



# Equivalent roles of marine subsidies and island characteristics in shaping island bird communities

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## Funding information

Fisheries and Oceans Canada; Mitacs;  
Natural Sciences and Engineering  
Research Council of Canada; Tula  
Foundation

**Handling Editor:** Dr. Gareth Jenkins

## Abstract

**Aim:** 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 examine the relative contributions of island characteristics, marine subsidies, species traits, and species interactions on avian community composition.

**Location:** Central Coast region of British Columbia, Canada.

**Taxon:** Terrestrial breeding birds.

**Methods:** We observed 3610 individuals of 32 bird species on 89 islands that spanned multiple orders of magnitude in area (0.0002–3 km<sup>2</sup>). 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 substrate, 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).

**Results:** Bird species distributions were determined almost equivalently by island biogeographic 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 influence, but no significant effect of any biological trait examined. Additionally, we found evidence that habitat preferences were a more important driver than competitive interactions.

**Main Conclusions:** Although most island biogeographic studies focus only on islands' physical characteristics, we found evidence for an equivalent role of marine subsidy in structuring island bird communities. Our study suggests that for small islands, disentangling the effects of island biogeographic characteristics, marine inputs, and biotic interactions is a useful next step in understanding species distributions.

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## KEYWORDS

avian ecology, biotic interactions, community structure, habitat filter, island biogeography theory, joint species distribution model, marine-derived nutrients, species composition, terrestrial birds

## 1 | 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; Kraft et al., 2015; van der Valk, 1981; 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 these mechanisms on species distributions (Pollock et al., 2014). Although the statistical framework was developed nearly 25 years ago (Chib & 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 (Ovaskainen et al., 2017; Warton et al., 2015).

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 among species of different dispersal abilities, while extinction rates are influenced by island size, an important factor in species' responses to environmental conditions (Valente et al., 2020) and biotic interactions (Bregman et al., 2015). Two species can co-exist on an island if they can tolerate some environmental conditions, if sufficient resources are available to both or if they facilitate each other's presence through mutualism or commensalism. However, they may not overlap on islands that are difficult to disperse to, where they cannot tolerate environmental conditions, or where they exclude one another through competition for shared resources (Cazelles et al., 2016; Zhao et al., 2021). 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 the species that inhabit them.

Spatial subsidies can alter the availability of resources in recipient ecosystems through the movement of nutrients, detritus, and organisms across ecosystems, leading to changes in community dynamics (Anderson et al., 2008; Polis et al., 1997). Marine-derived

nutrients can subsidize terrestrial ecosystems either through passive processes (e.g. the washing up of marine detritus by wind and waves) or active, animal-mediated processes (e.g. egestion, excretion, gametes, or carcass deposition; Subalusky & Post, 2019). The *Subsidized Island Biogeography Hypothesis* (SIB), a modification of TIB, suggests that an input of marine-derived nutrients may affect productivity in a way that facilitates the co-occurrence of more or fewer species on an island than predicted by TIB alone (Anderson & Wait, 2001). The mechanisms behind SIB involve a balance of the processes that determine species distribution patterns. Assuming a unimodal productivity-diversity relationship, SIB predicts that, beyond a certain level of productivity, biotic interactions will outweigh the local environmental conditions (i.e. the habitat filter). In nutrient-poor environments, SIB suggests that nutrient inputs will increase productivity, leading to increased species richness. This phenomenon is observed on Sardinian beaches, where macroalgal deposits have been found to increase species richness in foredune plant communities (Del Vecchio et al., 2017). However, at high levels of productivity, some species may become competitively dominant, leading to a decrease in species diversity. This is seen in salmon-rich streams in British Columbia, Canada, where nutrient-loving plant species dominate riparian communities, effectively decreasing plant species richness (Hocking & Reynolds, 2011). The productivity-diversity relationship 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 an ideal model system for testing predictions about the effects of marine influence on island species distributions.

Since its proposal, the few empirical tests of SIB have yielded mixed support (Barrett et al., 2003; Menegotto et al., 2019; Obrist et al., 2020), suggesting that the effects of marine subsidies on terrestrial ecosystems may be scale- and system-dependent. Marine subsidies may affect aspects of species communities that are not captured if only alpha diversity is evaluated, but the underlying mechanisms 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 (Obrist, Fitzpatrick, et al., 2022). At larger scales, dispersal limitations and environmental filters may have more influence than biotic interactions in structuring species communities. For instance, globally, climate and isolation were found to be the most important drivers of island bird assemblages (Sato et al., 2020). Effects depended on feeding guilds and habitat; 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 are often 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 & Reynolds, 2011; Wagner & Reynolds, 2019). However, there are competitive trade-offs in accessing those higher quality habitats; Pacific wrens living on streams with more salmon-derived nutrients experience more competition 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 to understanding how island species are assembled.

Here, we assess how marine subsidies influence the mechanisms that structure terrestrial breeding bird species communities on 89 islands in the Central Coast region of BC, Canada. These islands are continental—all lie within 10 km of mainland, with many stepping-stone islands in between. No island is further than 1 km from another island large enough to host all species found in our study. Since 14 of the 16 species in this study are migratory in at least a portion of their range (Sheard et al., 2020), we assumed that most species would not be strongly dispersal limited and focused our attention on the habitat filter and biotic interactions. We fit a spatially explicit joint species distribution model (JSDM) to estimate the relative contributions of island characteristics (island area, isolation, and habitat heterogeneity), 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. Although the surveyed islands are too small and topographically simple to host salmon-bearing streams, they are surrounded by a productive ocean and typically receive nutrient subsidies from beach-cast seaweeds (wrack) and animal-mediated deposits 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 but lower species richness on islands with more marine-derived nutrients, an effect that was stronger on smaller islands than larger ones (Obrist et al., 2020). We thus inferred that marine subsidies would impact species distributions, although the mechanism was unclear. This prompted us to generate two hypotheses: (1) the biotic interaction hypothesis—terrestrial breeding bird communities on islands are structured through interspecific competition and (2) the habitat filter hypothesis—species distribute across islands according to their environmental preferences and/or tolerances. This second hypothesis encompasses the possibility that the subsidy mechanism can only be tolerated by certain species; for example, river otters fertilize terrestrial vegetation but simultaneously cause habitat disturbances (Ben-David et al., 1998; Roe et al., 2010). These two hypotheses involve processes that are likely happening in unison, but our analysis intends to evaluate the relative contribution of each. In evaluating these hypotheses, we hope to unite

key theories about island biogeography, spatial subsidies, and species-specific responses to environmental gradients.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

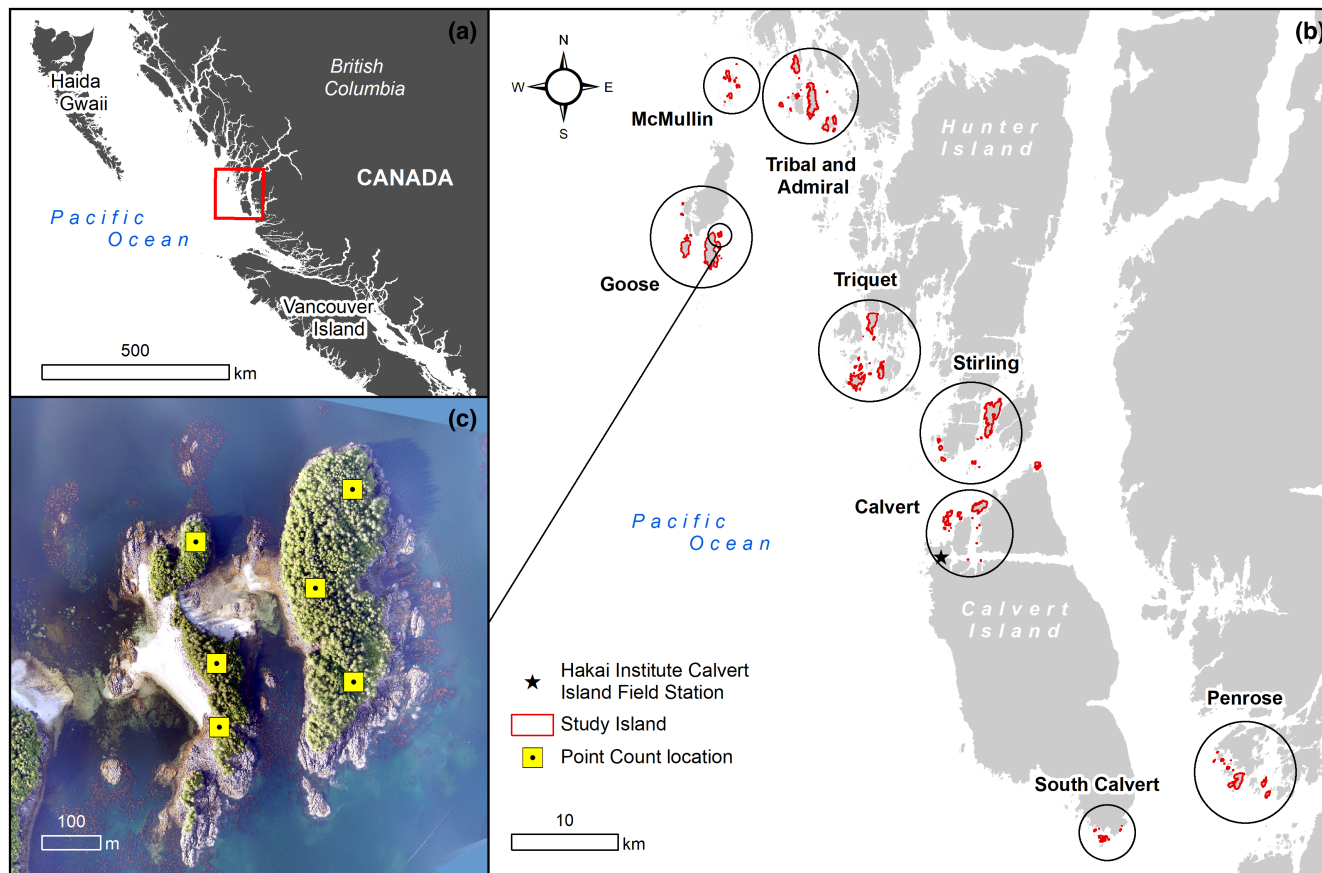
We surveyed terrestrial breeding bird communities on islands in the Central Coast region of BC, Canada (Figure 1a; 51° 26' to 52° 3' N and 127° 41' to 128° 28' W). A table with the observed bird species, including names in both local languages—Haítzaqv!a (Haítzaqv) and 'Uikala (Wuikinuxv)—and relative abundances can be found in Appendix S1: Table S1.1. This region hosts 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).

To select a representative sample of study islands 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 analysis begins with an initial partition of the data, followed by a hierarchical clustering of partitions. The Schwartz Bayesian Criterion (BIC) detected five clusters of island types, ranging from 134 to 432 islands per type (results in Appendix S1: Table S1.2). 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 selected islands up to 3 km<sup>2</sup> for sampling feasibility.

### 2.2 | Field surveys and data collection

#### 2.2.1 | 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. To improve model fit, we also removed two islands (TB04: 124 m<sup>2</sup> and CV05: 3560 m<sup>2</sup>) with no



**FIGURE 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. Projection: NAD\_1983\_BC\_Environment\_Albers.

observations of species abundant enough to include in the model (see 2.3.2), which left 281 locations across 89 islands. The number of point counts on each island was roughly proportional to island size. Chosen locations covered all habitat types on each island. To maintain independence, we placed point counts approximately 250m apart, although they were occasionally closer together on smaller islands. To account for this, and for detectability differences among species, we only retained observations from within 50m of the observer for analysis. We intended to reduce the effects of edge habitat by placing points more than 50m inland, but due to the small size of some of the islands, 56% of point counts occurred within 50m 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 competency to identify birds of BC by sight and sound. Initial comparisons with multiple observers in the field confirmed minimal inter-observer variation. 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).

### 2.2.2 | Nutrient subsidies

As in Obrist et al. (2020), we quantified marine inputs in three ways: (1) by weighing 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.

We measured wrack biomass in three quadrats along two transects at four locations ( $3 \times 2 \times 4$ ) on each island: at the north, east, south, and west-most points. Each transect was 20m 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 et al., 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 marine-derived nitrogen on islands, we took soil samples from four shore-adjacent plots on each island, corresponding to wrack biomass measurement sites. 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 per island. Because  $\delta^{15}\text{N}$  fractionates  $\sim 3.4\%$  per trophic level, this metric 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, feed primarily on fish in the ocean but returning to extensive latrine sites on land where they scent-mark and deposit faeces, 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). Additionally, other subsidy sources likely also impact soil  $\delta^{15}\text{N}$ ; for instance, both marine fog (Weathers & Likens, 1997) and sea spray (Art et al., 1974) could act as abiotic vectors of marine-derived nitrogen.

### 2.2.3 | Other 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 the studied islands are continental, and often close to other large islands (see Figure 1a), we represented 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 m<sup>2</sup>). Further details are in the Supplemental Information (Figure S1.1).

## 2.3 | Statistical analysis

### 2.3.1 | Hierarchical modelling of species communities (HMSC)

To evaluate community structure, we fit a joint species distribution model (JSDM) with Bayesian inference using the ‘Hmsc’ package (v. 3.0.11, Tikhonov et al., 2020) in R (v. 4.1.1, 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. Specifically, the random component calculates remaining occurrences and co-occurrences that are not accounted for by measured covariates at various hierarchical levels, and thus estimates biotic interactions after accounting for potential shared responses to the environment. This framework permits nested, hierarchical spatiotemporal models (Tikhonov et al., 2020). Since this type of model is newly applied, we provide thorough details of the model mechanics and mathematics in the Supplementary Information, closely following steps laid out in Ovaskainen et al. (2017), who developed the framework, and Stark et al. (2020), who applied it to eelgrass epifaunal communities.

### 2.3.2 | Model fit and evaluation

We fit a spatially explicit 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 S1: Figure S1.2). PSRF values close to 1 indicate minimal difference between chains (Brooks & 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<sup>2</sup> value appropriate for Poisson-distributed models and the area under the receiver operating characteristic curve (AUC) (Appendix S1: Table S1.3). Finally, we evaluated the model’s predictive power through three-fold cross validation (Appendix S1: Table S1.4). As a null model comparison, we refit the model without the environmental matrix while maintaining the hierarchical structure of our sampling design, the spatial structure, and the influence of species traits. The co-occurrence results of this model are in Figure S1.3.

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, and ones

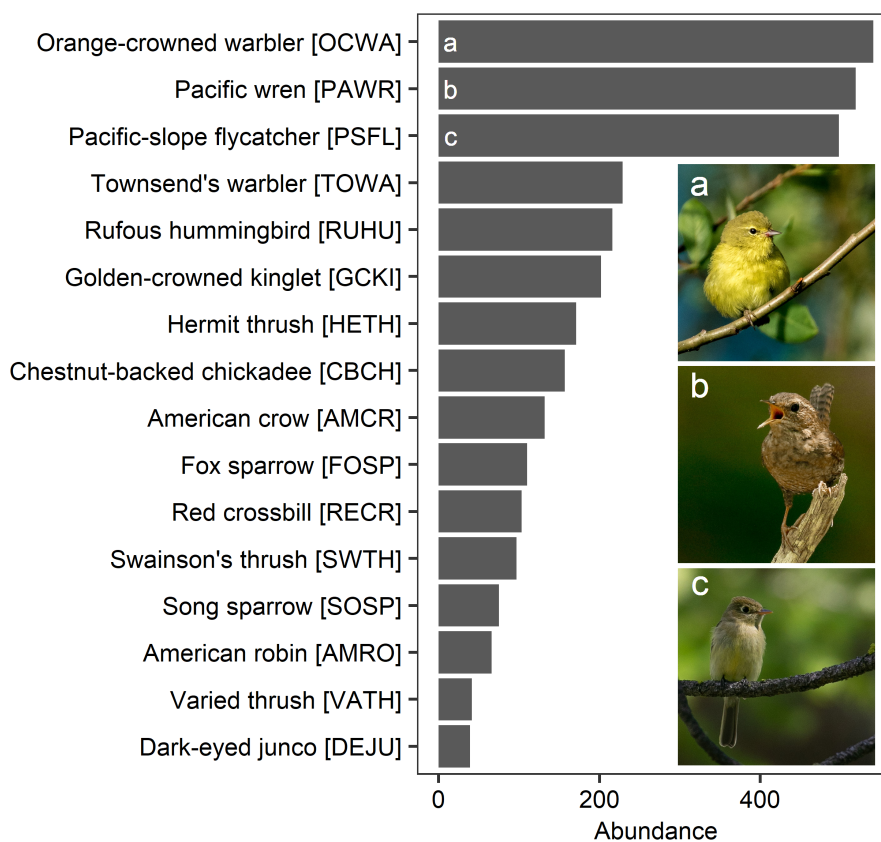
that related to "marine influence": forest-edge soil  $\delta^{15}\text{N}$ , distance to shore, wrack biomass, and proportion of rocky shoreline. We kept separate the interaction between island area and soil  $\delta^{15}\text{N}$ , and survey year. Although we recognize that habitat heterogeneity is not one of the two processes predicted to drive species richness in the classical *Theory of Island Biogeography* (MacArthur & Wilson, 1967), habitat heterogeneity is a fundamental tenet that is deeply intertwined with island biogeography (Kadmon & Allouche, 2007; Ricklefs & Lovette, 1999). As such, we considered it appropriate to examine in direct conjunction with isolation and island area. Variance partitioning also allowed us to calculate the variance explained by each level of random effect that we analysed, 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 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, 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. To confirm lack of competition between members of the same guild, we refit models separately for the insectivore and omnivore feeding guilds (Figure S1.4). Finally, in an additional analysis to confirm whether birds were dispersal limited, we conducted this same analysis once more, including Hand Wing Index as an additional parameter (Sheard et al., 2020). We found no statistical support for this trait (Figure S1.5).

### 2.3.3 | Nestedness and C-scores

To help explain our results, we estimated the degree of nestedness for terrestrial bird communities on the studied islands. Specifically, we calculated the NODF nestedness metric (Nestedness based on Overlap and Decreasing Fill, Almeida-Neto et al., 2008) using the 'vegan' package (v. 2.5.7, Oksanen et al., 2020) in R. Using the 'quasiswap' algorithm, which preserves row and column frequencies as well as marginal totals (Miklós & Podani, 2004), we simulated 5000 random matrices. We used these null matrices to determine whether observed NODF values were higher or lower than expected by chance by calculating standard effect sizes (SES). Specifically, we compared the observed NODF value to those calculated using the null matrices, which represent random assemblage. The formula for SES is [observed-expected]/



**FIGURE 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.

SD (Ulrich & Gotelli, 2012). Communities exhibiting significant nestedness have SES values of greater than 1.96, while those with less nestedness than expected by chance (i.e. anti-nested) have values less than -1.96 (Matthews et al., 2015; Ulrich & Gotelli, 2012).

We also assessed species communities using the C-score metric to check for potential competitive interactions. C-score is an index of how frequently species occur together at the same site (Stone & Roberts, 1992). As with NODF, we used the 'quasiswap' algorithm in the 'vegan' package in R to simulate 5000 random communities to determine whether our observed C-score was higher or lower than expected by chance. In this case, SES values of greater than 2 indicate significantly less co-occurrence than expected, while values of less than -2 indicate more co-occurrence than suggested by chance (Ulrich & Gotelli, 2007).

### 3 | 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 0.02, and best for fox sparrow with a pseudo- $R^2$  of 0.61. Pseudo- $R^2$  for all species can be found in Table S1.3.

#### 3.1 | Variance partitioning

Variance partitioning allowed us to obtain estimates for variance explained by parameters relating to the habitat filter and to biotic interactions (Figure 3, Figure S1.6). Variance explained by the habitat filter summed up to 60.8% and included the effects of marine influence (24.8%), island characteristics (23.5%), the interaction between island area and forest-edge soil  $\delta^{15}\text{N}$  (7.1%), and year (5.4%). Variance explained by biotic interactions added up to roughly half that explained by the habitat filter: 29.9%, including co-occurrences at the plot level (14.1%) and at the island level (15.8%). Finally, 9.3% of variance was also explained by a spatial parameter which accounted for the longitude and latitude of the point count at which each bird was observed.

There was considerable variation in the amount of variance explained by each partition of parameters for each species. For example, the influence of marine inputs ranged substantially from species

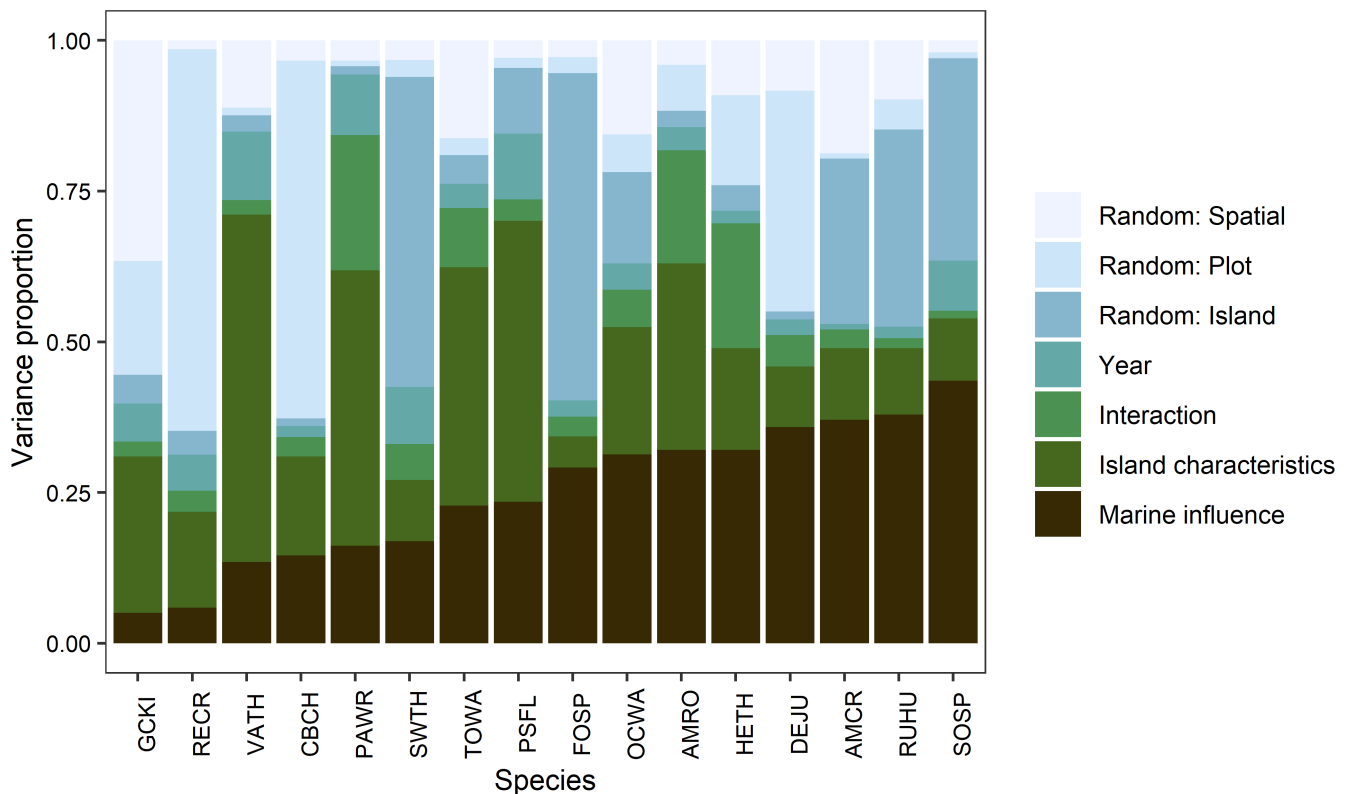


FIGURE 3 Proportions of variance explained by different grouping variables. The "marine influence" grouping includes wrack biomass,  $\delta^{15}\text{N}$  of the soil at the edge of the island, distance to shore, and the proportion of shoreline that is rocky, while "island characteristics" includes 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: Plot" term is the amount of variance explained by the random effect of point count ID—that is, 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—that is, 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.

to species, with 44% of the variation explained for song sparrows but only 5% for golden-crowned kinglets. Likewise, the island biogeography parameters (i.e. island area, isolation, and habitat heterogeneity) collectively explained 58% of variation in abundance of varied thrushes but only 5% for fox sparrows. Although 7.1% of overall variance was explained by the interaction between island area and forest-edge soil  $\delta^{15}\text{N}$ , this estimate ranged from under 2% for rufous hummingbirds and song sparrows to around 22% for Pacific wrens and hermit thrushes.

### 3.2 | Environmental filtering

As expected, species showed variable responses to environmental parameters, although we did find some overarching patterns (Figure 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, including 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.

### 3.3 | 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 S1.7).

### 3.4 | Co-occurrence patterns

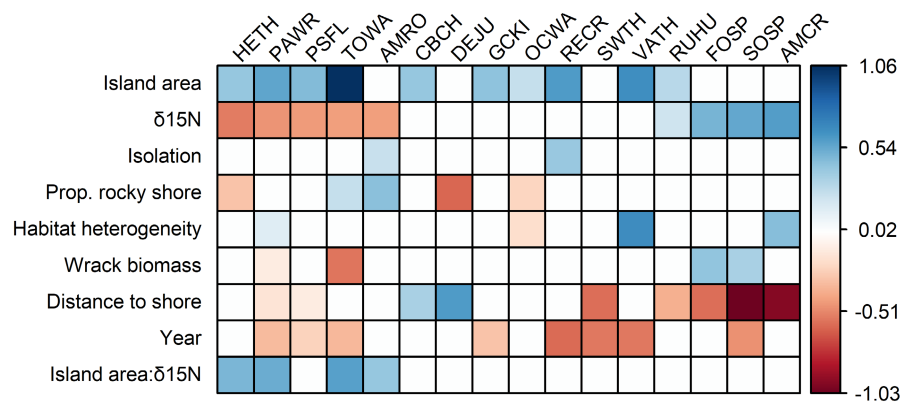
Although generally weak, we found evidence of a greater number of negative species associations at the plot level, and stronger, more positive associations at the island level (Figure 5). Dark-eyed junco was the only species to have negative associations with other species at the island scale. The median interaction value was  $0.06 \pm 0.39$  (SD) for plot level interactions,  $0.42 \pm 0.39$  for island level interactions and  $0.01 \pm 0.50$  at the coordinate level.

### 3.5 | Nestedness and C-scores

Without accounting for habitat-related parameters, bird communities were significantly anti-nested, meaning that they were less nested than expected if they were assembled by chance alone (NODF: 62.3, SES: -2.52). Similarly, species in these communities co-occurred significantly less often than expected by chance (C-score: 178.2, SES: 5.17).

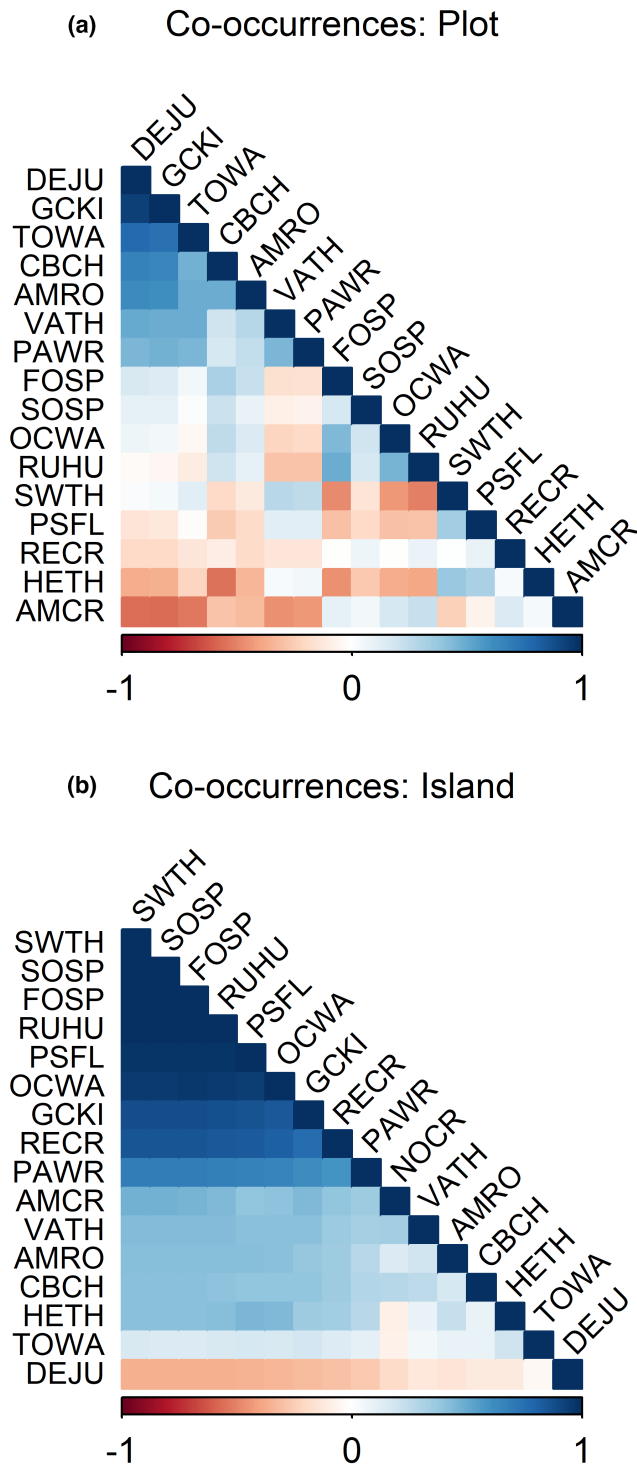
## 4 | DISCUSSION

Our field study aimed to examine the relative influence of the habitat filter and biotic interactions on the distribution of terrestrial breeding birds on 89 islands in the Central Coast region of British Columbia, Canada. We generated hypotheses about the relative



**FIGURE 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.





**FIGURE 5** 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 2](#).

importance of two simultaneously-occurring ecological processes: first, the biotic interaction hypothesis—that competition among species shapes island bird communities—and second, the habitat

filter hypothesis—that species distribute across islands according to their environmental preferences and tolerances. Using variance partitioning, we found evidence supporting our habitat filter hypothesis. Parameters related to the habitat filter explained approximately twice as much variance in species distributions compared to biotic interactions. Furthermore, among parameters relating to the habitat filter, marine influence and island characteristics were similarly important in predicting bird assemblages. When examining biotic interactions more closely, we observed more positive co-occurrences at the island scale, and more negative co-occurrences on the local plot scale. However, the modelled species-specific responses did not show evidence that these local negative co-occurrences were due to competition for marine-derived nutrients. Thus, our findings suggest that marine subsidies affected the distribution of bird species on the studied islands through environmental filtering to a greater degree than biotic interactions.

Using variance partitioning ([Figure 3](#)), we evaluated how different parameters related to the habitat filter and biotic interactions contribute to the explained variance in species distributions. We found evidence to support our second hypothesis, that species distributions on these islands were primarily driven by habitat preferences and tolerances. 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 roughly one half of the total variance explained by environmental parameters (60.8%). This final number includes the effect of year, which may capture annual variations in weather and ocean conditions that were not explicitly measured. Our findings echo those from 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). Similarly, a study on Galápagos island plant communities found the habitat filter more important than both biotic interactions and dispersal limitations (Carvajal-Endara et al., 2017). In contrast, competitive interactions have been cited as the primary drivers of bird communities in Amazonian habitat fragments (Bregman et al., 2015). In this case, the authors found stronger evidence of competition in smaller, degraded, and more isolated forest fragments; however, Itescu (2019) warns that patterns observed on island analogues are not always relevant for true island systems. Moreover, one empirical test on Eastern Nearctic islands found that neither the habitat filter nor biotic interactions predicted snake species' presences as well as random draws from the mainland species pool (Burbrink et al., 2015), providing support to theories that species distributions are best explained by randomized null models (Connor & Simberloff, 1979; Gotelli & Graves, 1996; Hubbell, 2001). Our study provides evidence that bird community structure varies across small islands with different environmental characteristics. By shedding light on the relative importance of these characteristics and biotic interactions, our research contributes to a better understanding of the factors driving species distributions on islands more generally.

Upon closer examination of the components making up the habitat filter, we found a substantial effect of marine influence on bird

species distributions in these island ecosystems. Variance partitioning showed that marine influence accounted for as much variation in bird species distributions as the more classically studied island characteristics (i.e. island size, isolation, and habitat heterogeneity) on these islands. On average, marine influence explained 24.8% of the variation in species distributions, while commonly studied island characteristics explained 23.5%. This high degree of marine influence suggests that nutrient inputs from the ocean can be particularly important on small islands with high perimeter-to-area ratios, such as those examined in this study (i.e.  $<3\text{ km}^2$ , Anderson & Wait, 2001). While previous studies have examined how the assemblage of island communities is influenced by various factors, including 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 & Phillimore, 2011), the effects of spatial subsidies had not been explicitly tested prior to this study (although their influence had been anticipated—for example Jonsson et al., 2009). A few studies have investigated the influence of marine subsidies on island alpha diversity (Barrett et al., 2003; Menegotto et al., 2019; Obrist et al., 2020), but the results have been highly variable, likely due to the context-dependent effects of spatial subsidies (Piovia-Scott et al., 2019; Spiller et al., 2010; Subalusky & Post, 2019). Our study provides an explanation for this variability, as our results support the interpretation that variation in species communities 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), our study suggests that species responses to their physical environments may be driven by variability in marine influence. Different environmental conditions due to marine influences promote the establishment and persistence of distinct groups of species, which may potentially also explain variability in alpha diversity. Overall, our study emphasizes the importance of considering the influence of the adjacent marine ecosystem, particularly on small islands, and contributes to our understanding of factors structuring species communities in heterogeneous environments.

We found that the amount of variance explained by different environmental parameters varied among species according to their natural histories. For example, marine influence better explained the occurrence of fox sparrows and song sparrows, two species commonly seen feeding intertidally. On the other hand, island characteristics better predicted the occurrences of forest-specialist birds, including varied thrushes, Pacific-slope flycatchers, and Pacific wrens. Of the studied species, four showed a preference for islands with higher marine-derived nitrogen in the soil (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). For four of these species, a positive interaction between marine-derived nitrogen and island size suggests that species avoid smaller islands with higher amounts of marine-derived nitrogen and are more common on larger islands with lower amounts of marine-derived nitrogen. Marine-derived nitrogen is likely a good

indicator of river otter activity on these islands. Their latrines create major onboarding spots for marine-derived nutrients that can flow in many directions through different processes, impacting island food webs (Ben-David et al., 1998; Obrist, Hanly, et al., 2022). In addition to creating hotspots of marine flow, river otter behaviour can also impact habitats through smaller, localized disturbances to coastal vegetation and soils. We speculate that some species with negative associations likely could not tolerate the edge-type habitats created by river otter disturbances. Indeed, 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). Furthermore, we found evidence for strong interannual variability for 7 of the 16 species examined. 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). 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 & Knops, 2001). In general, the observed species responses were in line with our expectations based on species' natural histories.

Taking environmental parameters into account, we examined the influence of biotic interactions on species distributions. We found a scale-dependent difference in the direction of species responses; negative co-occurrences were more common at the plot scale, while positive co-occurrences were more common at the island scale. Recent hypotheses suggest that competition occurs at smaller spatial scales, while positive interactions persist across scales (Araújo & Rozenfeld, 2014; Mod et al., 2020), so one possible explanation for this finding is that species compete for the same resources (e.g. subsidized habitats) locally but have shared broader habitat requirements (König et al., 2021; Ovasainen et al., 2016). However, we found no negative co-occurrences at the local scale (i.e. plot level, Figure 5a) between species that prefer islands with more marine-derived nitrogen in the soil (i.e. fox sparrows, song sparrows, American crows and rufous hummingbirds, Figure 4). Despite nitrogen limitation on the studied islands (Miller, 2019), species did not appear to out-compete one another for access to habitats with more marine-derived nitrogen; however, our analysis was not able to rule out the possibility of competition between sympatric species. Alternatively, given the relatively low densities of birds observed on these islands overall, we speculate that certain species are simply able to tolerate local environmental changes caused by river otters (e.g. major vegetation disturbances; Ben-David et al., 1998; Roe et al., 2010), while others are not. At the island scale, we found mainly positive species interactions. One possible explanation is that species assembled according to a nested pattern, that is that species in species-poor areas are simply subsets of those found in species-rich areas (Patterson & 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; Zurell et al. (2020) caution that positive co-occurrences are over-represented and more often indicate missed environmental parameters than true facilitation between species.

The importance of marine influence in our study may have been magnified by the small size of islands we examined. Indeed, the *Subsidized Island Biogeography Hypothesis* (SIB) posits that marine inputs have higher per-unit-area effects on smaller islands due to their higher perimeter-to-area ratios (Anderson & Wait, 2001). Given our interest in the influence of marine inputs, as well as for sampling feasibility, we only surveyed small islands (<3 km<sup>2</sup>) in this region of approximately 1500 islands. As such, the results from our study are only directly relevant for small, coastal islets and islands. Although much can be learned from studying larger islands and mainland systems, by focusing on small islands in this study, we were able to uncover some of the more nuanced effects of nutrient subsidies on terrestrial bird communities. In more complex systems, it can be difficult to discern the impact of multiple resources on many trophic entities, especially when resources arrive at different points in time and space (Anderson et al., 2008). Future multitrophic studies might shed light on inter-taxon species interactions that could drive patterns in species distributions on islands. For instance, perhaps birds, as mobile, upper-level consumers, simply reflect the changes in underlying plant, microbe, and invertebrate communities, which may demonstrate both stronger responses to nutrient fluxes and to parameters limiting dispersal (Subalusky & Post, 2019).

In conclusion, we found evidence that the habitat filter was more important than biotic interactions in determining the distribution of terrestrial breeding birds on small islands in British Columbia, Canada. Notably, our study demonstrates the importance of considering cross-boundary nutrient dynamics when evaluating species communities (Loreau et al., 2003), particularly on small islands (Anderson & Wait, 2001). We found that marine influence and island characteristics nearly equivalently described terrestrial breeding bird community assemblages on small temperate islands. Although the results and inferences of this study are primarily relevant to small, coastal islands and islets, obtaining such nuanced results can aid our understanding of both processes driving species distributions more generally, and of the importance of the consideration of the surrounding media in both island and island-analogue systems.

#### ACKNOWLEDGEMENTS

We are grateful to the Haítzaqv and Wuikinuxv First Nations for their support in conducting this research. We also thank many field and laboratory technicians for their hard work on the '100 Islands' project, particularly the bird crew: Kate Prince, Ian Thomas, Janine McManus, Rob White, Blair Dudeck and Julian Heavyside. Thank you also to the Hakai Institute staff at the Calvert Island Ecological Field Station for field and laboratory support, and to Carl Humchitt for his guidance and knowledge both on the water and on land. In addition, we thank members of the Reynolds lab and the Earth to Ocean Research Group, as well as Dr. David Green, Dr. Leithen M'Gonigle and Dr. Richard Johnston for their input and statistical advice.

This work was supported by the Hakai Institute (Tula Foundation), MITACS, NSERC Discovery Grants to J.D.R., B.M.S. and C.T.D., NSERC CGS-M and CGS-D grants to DSO, and a Fisheries and Oceans Canada Aquatic Science Supplement to DSO. This study was conducted with permission from both Haítzaqv (Heiltsuk) and Wuikinuxv governments. It was also conducted in British Columbia Provincial Protected Areas within the Hakai Lúxvbális Conservancy, the Calvert Island Conservancy, the Outer Central Coast Islands Conservancy, the Penrose Island Marine Provincial Park and the Penrose-Ripon Conservancy under BC Parks Permit no. 107190. Avian point count surveys were conducted under SFU Animal Care Permit no. 1165B-15.

#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

Data for this study are publicly available from the Hakai Institute Public Data Forum at <https://doi.org/10.21966/10tk-4956>. Code to rerun analysis is available at <http://doi.org/10.5281/zenodo.8475>.

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## BIOSKETCH

**Debora S. Obrist** is broadly interested in the effects of marine-derived nutrients on terrestrial ecosystems. This study was conducted as part of her PhD thesis work at Simon Fraser University on the effects of marine subsidies on avian island biogeography and trophic ecology in the Central Coast region of British Columbia. She and co-authors are part of the Hakai Institute's 100 Islands Project (<https://hakai.org>), a collaborative effort to answer questions about how island biogeography and marine subsidies affect ecological patterns on islands.

**Author contributions:** D.S.O, C.T.D., B.M.S. and J.D.R. conceived the ideas for the study. D.S.O., J.C.K., O.T.F., S.B.W., W.N. and L.Y.R. collected the data. D.S.O. and P.J.H. conducted statistical analyses. D.S.O. wrote the first draft of the manuscript. All authors contributed substantially to editing and revising the manuscript.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Obrist, D. S., Hanly, P. J., Kennedy, J. C., Fitzpatrick, O. T., Wickham, S. B., Nijland, W., Reshitnyk, L. Y., Darimont, C. T., Starzomski, B. M., & Reynolds, J. D. (2024). Equivalent roles of marine subsidies and island characteristics in shaping island bird communities. *Journal of Biogeography*, 51, 40–53. <https://doi.org/10.1111/jbi.14728>