, and M. Cymerski. 2015. Seabird colony effects on soil properties and vegetation zonation patterns on King George Island , Maritime Antarctic. *Polar Biology* 38:1645–1655.

Appendix A.

Supporting information for Chapter 2

Table A1. List of species included in analyses in taxonomic order, with relative abundance based on detections within 50 metres of an observer in point count surveys. Species were selected for analyses if they were known to breed in the Central Coast Region of British Columbia, based on Breeding Bird Atlas of BC (<https://www.birdatlas.bc.ca>).

Alpha Code	Common Name	Scientific Name	No. of Detections
SOGR	Sooty grouse	<i>Dendragapus fuliginosus</i>	11
ECDO	Eurasian collared-dove	<i>Streptopelia decaocto</i>	2
RUHU	Rufous hummingbird	<i>Selasphorus rufus</i>	230
HAWO	Hairy woodpecker	<i>Leuconotopicus villosus</i>	9
NOFL	Northern flicker	<i>Colaptes auratus</i>	8
OSFL	Olive-sided flycatcher	<i>Contopus cooperi</i>	1
PSFL	Pacific-slope flycatcher	<i>Empidonax difficilis</i>	525
STJA	Steller's jay	<i>Cyanocitta stelleri</i>	12
CORA	Common raven	<i>Corvus corax</i>	23
NOCR	Northwestern crow	<i>Corvus caurinus</i>	152
CBCH	Chestnut-backed chickadee	<i>Poecile rufescens</i>	172
BRCR	Brown creeper	<i>Certhia americana</i>	52
PAWR	Pacific wren	<i>Troglodytes pacificus</i>	543
GCKI	Golden-crowned kinglet	<i>Regulus satrapa</i>	215
RCKI	Ruby-crowned kinglet	<i>Regulus calendula</i>	2
VATH	Varied thrush	<i>Ixoreus naevius</i>	47
AMRO	American robin	<i>Turdus migratorius</i>	76
SWTH	Swainson's thrush	<i>Catharus ustulatus</i>	117
HETH	Hermit thrush	<i>Catharus guttatus</i>	183
CEDW	Cedar waxwing	<i>Bombycilla cedrorum</i>	4
OCWA	Orange-crowned warbler	<i>Oreothlypis celata</i>	571
YWAR	Yellow warbler	<i>Setophaga petechia</i>	2
YRWA	Yellow-rumped warbler	<i>Setophaga coronata</i>	26
TOWA	Townsend's warbler	<i>Setophaga townsendi</i>	234
WIWA	Wilson's warbler	<i>Cardellina pusilla</i>	23
SAVS	Savannah sparrow	<i>Passerculus sandwichensis</i>	1
WCSP	White-crowned sparrow	<i>Zonotrichia leucophrys</i>	1
FOSP	Fox sparrow	<i>Passerella iliaca</i>	128
SOSP	Song sparrow	<i>Melospiza melodia</i>	84
DEJU	Dark-eyed junco	<i>Junco hyemalis</i>	39
RECR	Red crossbill	<i>Loxia curvirostra</i>	109



Figure A1. Temperate rainforest study islands, surrounded by a dynamic, productive matrix. Photo taken with a small Remotely Piloted Aerial System (sRPAS).

Island selection process

Islands representative of the biogeographical and geomorphological variation in the region were chosen by using a two-step clustering method in SPSS statistical software (V23, IBM). This analysis considered 5 descriptors per island for the 1470 islands in the region: distance from mainland, area, exposure, normalized (size-independent) perimeter-to-area ratio, and percentage of area occupied by surrounding landmasses within 500 m of the island. For exposure, we used the British Columbia ShoreZone dataset, which classifies a unit of shoreline with a given exposure classification from very exposed to very protected. These classifications are based on wave exposure categories derived from wind fetch distances. The analysis used these variables to identify 5 clusters of island types (Table 2S). To facilitate sampling in a remote location, we selected 9 physical groupings of islands with 6-17 islands per group.

Table A2. Results of cluster analysis.

Cluster	# of Islands	Description
1	134	high exposure, close to mainland, few neighbouring islands
2	264	low exposure, close to mainland
3	432	high exposure, far from mainland, few neighbouring islands
4	426	low exposure, far from mainland, many neighbouring islands
5	197	low exposure, very close to mainland, many neighbouring islands, low P:A

Estimating isolation

To create an isolation metric, we considered that the classical TIB prediction that species richness varies with distance to mainland does not apply to this system because birds are highly mobile, and numerous large islands serve as a functional "mainland" source population. Rather than using the classical "distance to mainland" metric, we predicted the minimum size of an island that acts as a functional "mainland", and then used distance to the nearest island of that size as a predictor for our models.

To do this, we used the 'nls' (non-linear least squares) function in R to fit a non-linear model to the unlogged, rarefied species richness data as a response to the unlogged area, using the Michaelis-Menten function for asymptotic data with a y-intercept of zero. The Michaelis-Menten formula is $y = a \cdot x / (x + b)$ (plus intercept which is 0), where a is the y value at highest rate of increase, and b is the x value at approximately 1/2 of the asymptote. We then extracted the area at which species richness reached 90% of the asymptotic value, and measured distance to the nearest island of that size. We compared these results with those obtained from extracting the area for 95% and 99% of the asymptote, and, although the size of island falling into these categories is widely variable, the number of species found on an island of 90% the asymptote is less than 1 fewer than on an island with area 99% of the asymptote, so we used the distance to the closest island able to hold 90% of the maximum number of observed species as a metric for isolation (Figure A2).

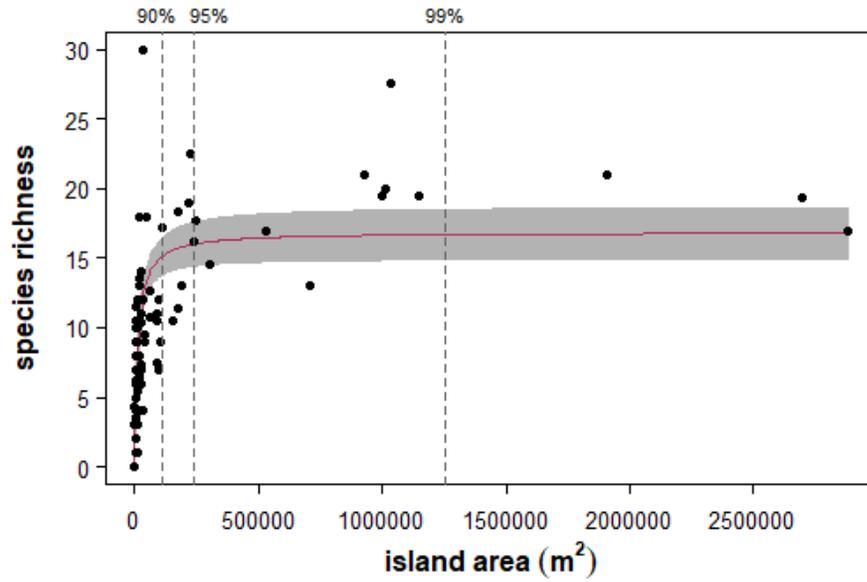


Figure A2. Species richness of terrestrial breeding birds plotted against island area. The red line represents the Michaelis-Menten function. Shaded area is the 95% confidence interval.

Analyses

In a preliminary analysis, we evaluated the effects of isolation and habitat heterogeneity on bird species richness and population density. In the species richness analysis, there was no difference between the model including both area and isolation, and the model with area alone, even when considering Burnham and Anderson's least stringent cutoff of a difference of $<2 \Delta AICc$ units (Burnham and Anderson 2002). Considering habitat heterogeneity in the model also proved to be uninformative (ie. the parameter did not improve model fit). All four models (area, area + isolation, area + habitat heterogeneity, and area + isolation + habitat heterogeneity) were better than the null model, which carried zero weight. In the population density model, adding habitat heterogeneity to the area model did not improve model quality, but both the area only model and area and habitat heterogeneity models were better than any models containing the isolation parameter.

Table A1. Initial suite of models to determine if isolation and habitat heterogeneity helped explain variation in species richness and improved model fit compared to island area alone. Even by the least stringent standards of $<2 \Delta AICc$, these additional parameters are uninformative.

Model	K	AICc	$\Delta AICc$	AICc weight	Cumulative weight	Log-likelihood
area + isolation	6	-34.61	0.00	0.46	0.46	23.80
area	5	-33.72	0.89	0.30	0.76	22.21
area + isolation + habitat heterogeneity	7	-32.31	2.30	0.15	0.91	23.83
area + habitat heterogeneity	6	-31.43	3.18	0.09	1.00	22.21
null	4	49.15	83.75	0.00	1.00	-20.34

Table A4. Initial suite of models to determine if isolation and habitat heterogeneity helped explain variation in population density and improved model fit compared to island area alone.

Model	K	AICc	$\Delta AICc$	AICc weight	Cumulative weight	Log-likelihood
area	5	653.82	0.00	0.47	0.47	-321.56
area + habitat heterogeneity	6	654.89	1.07	0.28	0.75	-320.94
area + isolation	6	655.99	2.17	0.16	0.91	-321.50
area + isolation + habitat heterogeneity	7	657.22	3.40	0.09	1.00	-320.94
null	4	670.54	16.72	0.00	1.00	-331.04

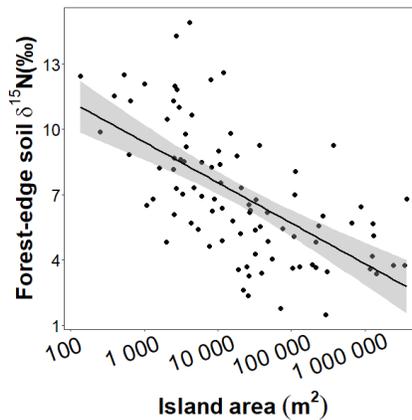


Figure A3. Correlation between marine input in the form of forest-edge soil $\delta^{15}N$ and island area on 91 islands on the Central Coast of British Columbia, Canada.

Correlation coefficient is -0.62, meaning that the variables are moderately correlated. Forest-edge soil $\delta^{15}N$ are averages from 4 plots representing the 4 cardinal directions at 0m from shore, so should not be affected by perimeter-to-area ratios.

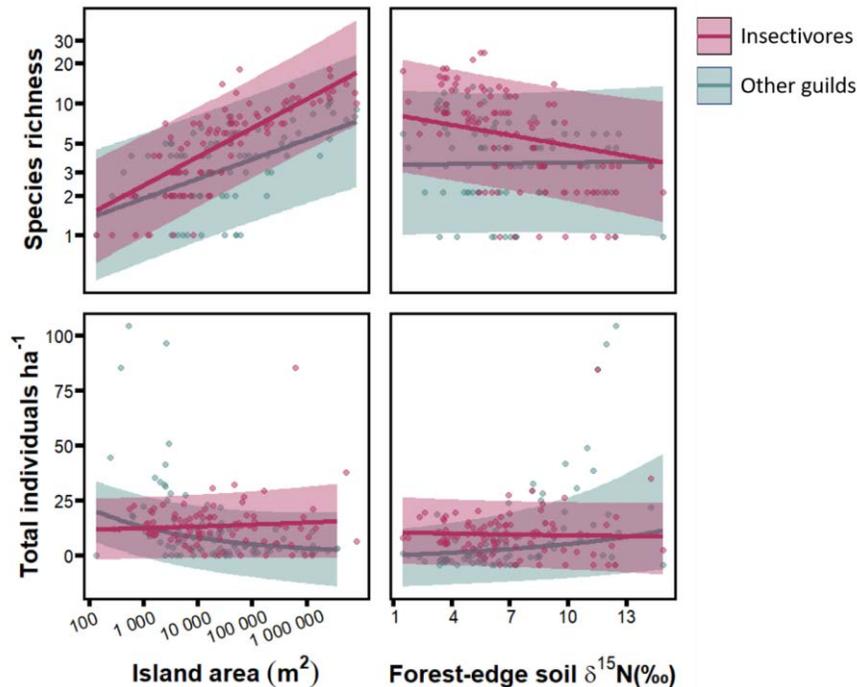


Figure A4. We fit separate global models for insectivore and “other guilds” species richness and total density to determine if any particular feeding guild was “dropping out” at higher levels of $\delta^{15}\text{N}$. We classified species based on the 5 diet categories described in the Elton Traits 1.0 database (Wilman et al. 2014). The “other” guild included “Omnivore”, “FruNect”, “VertFishScav”, and “PlantSeed” feeding categories. We combined these other guilds because they were poorly represented overall in our study with just a few species in each.

The majority (~2700 out of 3600) of our observations were of insectivorous birds. Area had a strong positive effect on species richness of both invertebrates and other guilds; however, the effect of $\delta^{15}\text{N}$ was only significant for insectivores. Neither area nor $\delta^{15}\text{N}$ had a significant effect on insectivore density, but area had a strong negative effect and $\delta^{15}\text{N}$ a positive albeit highly uncertain effect on the total bird density of other guilds. The interaction between area and $\delta^{15}\text{N}$ was also positive for the density of individuals in other guilds.

Relative Variable Importance (RVI)

To obtain meaningful RVIs, each parameter must occur in an equal number of models, so we considered all subsets of fixed effects and model-averaged across all outcomes to obtain coefficients and associated standard errors using the ‘MuMIn’ package in R (Barton 2019). Testing all possible combinations of parameters is not recommended when trying to determine “significance” or trying to isolate a top model but is an effective technique to determine RVIs (Arnold 2010; Burnham and Anderson 2004).

Supporting References for Chapter 2

Burnham, K. P., Anderson, D. R. 2002. Model Selection and Inference: A Practical Information-Theoretic Approach. 2nd Edition, Springer-Verlag, New York.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., Jetz, W. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* 95, 2027-2027.

Barton, K. 2019. MuMIn: Multi-model inference. R package version 1.43.6.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, 74, 1175-1178.

Burnham, K. P., Anderson, D. R. 2004. Multimodel inference - understanding AIC and BIC in model selection. *Sociological Methods and Research*. 33, 261-304.

Appendix B.

Supporting information for Chapter 3

Calculating “isolation”

To calculate a metric for “isolation”, we used the ‘*nls*’ (non-linear least squares) function in R to fit a non-linear model to the unlogged, rarefied species richness data as a response to the unlogged area, using the Michaelis-Menten function for asymptotic data with a y-intercept of zero with the following formula:

$$y = \frac{a * x}{(x + b)}$$

where *a* is the *y* value at highest rate of increase, and *b* is the *x* value at approximately 1/2 of the asymptote. We determined the area on an island where species richness reaches 90% of the asymptotic value, and for each island in our study, measured distance to the next nearest landmass of that size (including those not in our study). We evaluated the sensitivity of choosing the 90% asymptote by comparing results with those obtained from extracting the area for 95% and 99% of the asymptote, and, although the size of island falling into these categories is widely variable (Figure S1.1 below), the number of species found on an island of 90% the asymptote is less than 1 fewer than on an island with area 99% of the asymptote. As a result, we used the distance to the nearest island able to hold 90% of the maximum number of observed species as a metric for isolation.

How the HMSC model works

HMSC fits generalized linear models for the occurrence of each species, *j* (where *j* = 1, ..., *m*) in each sampling site, *i* (where *i* = 1, ..., *n*). These data are summarized in the matrix **Y**, a site-by-species matrix. The model, then, is denoted as

$$y_{ij} \sim D(L_{ij}, \sigma_j^2), \tag{1}$$

where y_{ij} represents the abundance of species *j* at site *i*, *D* represents the distribution of the response variable y_{ij} , L_{ij} represents the linear predictor, and

σ_j^2 represents a variance term. The linear predictor L_{ij} is estimated as a function of fixed (F) and random (R) components, such that

$$L_{ij} = L_{ij}^F + L_{ij}^R, \quad (2)$$

of which the fixed effects are modeled as

$$L_{ij}^F = \sum_k x_{ik} \beta_{jk}, \quad (3)$$

where x_{ik} is the environmental covariate x at site i (i.e., data from a site-by-environmental covariate matrix, \mathbf{X}) and β_{jk} is the abundance response of species j to the k th environmental covariate. In our case, \mathbf{X} included island area, isolation, habitat heterogeneity, distance to shore of each point count location, and island-level averages of wrack biomass, forest-edge soil $\delta^{15}\text{N}$, proportion of rocky shoreline, and year. It is assumed that the regression parameters adhere to a multivariate normal distribution, such that

$$\beta_j \sim N(\mu_j, V), \quad (4)$$

where β_j represents a vector of regression coefficients for species j . The expected environmental responses for species j are then represented by the vector μ_j , and variation around this expectation is represented by variance-covariance matrix \mathbf{V} . If the environmental responses depend on species-specific traits, this can be incorporated in the model by setting

$$\mu_{jk} = \sum_l t_{jl} \gamma_{lk}, \quad (5)$$

where t_{jl} denotes trait l for species j from the trait matrix \mathbf{T} , a species-by-trait matrix, and γ_{lk} represents the effect of trait l on the response to environmental covariate k . In this model, traits we considered were body mass, feeding guild, and categorical feeding height and nesting height.

Finally, the random component of equation (2) calculates remaining occurrences and co-occurrences that are not accounted for by measured covariates at various levels of the hierarchical structure of the observations. In our case, we collected bird abundance data on a point count level, with typically several point count locations on

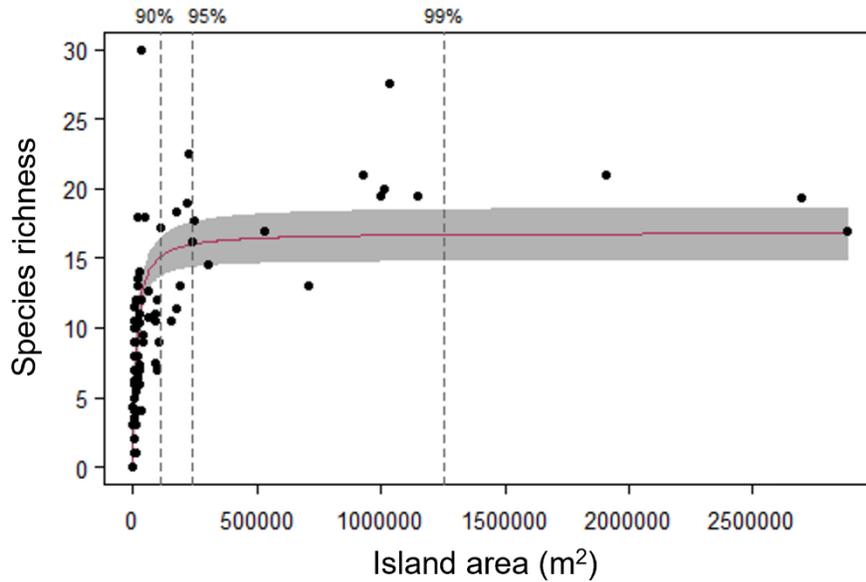
each island. Ignoring spatial autocorrelations can lead to overestimation of significance and biases in estimates of fixed effects (Legendre et al. 2002). As such, we included a spatial component by setting a matrix of the longitude and latitude of each point count location as an additional random effect, allowing us to take the spatial distance between all pairwise combinations of samples into account. The random component of the model is estimated with latent factor analysis (Ovaskainen et al. 2016). The linear predictor of our random effects can be written as

$$L_{ij}^R = \varepsilon_{ij}^{pcid} + \varepsilon_{ij}^{island} + \varepsilon_{ij}^{spatial}, \quad (6)$$

where ε_{ij} represents variation at the level of the three random effects we included: point count ID (*pcid*), island, and the spatially explicit distances between pairwise combinations of samples (*spatial*). It is assumed that the two non-spatial random effects components have multivariate normal distributions $\varepsilon_{ij}^{pcid} \sim N(0, \Omega^{pcid})$ and $\varepsilon_{ij}^{island} \sim N(0, \Omega^{island})$, where each Ω represents a variance-covariance matrix. Residual variances reveal correlations that cannot be accounted for by the fixed effects in the model. From these variance-covariance matrices, the co-occurrence matrix \mathbf{R} is generated. If j_1 and j_2 are two species in the model,

$$R_{j_1 j_2} = \Omega_{j_1 j_2} \sqrt{\Omega_{j_1 j_1} \Omega_{j_2 j_2}}, \quad (7)$$

where $R_{j_1 j_2}$ describes the extent to which species j_1 co-occurs more positively or negatively with species j_2 than by chance alone, after accounting for possible shared responses to the environment given the fixed effects in the model.



Figures:

Figure B1. Species richness of terrestrial breeding birds plotted against island area. The red line represents the Michaelis-Menten function. Shaded area is the 95% confidence interval.

Dotted lines represent 90%, 95%, and 99% of the calculated asymptote.

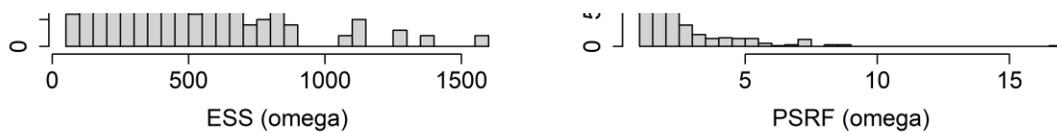


Figure B2 Effective sample size (ESS) and potential scale reduction factors (PSRF) for joint species distribution model of terrestrial breeding birds in BC, Canada. ESS and PSRF are metrics to evaluate chain convergence in Markov Chain Monte Carlo sampling. If ESS is similar to the theoretical number of samples, autocorrelation among consecutive samples is low. In this case, we evaluated 40000 samples in 2 chains (theoretical sample size = 80000). PSRF values closer to 1 indicates better mixing of chains.

Tables

Table B1 Name and number of individuals detected per bird species observed in the study. Third and fourth columns correspond to the names recorded on file by the Haítzaqv and Wuikinuxv First Nations. Number of detections are within 50 m of an observer in point count surveys. Species were included in analyses if they are known to breed in the Central Coast region of British Columbia, Canada (<https://www.birdatlas.bc.ca>).

English	Latin	Haítzaqv (Haítzaqv)	'Uik'ala (Wuikinuxv)	Number of detections (n = 3610)
Orange-crowned warbler	<i>Leiothlypis celata</i>	-	-	571
Pacific wren	<i>Troglodytes pacificus</i>	C'sk'í	-	543
Pacific-slope flycatcher	<i>Empidonax difficilis</i>	-	-	525
Townsend's warbler	<i>Setophaga townsendi</i>	-	-	234
Rufous hummingbird	<i>Selasphorus rufus</i>	Kvák'v'm'fa	k'va'ák'v'm'lhtua/ kvák'v'm'fa	230
Golden-crowned kinglet	<i>Regulus satrapa</i>	-	-	215
Hermit thrush	<i>Catharus guttatus</i>	h'x'v:h'x'v'ní	c'úp'ala/k'í'à'z'èli	183
Chestnut-backed chickadee	<i>Poecile rufescens</i>	Ziziziála	-	172
American crow	<i>Corvus caurinus</i>	k'á'qa	-	152
Fox sparrow	<i>Passerella iliaca</i>	-	-	128
Swainson's thrush	<i>Catharus ustulatus</i>	h'x'v:h'x'v'ní	-	117
Red crossbill	<i>Loxia curvirostra</i>	-	-	109
Song sparrow	<i>Melospiza melodia</i>	-	-	84
American robin	<i>Turdus migratorius</i>	C'ú'p'álá	-	76
Brown creeper	<i>Certhia americana</i>	-	-	52
Varied thrush	<i>Ixoreus naevius</i>	h'x'v:h'x'v'ní	c'úp'ala/k'í'à'z'èli	47
Dark-eyed junco	<i>Junco hyemalis</i>	-	-	39
Yellow-rumped warbler	<i>Setophaga coronata</i>	-	-	26
Common raven	<i>Corvus corax</i>	G'v'u'í	g'v'u'w'í	23
Wilson's warbler	<i>Cardellina pusilla</i>	-	-	23
Steller's jay	<i>Cyanocitta stelleri</i>	Kváy'alaqs	-	12
Sooty grouse	<i>Dendragapus fuliginosus</i>	m'í'k'í's	-	11
Hairy woodpecker	<i>Leuconotopicus villosus</i>	l'á'lap'í'ka	dh'à'dhanu	9
Northern flicker	<i>Colaptes auratus</i>	l'á'lap'í'ka	dh'à'dhanu	8
Pine siskin	<i>Spinus pinus</i>	-	-	8
Cedar waxwing	<i>Bombycilla cedrorum</i>	Tátix'as	-	4
Eurasian collared-dove	<i>Streptopelia decaocto</i>	Hám'í	ham'í'em	2
Ruby-crowned kinglet	<i>Regulus calendula</i>	-	-	2

Yellow warbler	<i>Setophaga petechia</i>	-	-	2
Olive-sided flycatcher	<i>Contopus cooperi</i>	-	-	1
Savannah sparrow	<i>Passerculus sandwichensis</i>	-	-	1
White-crowned sparrow	<i>Zonotrichia leucophrys</i>	-	-	1

Table B2. Results of cluster analysis to select a geographically and geomorphologically representative suite of islands. Island size, distance to mainland, percentage of area within 500 m covered by neighbouring landmasses, and size-independent perimeter-to-area ratios were calculated using WorldView2 satellite imagery at 2 m resolution, and exposure was based on the British Columbia ShoreZone dataset (Howes et al. 1994). This shorezone classification includes six classes between very exposed and very protected. Wave exposure categories are derived from wind fetch distances. We identified five types (i.e., clusters) of islands through this cluster analysis.

Cluster	# of Islands	Description
1	134	high exposure, close to mainland, few neighbouring islands
2	264	low exposure, close to mainland
3	432	high exposure, far from mainland, few neighbouring islands
4	426	low exposure, far from mainland, many neighbouring islands
5	197	low exposure, very close to mainland, many neighbouring islands, low P:A

Table B3. Explanatory model fits for each species included in a spatially explicit joint species distribution model with a Poisson distribution. We calculated values by simulating posterior predictive distributions using the same data that were used to fit the model. RMSE is the root mean square error. SR2 is the squared Spearman correlation between observed and predicted values (a pseudo-R²). O.AUC and O.TjurR2 indicate how well the model predicts occurrences (i.e., presence, where count > 0). AUC is the area under the curve and TjurR2 is Tjur’s coefficient of discrimination. C.SR2 and C.RMSE are the SR2 and RMSE, conditional on presence. All calculations were conducted using the ‘Hmsc’ package in R v. 4.1.1. (Tikhonov et al. 2020, R Core Team 2021)

Common name	RMSE	SR2	O.AUC	O.TjurR2	C.SR2	C.RMSE
American robin	0.58	0.02	0.75	0.11	0.36	0.10
Chestnut-backed chickadee	0.67	0.59	0.97	0.37	0.31	0.62
Dark-eyed junco	0.44	0.37	0.95	0.36	0.20	0.08
Fox sparrow	0.59	0.64	0.96	0.55	0.23	0.44
Golden-crowned kinglet	0.82	0.58	0.93	0.27	0.38	0.20
Hermit thrush	0.91	0.18	0.80	0.14	0.44	0.01
American crow	0.71	0.34	0.89	0.33	0.33	0.54
Orange-crowned warbler	1.44	0.22	0.73	0.08	0.39	0.08
Pacific wren	1.32	0.35	0.86	0.27	0.35	0.11
Pacific-slope flycatcher	1.28	0.30	0.85	0.25	0.35	0.07

Red crossbill	0.45	0.44	0.98	0.38	0.24	0.96
Rufous hummingbird	0.87	0.26	0.79	0.16	0.44	0.07
Song sparrow	0.55	0.51	0.95	0.52	0.22	0.30
Swainson's thrush	0.56	0.40	0.93	0.45	0.26	0.51
Townsend's warbler	0.94	0.47	0.87	0.29	0.40	0.25
Varied thrush	0.47	0.12	0.85	0.18	0.28	0.14

Table B4. Predictive model fits for each species included in a spatially explicit joint species distribution model (JSDM). To evaluate predictive power, we conducted a four-fold cross-validation, where samples were randomly divided among four partitions. The model was fit separately for each partition. Here, we report cross-validation-based predictive model fit values for each species.

Common name	RMSE	SR2	O.AUC	O.TjurR2	C.SR2	C.RMSE
American robin	0.54	0.02	0.50	0.00	0.90	0.06
Chestnut-backed chickadee	1.19	0.09	0.50	0.00	0.85	0.03
Dark-eyed junco	0.61	0.06	0.50	0.00	0.96	0.00
Fox sparrow	0.99	0.20	0.50	0.00	0.91	0.03
Golden-crowned kinglet	1.14	0.02	0.50	0.00	0.80	0.00
Hermit thrush	0.93	0.03	0.50	0.00	0.79	0.00
American crow	1.14	0.07	0.50	0.00	0.88	0.20
Orange-crowned warbler	1.66	0.06	0.50	0.00	0.47	0.04
Pacific wren	1.39	0.26	0.50	0.00	0.49	0.08
Pacific-slope flycatcher	1.38	0.17	0.50	0.00	0.49	0.04
Red crossbill	1.67	0.02	0.50	0.00	0.93	0.14
Rufous hummingbird	0.92	0.11	0.50	0.00	0.71	0.00
Song sparrow	0.77	0.18	0.50	0.00	0.94	0.04
Swainson's thrush	0.84	0.16	0.50	0.00	0.92	0.14
Townsend's warbler	1.20	0.17	0.50	0.00	0.77	0.02
Varied thrush	0.49	0.06	0.50	0.00	0.95	0.04

Appendix C.

Supporting information for Chapter 4

Study species names

Table C1. Names of species used in study, including those known and recorded on file by the Haïtzaqv and Wuikinuxv Nations.

English	Latin	Haïtzaqv̄a (Haïtzaqv)	'Uik̄ala (Wuikinuxv)
Plants:			
Salal	<i>Gaultheria shallon</i>	nk̄v̄t̄	nk̄w̄a's
False lily-of-the-valley	<i>Maiathemum dilatatum</i>	-	t̄m̄c̄
Isopods:			
Rough woodlouse	<i>Porcellio scaber</i>	-	-
Rock slater	<i>Ligidium gracile</i>	-	-
Weevils:			
Conifer seedling weevil	<i>Steremnius carinatus</i>	-	-
-	<i>Steremnius tuberosus</i>	-	-
Ground beetles:			
-	<i>Pterostichus algidus</i>	-	-
-	<i>Pterostichus amethystinus</i>	-	-
-	<i>Pterostichus crenicollis</i>	-	-
-	<i>Pterostichus lama</i>	-	-
Snail-killer carabid	<i>Scaphinotus angusticollis</i>	-	-
Songbirds:			
Chestnut-backed chickadee	<i>Poecile rufescens</i>	z̄iz̄iz̄iá̄la	-
Fox sparrow	<i>Passerella iliaca</i>	-	-
Orange-crowned warbler	<i>Leiothlypis celata</i>	-	-
Pacific wren	<i>Troglodytes pacificus</i>	C̄sk̄ñ̄	-
Song sparrow	<i>Melospiza melodia</i>	-	-

Island selection

To select a subset of the 1470 islands in the region, we conducted a two-step clustering method in SPSS statistical software (V23, IBM). The subset was chosen to represent the biogeographical and geomorphological variation in the region, considering five descriptors per island: distance from mainland, area, exposure, normalized (size-independent) perimeter-to-area ratio, and percentage of area occupied by surrounding landmasses (other islands) within 500 m of the island to account for the relative isolation of each island. Distance to mainland, island size, perimeter-to-area ratio, and surrounding landmasses were derived from WorldView2 satellite imagery with 2 m resolution. For exposure, we used the British Columbia ShoreZone dataset (Howes et al. 1994) which classifies a unit of shoreline with a given exposure classification. There are six classes, ranging from very exposed to very protected. These wave exposure categories are derived from wind fetch distances. The cluster analysis used these variables to identify five types (i.e., clusters) of islands (Table S1). To facilitate sampling in a remote location, we selected nine physical groupings of islands with 6-17 islands per group.

Table C2. Results of cluster analysis described above.

Cluster	# of Islands	Description
1	134	high exposure, close to mainland, few neighbouring islands
2	264	low exposure, close to mainland
3	432	high exposure, far from mainland, few neighbouring islands
4	426	low exposure, far from mainland, many neighbouring islands
5	197	low exposure, very close to mainland, many neighbouring islands, low P:A

Sample Collection

Table C3. Numbers of samples taken by taxon and by island size. In Island ID, the first two letters correspond to the name of the island group surveyed.

AD = Admiral, CV = Calvert, GS = Goose, MM = MacMullins, PR = Penrose, SC = South Calvert, ST = Stirling, TB = Tribal, and TQ = Triquet.

Island ID	Area (m ²)	Soil	Salal	False Lily-of-the Valley	Herbivores (weevils)	Detritivores (isopods)	Carnivores (beetles)	Song-birds (feces)	Song-birds (feathers)
AD01	39976	10	14	4	0	0	0	3	3
AD02	247740	12	20	7	0	0	2	5	5
AD03	960	7	7	7	0	0	2	0	0
AD04	1772	7	9	9	0	0	0	1	1
AD05	17632	9	11	9	0	0	0	1	2
AD06	175748	13	23	16	0	0	0	11	10
AD07	552	7	7	7	0	0	0	0	0
CV01	8855	9	11	11	3	0	3	0	3
CV02	6868	8	10	10	5	0	2	0	0
CV03	7012	9	11	12	5	0	5	0	0
CV04	2392	6	7	9	2	0	3	6	8
CV05	3560	8	10	10	3	0	4	0	0
CV06	22218	10	14	16	3	0	6	5	6
CV07	93152	11	17	18	4	0	4	1	5
CV08	173848	14	26	28	4	1	5	4	4
CV09	4672	8	10	8	0	1	0	1	1
CV10	9828	7	9	2	1	0	4	1	1
CV11	3828	8	10	7	1	0	1	0	0
CV12	13612	9	11	5	3	1	4	2	3
CV13	300392	14	26	23	3	2	3	8	13
CV14	480	7	7	7	2	0	2	0	0
CV15	31700	10	14	14	0	0	0	2	2
CV16	926825	18	38	22	0	0	0	8	8
CV17	224270	13	23	10	0	0	0	4	5
GS01	2280	7	6	8	4	7	4	0	4
GS02	3048	8	3	3	5	5	5	0	0
GS03	1000108	16	19	25	5	0	5	3	5
GS05	17200	9	11	0	5	0	5	5	6
GS06	2880440	33	80	49	4	0	4	5	12
GS07	63548	11	12	0	2	4	3	0	0
GS09	23156	10	15	6	1	2	2	0	0
MM01	3252	8	9	8	3	6	5	0	0

MM02	12604	10	14	6	2	3	51	6	7
MM03	5172	9	11	10	5	4	5	4	7
MM04	2172	7	8	6	4	9	6	3	3
MM05	22244	10	13	12	1	5	4	9	11
MM06	218168	13	23	16	1	7	55	22	30
MM07	2604	6	3	8	0	0	0	0	3
MM08	1800	7	2	7	0	5	5	0	2
MM09	2740	6	0	3	0	3	4	0	1
MM10	112324	4	9	10	2	4	5	10	17
MM11	20732	5	6	3	0	2	4	0	0
PR01	155844	11	17	16	3	0	3	0	0
PR02	191988	11	18	17	2	2	3	0	0
PR03	5228	8	10	3	2	2	0	0	0
PR04	45648	10	14	1	4	1	2	0	0
PR05	2396	7	8	5	4	0	1	0	0
PR06	7616	8	9	5	3	0	3	2	2
PR07	2584	1	3	2	0	0	0	0	0
PR08	38936	10	14	2	0	0	0	1	1
PR09	7132	8	10	2	0	0	0	0	0
PR10	10224	9	11	2	0	0	0	1	1
PR11	3748	7	9	1	0	0	0	0	0
PR12	5096	1	3	2	0	0	0	0	0
PR13	1014904	19	41	10	0	0	0	0	2
SC01	238564	13	23	21	1	3	5	15	22
SC02	9180	9	11	10	2	7	2	1	2
SC03	27264	9	11	8	1	1	2	2	3
SC04	2448	7	9	6	1	0	1	0	0
SC05	9820	7	9	8	0	2	0	1	2
SC06	1160	7	9	5	0	4	0	0	0
ST01	2192	7	7	7	0	0	0	2	2
ST02	22568	9	11	8	2	3	4	1	1
ST03	31132	10	14	9	1	1	1	2	2
ST05	96724	3	9	8	0	0	0	3	3
ST07	1416	7	7	5	0	1	2	2	2
ST08	15576	9	10	5	0	0	0	0	0
ST09	226	7	0	6	0	0	0	0	0
ST10	90388	11	17	14	0	0	0	3	3
ST12	59873	10	14	12	0	0	0	0	2
ST14	2699381	39	101	96	0	0	0	13	16
TB01	1909728	26	68	57	0	1	0	4	4
TB02	18716	8	10	9	2	5	2	1	2
TB03	85788	10	14	10	0	1	0	2	3
TB04	124	7	7	4	0	0	0	0	0
TB05	707600	15	31	25	0	2	0	3	4

TB06	2884	7	9	9	1	0	1	3	2
TB07	351	7	7	6	1	0	1	0	0
TB08	92216	9	11	11	2	3	3	6	7
TB10	9272	10	11	11	3	0	4	0	0
TB12	3168	7	8	10	0	2	2	0	0
TQ01	10184	9	11	4	3	4	0	5	8
TQ02	2252	7	8	5	3	0	4	3	5
TQ03	27785	9	11	11	3	2	1	0	1
TQ04	21958	10	14	14	2	0	1	4	4
TQ05	4140	8	8	5	5	1	0	1	2
TQ06	2236	7	8	8	2	1	0	0	0
TQ07	528840	22	45	43	0	3	0	9	16
TQ08	6616	8	10	10	0	4	0	1	2
TQ10	106376	13	23	25	0	0	0	8	9
TQ11	904	7	9	10	0	1	0	1	1
TQ12	15936	10	14	16	0	0	0	1	2
TQ13	1036682	24	48	45	0	3	0	6	6
TQ15	26912	8	11	11	0	3	0	0	1
TQ17	576	7	7	4	0	3	0	0	0
TQ18	32740	10	14	12	1	4	1	0	0
TQ20	1147628	21	50	44	0	1	0	4	4
Totals:		973	1485	1166	137	142	271	241	337

Stable isotope composition of subsidy sources

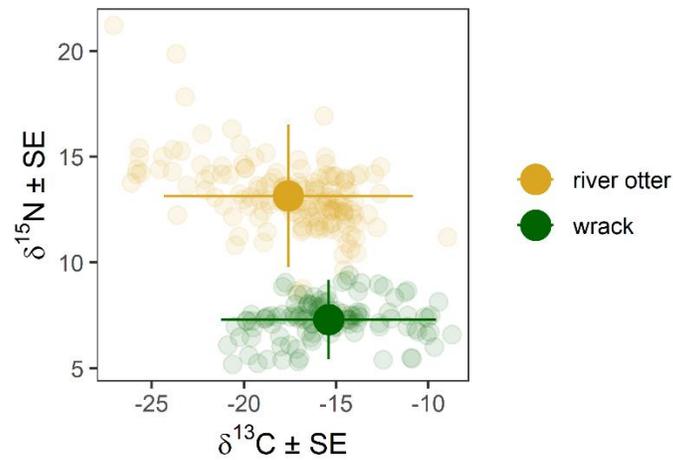


Figure C1. Stable isotope signatures of marine inputs on the central coast of British Columbia. Large circles indicate means, bars represent standard errors, and small circles represent raw data points.

River otter spraint samples were provided by Andrew Sheriff (collected in 2015, 2016, and 2017), and wrack samples were collected by Sara Wickham (2018). Samples of both types were collected on or near study islands.

Enrichment model R² values

Table C4. R² values for $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and %N models. The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ models included the following standardized parameters: \log_{10} island area (m²), \log_e distance to shore (m), an interaction term between area and distance to shore, sqrt wrack biomass (kg/m²), slope (degrees), and the random effect of island due to repeat sampling on certain islands for most groups. The %N model included these same parameters with the addition of standardized $\delta^{15}\text{N}$.

Group	$\delta^{15}\text{N}$		$\delta^{13}\text{C}$		%N	
	Marginal R ²	Conditional R ²	Marginal R ²	Conditional R ²	Marginal R ²	Conditional R ²
Soil	0.57	0.69	0.11	0.34	0.16	0.24
Salal	0.65	0.79	0.17	0.39	0.07	0.15
False Lily-of-the-Valley	0.63	0.82	0.23	0.39	0.16	0.70
Herbivores (weevils)	0.52	0.67	0.04	0.23	0.04	0.04
Detritivores (isopods)	0.51	0.71	0.14	0.43	0.08	0.23
Carnivores (beetles)	0.50	0.64	0.07	0.28	0.08	0.24
Songbirds (feces)	0.30	0.47	0.05	0.08	0.17	0.31
Songbirds (feathers)	0.16	0.31	0.08	0.08	0.05	0.17

Enrichment model coefficient estimates

Table C5. Model-averaged coefficient estimates of $\delta^{15}\text{N}$ of each taxon from models including standardized \log_{10} island area (m²), \log_e distance to shore (m), sqrt wrack biomass (kg/m²), and mean island slope (°).

Taxon	Fit	Fit SE	Lower CI	Upper CI	Parameter
Soil	-2.72	0.22	-3.15	-2.29	Island area
Salal	-4.50	0.31	-5.11	-3.89	Island area
False lily-of-the-valley	-4.70	0.41	-5.50	-3.90	Island area
Weevils (herbivores)	-3.39	0.44	-4.25	-2.53	Island area
Isopods (detritivores)	-1.65	0.22	-2.08	-1.22	Island area
Beetles (carnivores)	-2.35	0.24	-2.82	-1.88	Island area
Songbirds (feces)	-1.82	0.34	-2.49	-1.15	Island area
Songbirds (feathers)	-1.36	0.30	-1.95	-0.77	Island area

Soil	-1.33	0.09	-1.51	-1.15	Distance to shore
Salal	-1.43	0.09	-1.61	-1.25	Distance to shore
False lily-of-the-valley	-1.98	0.11	-2.20	-1.76	Distance to shore
Weevils (herbivores)	-0.66	0.35	-1.35	0.03	Distance to shore
Isopods (detritivores)	-0.23	0.16	-0.54	0.08	Distance to shore
Beetles (carnivores)	-0.33	0.14	-0.60	-0.06	Distance to shore
Songbirds (feces)	-0.72	0.27	-1.25	-0.19	Distance to shore
Songbirds (feathers)	-0.42	0.24	-0.89	0.05	Distance to shore
Soil	-0.33	0.10	-0.53	-0.13	Island area * distance
Salal	-1.15	0.10	-1.35	-0.95	Island area * distance
False lily-of-the-valley	-0.73	0.12	-0.97	-0.49	Island area * distance
Weevils (herbivores)	-0.62	0.26	-1.13	-0.11	Island area * distance
Isopods (detritivores)	-0.42	0.13	-0.67	-0.17	Island area * distance
Beetles (carnivores)	-0.43	0.14	-0.70	-0.16	Island area * distance
Songbirds (feces)	0.23	0.29	-0.34	0.80	Island area * distance
Songbirds (feathers)	-0.06	0.27	-0.59	0.47	Island area * distance
Soil	-0.06	0.21	-0.47	0.35	Mean island slope
Salal	-0.33	0.35	-1.02	0.36	Mean island slope
False lily-of-the-valley	-0.43	0.44	-1.29	0.43	Mean island slope
Weevils (herbivores)	0.10	0.52	-0.92	1.12	Mean island slope
Isopods (detritivores)	-0.50	0.22	-0.93	-0.07	Mean island slope
Beetles (carnivores)	-0.48	0.24	-0.95	-0.01	Mean island slope
Songbirds (feces)	-0.01	0.37	-0.74	0.72	Mean island slope
Songbirds (feathers)	-0.20	0.34	-0.87	0.47	Mean island

					slope
Soil	0.09	0.22	-0.34	0.52	Wrack biomass
Salal	0.78	0.33	0.13	1.43	Wrack biomass
False lily-of-the-valley	0.92	0.42	0.10	1.74	Wrack biomass
Weevils (herbivores)	-0.29	0.49	-1.25	0.67	Wrack biomass
Isopods (detritivores)	0.12	0.31	-0.49	0.73	Wrack biomass
Beetles (carnivores)	0.27	0.41	-0.53	1.07	Wrack biomass
Songbirds (feces)	0.34	0.39	-0.42	1.10	Wrack biomass
Songbirds (feathers)	0.53	0.32	-0.10	1.16	Wrack biomass

Table C6. Model-averaged coefficient estimates of $\delta^{13}\text{C}$ of each taxon from models including standardized \log_{10} island size (m^2), In distance to shore (m), sqrt wrack biomass (kg/m^2), and mean island slope ($^\circ$).

Taxon	Fit	SE	Lower CI	Upper CI	Parameter
Soil	0.2	0.05	0.1	0.3	Island area
Salal	-0.25	0.11	-0.46	-0.05	Island area
False lily-of-the-valley	-0.07	0.14	-0.33	0.2	Island area
weevils (herbivores)	-0.01	0.09	-0.18	0.16	Island area
Isopods (detritivores)	-0.23	0.15	-0.52	0.07	Island area
Beetles (carnivores)	-0.16	0.16	-0.46	0.15	Island area
Songbirds - feces	-0.22	0.18	-0.56	0.13	Island area
Songbirds - feathers	-0.44	0.11	-0.65	-0.24	Island area
Soil	-0.04	0.03	-0.1	0.02	Distance to shore
Salal	-0.62	0.06	-0.73	-0.51	Distance to shore
False lily-of-the-valley	-1.26	0.09	-1.43	-1.09	Distance to shore
weevils (herbivores)	0.01	0.06	-0.11	0.12	Distance to shore
Isopods (detritivores)	-0.28	0.09	-0.46	-0.1	Distance to shore
Beetles (carnivores)	-0.07	0.08	-0.23	0.08	Distance to shore
Songbirds - feces	-0.23	0.17	-0.57	0.11	Distance to shore

Songbirds - feathers	-0.15	0.14	-0.41	0.12	Distance to shore
Soil	0.15	0.02	0.1	0.19	Island area * distance
Salal	0.1	0.04	0.03	0.18	Island area * distance
False lily-of-the-valley	0.32	0.06	0.2	0.44	Island area * distance
weevils (herbivores)	0.06	0.06	-0.05	0.18	Island area * distance
Isopods (detritivores)	0.05	0.09	-0.13	0.24	Island area * distance
Beetles (carnivores)	-0.01	0.09	-0.2	0.17	Island area * distance
Songbirds - feces	0.17	0.15	-0.12	0.46	Island area * distance
Songbirds - feathers	0.13	0.1	-0.06	0.33	Island area * distance
Soil	0.01	0.06	-0.11	0.13	Mean island slope
Salal	-0.27	0.11	-0.48	-0.06	Mean island slope
False lily-of-the-valley	-0.43	0.17	-0.76	-0.1	Mean island slope
weevils (herbivores)	0.04	0.09	-0.12	0.21	Mean island slope
Isopods (detritivores)	-0.27	0.17	-0.61	0.06	Mean island slope
Beetles (carnivores)	-0.34	0.17	-0.66	-0.01	Mean island slope
Songbirds - feces	-0.39	0.16	-0.71	-0.07	Mean island slope
Songbirds - feathers	-0.21	0.1	-0.4	-0.02	Mean island slope
Soil	-0.06	0.05	-0.16	0.04	Wrack biomass
Salal	0.04	0.12	-0.2	0.28	Wrack biomass
False lily-of-the-valley	-0.37	0.16	-0.69	-0.05	Wrack biomass
weevils (herbivores)	-0.09	0.06	-0.21	0.03	Wrack biomass
Isopods (detritivores)	-0.03	0.15	-0.33	0.27	Wrack biomass
Beetles (carnivores)	-0.22	0.15	-0.52	0.08	Wrack biomass
Songbirds - feces	0.01	0.15	-0.29	0.3	Wrack

Songbirds - feathers	0.02	0.08	-0.14	0.17	biomass Wrack biomass
----------------------	------	------	-------	------	-----------------------------

Table C7. Model-averaged coefficient estimates of %N of each taxon from models including standardized log₁₀ island size (m²), log_e distance to shore (m), sqrt wrack biomass (kg/m²), and mean island slope (°).

Taxon	Fit	Fit SE	Lower CI	Upper CI	Parameter
Soil	0.09	0.02	0.06	0.13	δ ¹⁵ N
Salal	0.09	0.01	0.06	0.11	δ ¹⁵ N
False lily-of-the-valley	0.28	0.04	0.20	0.37	δ ¹⁵ N
Weevils (herbivores)	0.04	0.05	-0.06	0.13	δ ¹⁵ N
Isopods (detritivores)	-0.16	0.13	-0.40	0.09	δ ¹⁵ N
Beetles (carnivores)	-0.12	0.08	-0.27	0.03	δ ¹⁵ N
Songbirds - feces	-0.83	0.44	-1.69	0.03	δ ¹⁵ N
Songbirds - feathers	0.09	0.04	0.01	0.17	δ ¹⁵ N
Soil	-0.04	0.02	-0.08	0.00	Island area
Salal	0.05	0.02	0.01	0.08	Island area
False lily-of-the-valley	-0.01	0.10	-0.21	0.19	Island area
Weevils (herbivores)	0.01	0.05	-0.09	0.11	Island area
Isopods (detritivores)	0.18	0.12	-0.06	0.42	Island area
Beetles (carnivores)	-0.08	0.11	-0.30	0.15	Island area
Songbirds - feces	0.78	0.61	-0.41	1.97	Island area
Songbirds - feathers	0.08	0.06	-0.03	0.19	Island area
Soil	-0.05	0.01	-0.08	-0.03	Distance to shore
Salal	0.03	0.01	0.01	0.05	Distance to shore
False lily-of-the-valley	0.04	0.03	-0.02	0.10	Distance to shore
Weevils (herbivores)	-0.05	0.04	-0.13	0.04	Distance to shore
Isopods (detritivores)	0.16	0.09	-0.03	0.34	Distance to shore
Beetles (carnivores)	-0.09	0.06	-0.21	0.02	Distance to shore
Songbirds - feces	1.33	0.53	0.29	2.36	Distance to shore
Songbirds - feathers	0.03	0.05	-0.08	0.13	Distance to shore
Soil	0.00	0.02	-0.04	0.03	Mean island slope
Salal	-0.03	0.01	-0.05	0.00	Mean island slope

False lily-of-the-valley	0.12	0.09	-0.05	0.29	Mean island slope
Weevils (herbivores)	0.04	0.07	-0.09	0.17	Mean island slope
Isopods (detritivores)	0.10	0.12	-0.13	0.33	Mean island slope
Beetles (carnivores)	-0.22	0.12	-0.44	0.01	Mean island slope
Songbirds - feces	-0.20	0.66	-1.49	1.08	Mean island slope
Songbirds - feathers	-0.06	0.06	-0.19	0.06	Mean island slope
Soil	0.02	0.02	-0.02	0.05	Wrack biomass
Salal	0.02	0.02	-0.01	0.05	Wrack biomass
False lily-of-the-valley	-0.05	0.11	-0.25	0.16	Wrack biomass
Weevils (herbivores)	0.08	0.05	-0.03	0.19	Wrack biomass
Isopods (detritivores)	-0.07	0.13	-0.33	0.18	Wrack biomass
Beetles (carnivores)	-0.27	0.16	-0.58	0.04	Wrack biomass
Songbirds - feces	-1.33	0.57	-2.44	-0.22	Wrack biomass
Songbirds - feathers	-0.10	0.06	-0.22	0.03	Wrack biomass

Relative Variable Importance (RVIs)

Table C8. Relative variable importance of parameters included in models evaluating effects on soil, plants, invertebrates, and songbird $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and %N.

^{15}N-Enrichment Analysis						
Taxon	Island area (n = 12)	Distance to shore (n = 12)	Area * distance (n = 4)	Mean island slope (n = 10)	Wrack biomass (n = 10)	
Soil	1.00	1.00	0.99	0.28	0.28	
Salal	1.00	1.00	1.00	0.39	0.84	
False lily-of-the-valley	1.00	1.00	1.00	0.39	0.79	
Weevils (herbivores)	1.00	1.00	0.86	0.26	0.28	
Isopods (detritivores)	1.00	1.00	0.97	0.79	0.28	
Beetles (carnivores)	1.00	1.00	0.98	0.72	0.34	
Songbirds - feces	1.00	0.95	0.31	0.27	0.34	
Songbirds - feathers	1.00	0.71	0.19	0.32	0.56	
^{13}C-Enrichment Analysis						
Taxon	Island area (n = 12)	Distance to shore (n = 12)	Area * distance (n = 4)	Mean island slope (n = 10)	Wrack biomass (n = 10)	
Soil	1.00	1.00	1.00	0.28	0.42	
Salal	1.00	1.00	0.93	0.87	0.30	
False lily-of-the-valley	1.00	1.00	1.00	0.82	0.90	
Weevils (herbivores)	0.29	0.29	0.04	0.32	0.52	
Isopods (detritivores)	0.61	0.97	0.17	0.56	0.27	
Beetles (carnivores)	0.40	0.38	0.04	0.79	0.54	
Songbirds - feces	0.55	0.54	0.12	0.85	0.29	
Songbirds - feathers	1.00	0.49	0.23	0.79	0.29	
%N Analysis						

Taxon	$\delta^{15}\text{N}$ (n = 16)	Island area (n = 16)	Distance to shore (n = 16)	Mean island slope (n = 16)	Wrack biomass (n = 16)
Soil	1.00	0.72	1.00	0.28	0.37
Salal	1.00	0.94	0.97	0.64	0.43
False lily-of- the-valley	1.00	0.27	0.48	0.50	0.30
Weevils (herbivores)	0.32	0.16	0.40	0.33	0.56
Isopods (detritivores)	0.45	0.50	0.59	0.33	0.29
Beetles (carnivores)	0.59	0.33	0.58	0.72	0.62
Songbirds - feces	0.68	0.44	0.89	0.30	0.82
Songbirds - feathers	0.83	0.48	0.30	0.39	0.55

Biplots of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ with wrack biomass and island slope

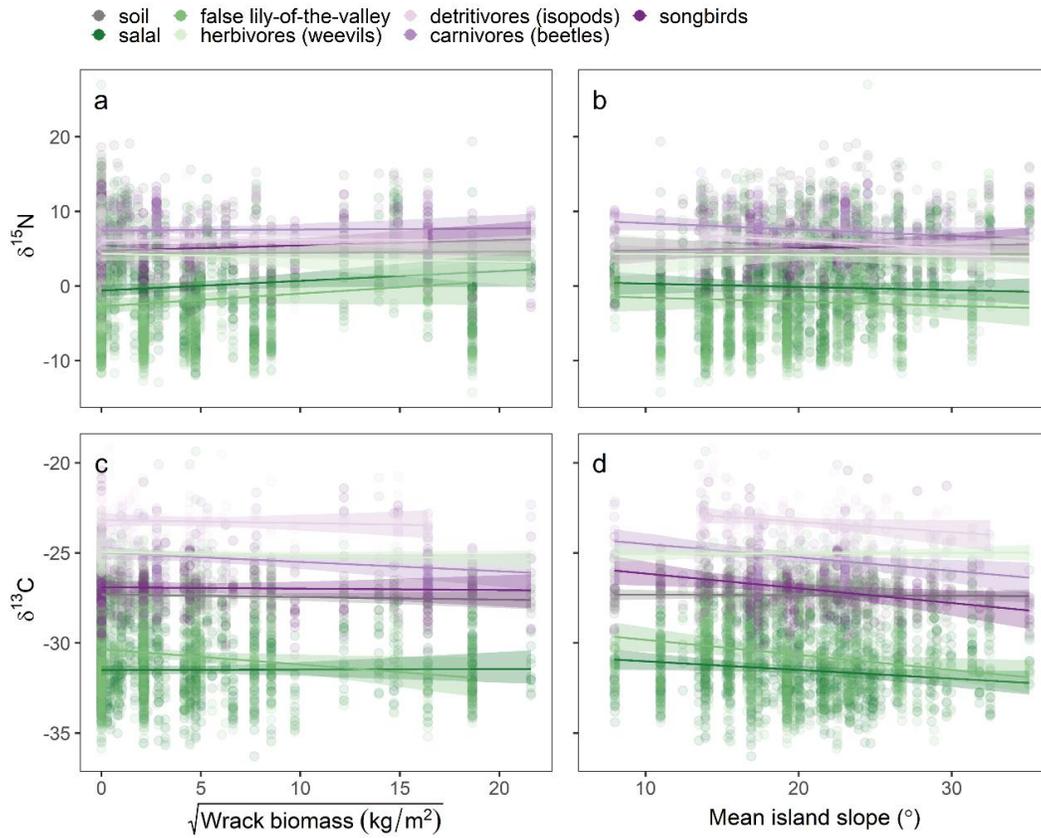


Figure C2. Effects of wrack biomass (kg/m^2) and mean island slope ($^\circ$) on $\delta^{15}\text{N}$ (a, b) and $\delta^{13}\text{C}$ (c, d) in soil, plants, invertebrates, and songbird feces.

Shaded areas represent 95% confidence interval around taxon-specific global model-predicted means.

AICc evaluation of %N models with and without $\delta^{15}\text{N}$

Table C9. Models of %N including $\delta^{15}\text{N}$ as a parameter were compared using AICc to those without $\delta^{15}\text{N}$ for each taxonomic group. All models include standardized \log_{10} island size (m^2), \log_e distance to shore (m), sqrt wrack biomass (kg/m^2), and mean island slope.

Taxon	Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Soil	With $\delta^{15}\text{N}$	8	680.48	0.00	1.00	1.00	-332.16
	Without $\delta^{15}\text{N}$	7	704.82	24.35	0.00	1.00	-345.35
Salal	With $\delta^{15}\text{N}$	8	217.02	0.00	1.00	1.00	-100.45
	Without $\delta^{15}\text{N}$	7	265.84	48.82	0.00	1.00	-125.87
False lily-of-the-valley	With $\delta^{15}\text{N}$	8	670.12	0.00	1.00	1.00	-326.90
	Without $\delta^{15}\text{N}$	7	706.88	36.76	0.00	1.00	-346.32
Weevils (Herbivores)	Without $\delta^{15}\text{N}$	7	198.22	0.00	0.67	0.67	-91.68
	With $\delta^{15}\text{N}$	8	199.68	1.45	0.33	1.00	-91.28
Isopods (Detritivores)	Without $\delta^{15}\text{N}$	7	427.37	0.00	0.72	0.72	-206.27
	With $\delta^{15}\text{N}$	8	429.31	1.94	0.28	1.00	-206.11
Beetles (Carnivores)	With $\delta^{15}\text{N}$	8	719.43	0.00	0.76	0.76	-351.44
	Without $\delta^{15}\text{N}$	7	721.70	2.27	0.24	1.00	-353.64
Songbirds (feces)	With $\delta^{15}\text{N}$	7	1160.29	0.00	0.56	0.56	-571.75
	Without $\delta^{15}\text{N}$	8	1160.78	0.49	0.44	1.00	-573.08
Songbirds (feathers)	With $\delta^{15}\text{N}$	8	479.67	0.00	0.88	0.88	-231.56
	Without $\delta^{15}\text{N}$	7	483.57	3.89	0.12	1.00	-234.57

Structural Equation Model Outputs

Table C10. Model output from $\delta^{15}\text{N}$ SEM using fecal samples for songbirds. FMI stands for “fraction of missing information”, and RIV is the “relative increase in variance”. Model diagnostics for this model include chi sq = 10.23, df = 5.00, cfi = 0.98, rmsea = 0.10, srmr = 0.05.

Left	Op	Right	Est	SE	T	DF	P-value	FMI	RIV	Lower CI	Upper CI
Beetle $\delta^{15}\text{N}$	~~	Isopod $\delta^{15}\text{N}$	-0.26	0.08	-3.30	434.80	0.00	0.48	0.91	-0.42	-0.11
Bird fecal $\delta^{15}\text{N}$	~	Isopod $\delta^{15}\text{N}$	-0.26	0.16	-1.62	211.19	0.11	0.69	2.17	-0.56	0.05
Beetle $\delta^{15}\text{N}$	~	Wrack biomass	-0.02	0.09	-0.24	382.84	0.82	0.51	1.04	-0.20	0.16
Bird fecal $\delta^{15}\text{N}$	~	Wrack biomass	-0.01	0.09	-0.11	658.55	0.91	0.39	0.63	-0.18	0.16
Soil $\delta^{15}\text{N}$	~	Wrack biomass	0.00	0.07	-0.02	3027.04	0.99	0.18	0.22	-0.14	0.14
Isopod $\delta^{15}\text{N}$	~	Wrack biomass	0.09	0.08	1.12	309.54	0.26	0.57	1.30	-0.06	0.23
Weevil $\delta^{15}\text{N}$	~	Plant $\delta^{15}\text{N}$	0.09	0.18	0.52	486.73	0.61	0.45	0.82	-0.26	0.44
Bird fecal $\delta^{15}\text{N}$	~	Weevil $\delta^{15}\text{N}$	0.10	0.17	0.58	192.13	0.56	0.72	2.54	-0.23	0.43
Plant $\delta^{15}\text{N}$	~~	Plant $\delta^{15}\text{N}$	0.13	0.03	4.97	Inf	0.00	0.00	0.00	0.08	0.18
Beetle $\delta^{15}\text{N}$	~	Weevil $\delta^{15}\text{N}$	0.13	0.13	1.06	419.39	0.29	0.49	0.95	-0.11	0.38
Bird fecal $\delta^{15}\text{N}$	~	Beetle $\delta^{15}\text{N}$	0.18	0.20	0.91	186.38	0.36	0.73	2.69	-0.21	0.58
Isopod $\delta^{15}\text{N}$	~~	Isopod $\delta^{15}\text{N}$	0.29	0.06	4.92	381.27	0.00	0.51	1.04	0.17	0.40
Bird fecal $\delta^{15}\text{N}$	~~	Bird fecal $\delta^{15}\text{N}$	0.36	0.07	4.92	412.74	0.00	0.49	0.96	0.22	0.51
Isopod $\delta^{15}\text{N}$	~	Plant $\delta^{15}\text{N}$	0.38	0.14	2.70	488.96	0.01	0.45	0.82	0.10	0.66
Beetle $\delta^{15}\text{N}$	~~	Beetle $\delta^{15}\text{N}$	0.41	0.13	3.26	416.13	0.00	0.49	0.95	0.16	0.66
Isopod $\delta^{15}\text{N}$	~	Soil $\delta^{15}\text{N}$	0.50	0.14	3.51	380.11	0.00	0.51	1.04	0.22	0.77
Bird fecal $\delta^{15}\text{N}$	~	Plant $\delta^{15}\text{N}$	0.78	0.23	3.44	239.65	0.00	0.64	1.80	0.33	1.22
Weevil $\delta^{15}\text{N}$	~~	Soil $\delta^{15}\text{N}$	0.83	0.25	3.37	1562.14	0.00	0.25	0.34	0.35	1.31
Weevil $\delta^{15}\text{N}$	~~	Weevil $\delta^{15}\text{N}$	0.90	0.33	2.71	780.44	0.01	0.36	0.55	0.25	1.55
Plant $\delta^{15}\text{N}$	~	Soil $\delta^{15}\text{N}$	0.93	0.05	18.04	Inf	0.00	0.00	0.00	0.83	1.03
Beetle $\delta^{15}\text{N}$	~	Isopod $\delta^{15}\text{N}$	0.95	0.17	5.58	483.60	0.00	0.45	0.83	0.62	1.28
Soil $\delta^{15}\text{N}$	~~	Soil $\delta^{15}\text{N}$	1.00	0.20	4.97	Inf	0.00	0.00	0.00	0.61	1.40

Table C11. Model output from $\delta^{13}\text{C}$ SEM using fecal samples for songbirds. FMI stands for “fraction of missing information”, and RIV is the “relative increase in variance”. Model diagnostics for this model include $\chi^2 = 8.75$, $df = 5.00$, $cfi = 0.88$, $rmsea = 0.09$, $srmr = 0.07$.

Left	Op	Right	Est	SE	T	DF	P-value	FMI	RIV	Lower CI	Upper CI
Weevil $\delta^{13}\text{C}$	~~	Soil $\delta^{13}\text{C}$	-0.39	0.17	-2.39	892.23	0.02	0.33	0.50	-0.72	-0.07
Plant $\delta^{13}\text{C}$	~	Soil $\delta^{13}\text{C}$	-0.17	0.15	-1.11	Inf	0.27	0.00	0.00	-0.47	0.13
Soil $\delta^{13}\text{C}$	~	Wrack biomass	-0.11	0.14	-0.79	Inf	0.43	0.06	0.06	-0.38	0.16
Weevil $\delta^{13}\text{C}$	~	Plant $\delta^{13}\text{C}$	-0.10	0.14	-0.71	324.68	0.48	0.55	1.23	-0.38	0.18
Bird fecal $\delta^{13}\text{C}$	~	Weevil $\delta^{13}\text{C}$	-0.09	0.14	-0.64	188.53	0.52	0.73	2.63	-0.37	0.19
Beetle $\delta^{13}\text{C}$	~	Wrack biomass	0.01	0.14	0.03	731.52	0.97	0.37	0.58	-0.28	0.29
Beetle $\delta^{13}\text{C}$	~~	Isopod $\delta^{13}\text{C}$	0.01	0.30	0.02	191.96	0.99	0.72	2.55	-0.59	0.59
Bird fecal $\delta^{13}\text{C}$	~	Beetle $\delta^{13}\text{C}$	0.01	0.16	0.09	207.40	0.93	0.69	2.24	-0.31	0.33
Bird fecal $\delta^{13}\text{C}$	~	Plant $\delta^{13}\text{C}$	0.02	0.16	0.14	170.83	0.89	0.76	3.19	-0.28	0.33
Isopod $\delta^{13}\text{C}$	~	Soil $\delta^{13}\text{C}$	0.03	0.13	0.27	226.58	0.79	0.66	1.95	-0.22	0.28
Isopod $\delta^{13}\text{C}$	~	Wrack biomass	0.07	0.13	0.51	732.06	0.61	0.37	0.58	-0.19	0.32
Bird fecal $\delta^{13}\text{C}$	~	Wrack biomass	0.12	0.13	0.87	504.40	0.38	0.44	0.80	-0.15	0.38
Beetle $\delta^{13}\text{C}$	~	Weevil $\delta^{13}\text{C}$	0.23	0.13	1.68	293.97	0.09	0.58	1.38	-0.04	0.49
Beetle $\delta^{13}\text{C}$	~	Isopod $\delta^{13}\text{C}$	0.41	0.36	1.14	224.12	0.26	0.67	1.98	-0.30	1.12
Isopod $\delta^{13}\text{C}$	~	Plant $\delta^{13}\text{C}$	0.46	0.13	3.55	261.59	0.00	0.62	1.60	0.21	0.72
Bird fecal $\delta^{13}\text{C}$	~	Isopod $\delta^{13}\text{C}$	0.62	0.18	3.49	203.90	0.00	0.70	2.30	0.27	0.96
Isopod $\delta^{13}\text{C}$	~~	Isopod $\delta^{13}\text{C}$	0.71	0.16	4.51	275.26	0.00	0.60	1.50	0.40	1.01
Bird fecal $\delta^{13}\text{C}$	~~	Bird fecal $\delta^{13}\text{C}$	0.75	0.17	4.50	251.87	0.00	0.63	1.68	0.42	1.07
Beetle $\delta^{13}\text{C}$	~~	Beetle $\delta^{13}\text{C}$	0.81	0.56	1.45	805.63	0.15	0.35	0.54	-0.28	1.91
Weevil $\delta^{13}\text{C}$	~~	Weevil $\delta^{13}\text{C}$	0.97	0.22	4.50	297.14	0.00	0.58	1.37	0.55	1.39
Plant $\delta^{13}\text{C}$	~~	Plant $\delta^{13}\text{C}$	0.97	0.21	4.58	Inf	0.00	0.00	0.00	0.56	1.39
Soil $\delta^{13}\text{C}$	~~	Soil $\delta^{13}\text{C}$	0.98	0.21	4.58	Inf	0.00	0.00	0.00	0.56	1.40

Table C12. Model output from $\delta^{15}\text{N}$ SEM using feather samples for songbirds. FMI stands for “fraction of missing information”, and RIV is the “relative increase in variance”. Model diagnostics for this model include chi sq = 7.88, df = 5.00, p-value = 0.16, cfi = 0.99, rmsea = 0.08, srmr = 0.06.

Left	Op	Right	Est	SE	T	DF	P-value	FMI	RIV	Lower CI	Upper CI
Bird feather $\delta^{15}\text{N}$	~	Weevil $\delta^{15}\text{N}$	-0.27	0.23	-1.16	161.06	0.25	0.78	3.63	-0.72	0.18
Beetle $\delta^{15}\text{N}$	~~	Isopod $\delta^{15}\text{N}$	-0.25	0.08	-3.29	559.32	0.00	0.42	0.73	-0.40	-0.10
Bird feather $\delta^{15}\text{N}$	~	Beetle $\delta^{15}\text{N}$	-0.07	0.28	-0.26	199.96	0.80	0.70	2.37	-0.61	0.47
Bird feather $\delta^{15}\text{N}$	~	Isopod $\delta^{15}\text{N}$	-0.02	0.22	-0.07	180.20	0.94	0.74	2.86	-0.44	0.41
Beetle $\delta^{15}\text{N}$	~	Wrack biomass	-0.01	0.09	-0.06	415.61	0.96	0.49	0.95	-0.18	0.17
Soil $\delta^{15}\text{N}$	~	Wrack biomass	0.00	0.07	0.02	3616.00	0.98	0.17	0.20	-0.14	0.14
Bird feather $\delta^{15}\text{N}$	~	Wrack biomass	0.01	0.12	0.11	1073.22	0.91	0.30	0.44	-0.22	0.25
Isopod $\delta^{15}\text{N}$	~	Wrack biomass	0.06	0.08	0.85	302.85	0.40	0.57	1.34	-0.08	0.21
Weevil $\delta^{15}\text{N}$	~	Plant $\delta^{15}\text{N}$	0.08	0.18	0.43	440.78	0.67	0.47	0.90	-0.28	0.44
Plant $\delta^{15}\text{N}$	~~	Plant $\delta^{15}\text{N}$	0.13	0.03	4.93	Inf	0.00	0.00	0.00	0.08	0.18
Beetle $\delta^{15}\text{N}$	~	Weevil $\delta^{15}\text{N}$	0.14	0.13	1.11	527.25	0.27	0.43	0.77	-0.11	0.38
Isopod $\delta^{15}\text{N}$	~~	Isopod $\delta^{15}\text{N}$	0.28	0.06	4.89	473.51	0.00	0.46	0.84	0.17	0.40
Beetle $\delta^{15}\text{N}$	~~	Beetle $\delta^{15}\text{N}$	0.40	0.12	3.35	589.33	0.00	0.41	0.70	0.16	0.63
Isopod $\delta^{15}\text{N}$	~	Plant $\delta^{15}\text{N}$	0.40	0.14	2.80	778.14	0.01	0.36	0.55	0.12	0.68
Isopod $\delta^{15}\text{N}$	~	Soil $\delta^{15}\text{N}$	0.50	0.14	3.43	427.17	0.00	0.48	0.93	0.21	0.78
Bird feather $\delta^{15}\text{N}$	~~	Bird feather $\delta^{15}\text{N}$	0.67	0.14	4.90	560.73	0.00	0.42	0.73	0.40	0.93
Bird feather $\delta^{15}\text{N}$	~	Plant $\delta^{15}\text{N}$	0.81	0.31	2.60	258.05	0.01	0.62	1.63	0.20	1.42
Weevil $\delta^{15}\text{N}$	~~	Soil $\delta^{15}\text{N}$	0.83	0.25	3.33	1663.73	0.00	0.24	0.32	0.34	1.32
Weevil $\delta^{15}\text{N}$	~~	Weevil $\delta^{15}\text{N}$	0.92	0.34	2.68	868.73	0.01	0.34	0.51	0.25	1.59
Plant $\delta^{15}\text{N}$	~	Soil $\delta^{15}\text{N}$	0.93	0.05	17.90	Inf	0.00	0.00	0.00	0.83	1.03
Beetle $\delta^{15}\text{N}$	~	Isopod $\delta^{15}\text{N}$	0.93	0.17	5.65	461.54	0.00	0.46	0.86	0.61	1.25
Soil $\delta^{15}\text{N}$	~~	Soil $\delta^{15}\text{N}$	1.00	0.20	4.93	Inf	0.00	0.00	0.00	0.61	1.40

Table C13. Model output from $\delta^{13}\text{C}$ SEM using feather samples for songbirds. Model diagnostics for this model include chi-sq = 296.71, df = 5.00, cfi = 0.00, rmsea = 0.78, srmr = 0.11. FMI stands for “fraction of missing information”, and RIV is the “relative increase in variance”. Note: this model does not pass diagnostic tests.

Left	Op	Right	Est	SE	T	DF	P-value	FMI	RIV	Lower CI	Upper CI
Weevil $\delta^{13}\text{C}$	~~	Soil $\delta^{13}\text{C}$	-0.41	0.17	-2.46	693.00	0.01	0.38	0.61	-0.73	-0.08
Bird feather $\delta^{13}\text{C}$	~	Weevil $\delta^{13}\text{C}$	-0.36	0.16	-2.30	181.92	0.02	0.74	2.81	-0.67	-0.05
Plant $\delta^{13}\text{C}$	~	Soil $\delta^{13}\text{C}$	-0.17	0.15	-1.13	Inf	0.26	0.00	0.00	-0.46	0.13
Weevil $\delta^{13}\text{C}$	~	Plant $\delta^{13}\text{C}$	-0.14	0.14	-1.00	388.08	0.32	0.51	1.02	-0.42	0.14
Soil $\delta^{13}\text{C}$	~	Wrack biomass	-0.11	0.14	-0.81	Inf	0.42	0.06	0.06	-0.38	0.16
Beetle $\delta^{13}\text{C}$	~~	Isopod $\delta^{13}\text{C}$	-0.09	1.06	-0.09	463.98	0.93	0.46	0.86	-2.16	1.98
Bird feather $\delta^{13}\text{C}$	~	Wrack biomass	-0.09	0.15	-0.60	822.50	0.55	0.35	0.53	-0.38	0.20
Bird feather $\delta^{13}\text{C}$	~	Isopod $\delta^{13}\text{C}$	-0.01	0.19	-0.05	217.00	0.96	0.68	2.08	-0.38	0.36
Beetle $\delta^{13}\text{C}$	~	Wrack biomass	0.01	0.26	0.03	799.89	0.98	0.35	0.54	-0.51	0.52
Isopod $\delta^{13}\text{C}$	~	Wrack biomass	0.07	0.13	0.54	586.75	0.59	0.41	0.70	-0.19	0.33
Bird feather $\delta^{13}\text{C}$	~	Beetle $\delta^{13}\text{C}$	0.08	0.18	0.46	289.80	0.65	0.58	1.41	-0.27	0.43
Isopod $\delta^{13}\text{C}$	~	Soil $\delta^{13}\text{C}$	0.09	0.13	0.67	324.22	0.51	0.55	1.24	-0.17	0.34
Beetle $\delta^{13}\text{C}$	~	Weevil $\delta^{13}\text{C}$	0.25	0.13	1.86	273.30	0.07	0.60	1.51	-0.01	0.50
Bird feather $\delta^{13}\text{C}$	~	Plant $\delta^{13}\text{C}$	0.27	0.17	1.61	332.88	0.11	0.55	1.20	-0.06	0.60
Isopod $\delta^{13}\text{C}$	~	Plant $\delta^{13}\text{C}$	0.42	0.13	3.24	240.12	0.00	0.64	1.79	0.17	0.68
Beetle $\delta^{13}\text{C}$	~	Isopod $\delta^{13}\text{C}$	0.49	1.21	0.40	466.19	0.69	0.46	0.86	-1.88	2.86
Isopod $\delta^{13}\text{C}$	~~	Isopod $\delta^{13}\text{C}$	0.75	0.16	4.59	281.31	0.00	0.59	1.46	0.43	1.07
Bird feather $\delta^{13}\text{C}$	~~	Bird feather $\delta^{13}\text{C}$	0.96	0.21	4.52	179.14	0.00	0.74	2.90	0.54	1.37
Plant $\delta^{13}\text{C}$	~~	Plant $\delta^{13}\text{C}$	0.97	0.21	4.66	Inf	0.00	0.00	0.00	0.56	1.38
Soil $\delta^{13}\text{C}$	~~	Soil $\delta^{13}\text{C}$	0.98	0.21	4.66	Inf	0.00	0.00	0.00	0.57	1.40
Weevil $\delta^{13}\text{C}$	~~	Weevil $\delta^{13}\text{C}$	1.01	0.22	4.58	350.44	0.00	0.53	1.14	0.58	1.44
Beetle $\delta^{13}\text{C}$	~~	Beetle $\delta^{13}\text{C}$	1.22	12.11	0.10	4953.56	0.92	0.14	0.17	-22.51	24.94

Supporting References for Chapter 4

Howes, D., J. Harper, and E. Owens. 1994. Physical Shore-Zone Mapping System for British Columbia. Technical report by the Coastal Task Force of the Resource Inventory Committee (RIC), R. I. C. Secretariat.:97.