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Nestedness and Modularity of Avian Metacommunities Across Gradients of Chesapeake Bay Island Characteristics

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NESTEDNESS AND MODULARITY OF AVIAN METACOMMUNITIES ACROSS

GRADIENTS OF CHESAPEAKE BAY ISLAND CHARACTERISTICS

by

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ABSTRACT

NESTEDNESS AND MODULARITY OF AVIAN METACOMMUNITIES ACROSS ENVIRONMENTAL GRADIENTS OF CHESAPEAKE BAY ISLANDS, VIRGINIA

Grant Walter Bowers
Old Dominion University, 2022
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Islands are not only great models for understanding the ways in which communities are linked by the dispersal of their members to form metacommunities, but are of particular interest to conservationists. One important aspect of metacommunity structure is the degree of nestedness—whether or not less speciose communities are perfect subsets of more speciose communities. Another important metric of metacommunity structure is modularity—the degree to which communities belong to modules composed of other communities that share the same species but have little species overlap with communities from different modules. Environmental gradients have received insufficient attention as predictors of metacommunity nestedness and modularity. I examined bird metacommunities on small islands within the Chesapeake Bay, USA. These islands serve as natural laboratories, representing a gradient of sizes, degrees of isolation, and variation in habitat type. My objective was to determine which, if any, of these variables best predicted patterns of nestedness and modularity. Presence-absence data were collected from thirteen islands in the southern end of Chesapeake Bay from June to August of 2021. Three matrices were developed (ranked by island size, isolation, and habitat type, respectively) and evaluated for both nestedness and modularity. Island size produced the greatest degree of nestedness, even when accounting for variation in species richness across islands.

None of the island characteristics exhibited patterns of modularity. Weighted matrices were developed based on the naturally uneven distributions of islands across these gradients and produced similar results to the non-weighted matrices. These results suggest that, on a broad scale, avian metacommunities across small (<10,000 ha), nearshore (<10 km) islands will display a nested structure along a gradient of island size, meaning the largest islands contain representatives from most species in the system, and smaller islands are largely redundant in species composition.

My thesis is dedicated to my parents, who encouraged my ambitions. It may be bittersweet to no longer be able to give me the answers to some of my questions, but I hope you know you have succeeded in teaching me to find them on my own.

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

BACKGROUND

Broadly speaking, the term "community" refers to a group of organisms of different species that live together in space and time, and community ecologists seek to understand the processes that create and shape these communities and the patterns therein (Vellend 2010). Much effort has been made to use empirical studies of environmental manipulation to painstakingly tease apart these processes within individual communities, but the more specific the conclusions, the more likely they will be unique to that community and fail to apply elsewhere (Lawton 1999). As such, I sought to find patterns that were precise enough to be predictive, yet general enough to be applied to more than a single system. In doing so, I drew upon several different fields and concepts of ecology and mathematics—some that have a long history, and some that represent newer insights.

ISLAND BIOGEOGRAPHY

The history of community ecology and island biogeography are closely intertwined (Santos et al. 2016). As far back as Alfred Wallace's (1863) descriptions of and explanations for Southeast Asian biogeography, researchers have been attempting to explain why islands possess the flora and fauna they do, and the processes underlying the observed patterns of distribution. The MacArthur-Wilson model of island biogeography is one of the foundations of today's studies of island biogeography. It is based on observations of the effects of island area and island distance on species richness (MacArthur and Wilson 1963). The distance of an island from the mainland determines the rate at which species arrive on the island, and the size of an island determines the rate at which species on the island go extinct. Species richness would tend towards the

equilibrium point between the rates of immigration and extinction. Despite being a deliberate oversimplification, the use of island area and distance alone to predict characteristics of an island's biota has been supported by experimental evidence in the years following (Simberloff and Wilson 1969). One of the model's main implications is that a larger island would harbor greater species richness than multiple smaller islands that represent the same total area when combined. This principle would eventually become the center of a debate known by the acronym SLOSS ("Single Large or Several Small") during the 1970s and 1980s (Tjørve 2010). The debate was concerned primarily with the design of natural reserves. However, the MacArthur-Wilson model ignored too many biological phenomena (e.g., differences between species, colonization among islands, etc.) to gain support as a tool for reserve design. As Simberloff and Abele (1976) point out, even within birds, differences in dispersal behavior between tropical and arctic species mean that a having a larger reserve is best for the former but having several smaller reserves is better suited to the latter. More recent iterations of the island biogeography model have incorporated more ecological and evolutionary phenomena, especially differences among species such as competitiveness and dispersal ability (Lomolino 2000a; Santos et al. 2016).

METACOMMUNITY ECOLOGY

The term metacommunity was originally used to describe a collection of similar habitat patches, each with their own similar communities (Wilson 1992). Leibold et al. (2004) described a metacommunity as a group of similar communities linked by the dispersal of some of their members and argued that the concept can explain phenomena that are contrary to what one would expect when studying communities at the local scale alone. Many authors had been exploring similar concepts for decades, converging on several different models that Leibold et al. (2004) would identify as four paradigms of metacommunity dynamics. The most basic of the

four is the neutral paradigm, which shares ties with the work of Hubbell (2001) on neutral theory. All patches are assumed to be identical, and all species are competitively equivalent. Species rise and decline through a slow, random walk. Diversity in the metacommunity persists only because the path to equilibrium (i.e., extinction of all but one species) is so slow that it is comparable to the rate of speciation, which offsets the loss of species. Within an individual patch, species can go extinct much more quickly, but can be rescued by random immigration from other patches (Leibold et al. 2004).

The patch dynamics paradigm consists of identical patches, but the species are distinct, and vary in their relative competitive abilities. In the simplest incarnation of this model, species coexist because of the competition-colonization tradeoff; one species outcompetes the other when both are present, but the other species is better at reaching areas where neither are present, giving it time to increase in numbers before the slower, more competitive species arrives in the patch (Levins and Culver 1971). If patches routinely become devoid of the more competitive species by either stochastic or deterministic processes, then there will always be enough patches for the colonizing species to occupy free of competition at any given time. Subsequent studies have incorporated tradeoffs beyond competition and colonization, such as tradeoffs between different colonization stages, into this model (Yu and Wilson 2001).

The species-sorting paradigm incorporates variation in patch characteristics in conjunction with variation in species characteristics (Leibold et al. 2004). As a result, species settle in the patches that best suit them, maintaining diversity without the need for turnover or speciation. The implication is that the dispersal ability of all species is high enough that species have colonized all patches in which they can persist. This paradigm reflects the long history of study into how

heterogeneous abiotic factors and species niche differences influence the species compositions of patchy environments (MacArthur 1958; Whittaker 1962; Tilman 1982).

When species disperse enough to be consistently found in patches where self-sustaining populations *cannot* persist, the metacommunity is instead described by the mass effects paradigm (Leibold et al. 2004). Patches and species characteristics are heterogeneous, and species live in patches that best suit them. However, species can disperse among patches so readily that there is a consistent population of each species beyond the boundaries of their ideal patch. These populations can be entirely sustained by dispersal from better patches, with the members of the populations themselves failing to reproduce enough to maintain their numbers without this influx (Mouquet and Loreau 2003).

Leibold et al. (2004) explicitly states that these paradigms should be synthesized, rather than viewed as discrete categories to divide up real-world metacommunities in the future. However, many subsequent authors took away the latter impression, and this problem compounded over time (Brown et al. 2017). Logue et al. (2011) argued that these "big four" paradigms were noncomprehensive regions of a continuum defined by factors like species similarity, patch heterogeneity, and dispersal ability, on which every metacommunity would occupy a unique point.

STRUCTURAL PROPERTIES OF METACOMMUNITIES

The ways in which species compositions differ between communities is a major component of understanding metacommunity dynamics (Leibold and Mikkelson 2002; Presley et al. 2012). When moving among communities, one might ask whether species drop off without replacement or undergo turnover? Are the changes evenly dispersed, randomly dispersed, or clumped?

Questions like these are of great academic interest and particular conservation relevance. When prioritizing areas for conservation, it is useful to understand which areas not only have the highest species richness, but also which areas contribute the most gamma diversity (the total diversity across all communities in a metacommunity) by harboring more unique species not found elsewhere (Tjørve 2010).

PRESENCE-ABSENCE MATRIX

To examine metacommunity structure, one must determine species composition of each community. A common way to organize this information is with a presence-absence matrix, where the presence or absence of a species in the community is indicated by either a 1 or a 0, respectively. These can also be displayed as a filled-in cell or a blank cell for graphical purposes. In this context, the matrices are bipartite, meaning that the rows and columns represent two different things (in this case, the communities and the species, respectively) (Leibold and Mikkelson 2002). This is unlike a unipartite matrix, in which the rows and columns both represent the same species list, and the 1s represent co-occurrence or some other kind of interaction. Unipartite matrices are more often used when studying the properties of interactions between species rather than of cooccurrence (Bascompte et al. 2003).

NESTEDNESS

In the context of community ecology, community nestedness is the degree to which the less-speciose communities of a system are proper subsets of the more-speciose communities (Patterson and Atmar 1986). Community nestedness is distinct from the concept of "species nestedness", often considered a property of a unipartite matrix, and better defined as the degree to which a species with few interactions will exclusively interact with the species with the most

interactions (Bascompte et al. 2003). Although the distinction between these concepts of nestedness may appear similar, the subtle distinction is important.

Patterson and Atmar's (1986) interpretation of nestedness involved ordering communities by species richness, but one could alternatively examine nestedness of communities ranked by other properties such as elevation (Presley et al. 2012). The implication of nestedness in a metacommunity is that there is variation in habitat quality and species versatility (i.e. whether the species are "specialists" or "generalists") in the system (Ulrich et al. 2009). Some habitats are of lesser quality, such that only a subset of generalists can be found within patches as patch quality decreases. These generalists can also survive in communities that are speciose, high-quality, competitive patches, that contain representatives of all species found in the broader metacommunity. Within nested communities, the less-speciose patches are largely redundant (Figure 1a), and may become even more redundant over time as all but the generalists go extinct (Patterson and Atmar 1986). The fact that less-rich patches will often contain nothing but generalists that are also present in the richer patches has important implications for conservation. Highly nested metacommunities are best suited to the "Single Large reserve" extreme of the SLOSS debate (Wright and Reeves 1992).

MODULARITY

Modularity is the degree to which the species within a presence-absence matrix fall into "modules". In this context, a module is a subset of species that often co-occur with each other (Figure 1b) and rarely co-occur with species outside the module (Borthagaray et al. 2014). In the context of metacommunity composition, this pattern has also been described as turnover with clumped boundaries, because when comparing different communities, species will be replaced by other species, and those replacements will happen all at once rather than randomly or in an
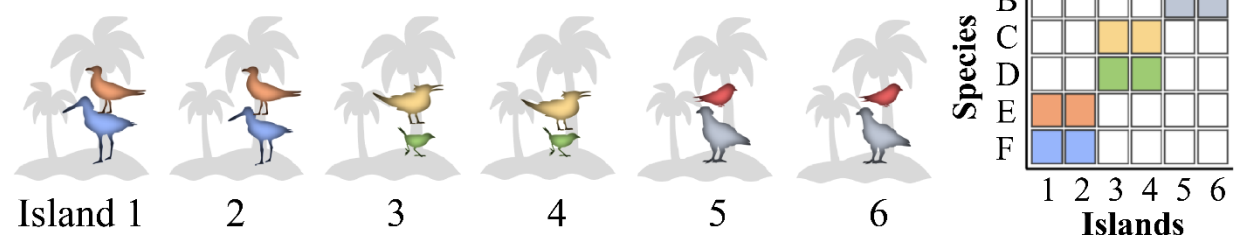
Figure 1: Examples of a perfectly nested distribution (a), and a perfectly modular distribution (b), using bird species on islands as an example.

overdispersed fashion (Leibold and Mikkelson 2002). As with nestedness, modularity can be used in unipartite matrices involving interactions (Newman 2006; Zhao et al. 2018), but the term can also apply to a bipartite matrix (Borthagaray et al. 2014).

High modularity suggests the existence of discrete, "Clementsian" communities, in which species ranges overlap almost exclusively with the ranges of other members of their community. This may be the result of a species pool that has coevolved to depend on one another and have similar habitat preferences (Clements 1916). From a conservation perspective, high disparity between community species composition requires a much larger number of communities to be protected than would a simple nested metacommunity in which the most species-rich patch encompasses all of the metacommunity's diversity (Angeler 2013). However, unlike a metacommunity composed of disparate but non-modular species compositions, highly modular

metacommunities can provide a built-in roadmap to guide conservation efforts. In a perfectly modular system, only one patch from each "module" need be preserved to preserve the full diversity of the metacommunity, because all patches within each module have identical species compositions.

AVIAN ECOLOGY

In a particular area, some birds will be resident, and some will be seasonal. Some birds will use the area ephemerally during migration, and other birds will visit exclusively to breed (Hardaway et al. 2002). Thus, avifaunal land use can be complex to assess. Moreover, many birds have the ability to disperse over large distances compared with the majority of terrestrial fauna (Wang et al. 2010). Even some small passerine birds can migrate huge distances annually (Dunn et al. 2020). This high dispersal ability makes them adept colonizers of new habitat within short periods of time, especially in the case of sea-going birds (Erwin et al. 2007). Additionally, contrary to the way patch dynamics are often modeled, "extinction" from an isolated patch is not necessarily the result of the death of the local population as is assumed by MacArthur and Wilson (1963) and Levins and Culver (1971) but could instead result from the deliberate choice to leave the patch. Entire flocks of birds can come and go among patches on a daily basis (pers. obs.).

THE CHESAPEAKE BAY ISLANDS

The Chesapeake Bay is an estuary located within Maryland and Virginia, USA. It is over 300 km in length, and ranges from 5 to 50 km in width (Wrayf et al. 1995). The Bay includes many small islands, especially in the wider southern end.

History and Geology

The Chesapeake Bay's formation was pre-empted by a meteor impact during the late Eocene (~35 Ma), when sea levels were such that the entire region was underwater. The massive crater formed what would become the Bay's southern end (Kenkmann et al. 2009). When sea levels fell sufficiently in later epochs, it exposed the Delmarva peninsula that defines the eastern border of the Bay. During the ice ages of the last several million years, the cyclical pattern of glacial and interglacial periods (in which the sea level falls and rises) caused the region to alternate between existing as a floodplain surrounding the lower Susquehanna River and existing as a large, shallow bay, respectively (Hobbs 2004). The Earth has been in the interglacial phase for the last 10,000 years or so (Dergachev 2015), and this has resulted in the Bay as it exists today.

In modern times, the Bay is undergoing more changes because of sea level rise (Boon et al. 2010). Some of this is the result of the global trend of sea level rise, but some of it is the result of the natural subsidence of the continental crust in the region (Engelhart et al. 2009). This creates an additional, relative sea level rise on top of global trends, meaning that the Bay region is experiencing roughly twice the global mean sea level rise (Boon et al. 2010).

As a result of this change, many of the islands in the Chesapeake Bay have lost substantial amounts of land. Many inhabited islands were abandoned, and islands that were once hundreds of hectares in area have lost more than half of their landmass or have submerged entirely (Erwin et al. 2011).

Biota

The islands of the Chesapeake Bay consist mainly of marshes, and sometimes upland areas containing sand dunes, grasses, shrubs, and even forests (Wrayf et al. 1995, pers. obs.). These

islands were presumably connected to the mainland during the last glacial period but were then isolated when sea levels rose in the last 10,000 years (Boon et al. 2010, Dergachev 2015), so it seems unlikely that any speciation events have occurred in this short amount of time (Johnson and Cicero 2004), especially considering that the ease at which species can move between them compared to more isolated islands would hinder speciation (Claramunt et al. 2012). As a result, the species present on the islands likely represent a subset of the regional species pool.

Of the various organisms inhabiting the islands, the birds that use the islands as breeding grounds have received the most attention by researchers and conservationists (Keller 1992; Erwin and Beck 2007; Erwin et al. 2007, 2011). Breeding grounds can serve as source populations for the surrounding area and, in the case of migrating species, ecosystems across entire regions can be influenced by birds that would be absent if not for the existence of breeding grounds or migration stopovers many hundreds of kilometers away (Higuchi 2012). Meanwhile, for species that do not seek out the islands for breeding or as migration stopovers, the islands may merely represent a tiny percentage of the total habitat available to them and offer no obvious benefits over mainland analogues. Because of this discrepancy between the conservation relevances of these two types of land use (migration versus mere residence), populations that are most often studied include breeding/migrating birds such as terns (*Sternidae*), gulls (*Laridae*), waders (*Ardei*), ducks (*Anatidae*), and shorebirds (*Charadrii*, *Scolopaci*) (Erwin et al. 2007, 2011). Other birds known to exist on these islands include many typical marsh and forest birds, including wrens (*Troglodytidae*), blackbirds (*Icteridae*), sparrows (*Passerellidae*), swallows (*Hirundinidae*), corvids (*Corvidae*), rails (*Rallidae*), and others (eBird 2021).

Restoration

Primarily because of their importance to breeding birds, the islands of the Chesapeake Bay have been the focus of several restoration projects. The restoration of Poplar Island by the US Army Corps of Engineers is by far the largest of these undertakings. The island shrank from about 460 ha in the late 19th century to less than 1 ha by 1998. At this point, it was decided that dikes would be built surrounding the few remnants of the island, and that they would be filled in by the dredged material left over from the nearby digging of shipping channels. The island was divided into cells, which were designed to replicate a variety of habitats for estuarine species, chiefly breeding birds (Erwin et al. 2007). While Poplar Island was essentially recreated from almost nothing, there are examples of entirely artificial islands serving a similar purpose, intentionally or otherwise. Bridge tunnel islands in the Chesapeake region have become breeding grounds for sea birds, despite the intended function being purely for transportation. The Hampton Roads Bridge Tunnel is one such example (Keller 1992).

STUDY GOALS

From June to August of 2021, I surveyed 12 small Chesapeake Bay islands in Virginia and one in Maryland twice each to collect presence-absence data for avian taxa occurring on each island. In Chapter 2, I describe how I collected these data, and how I analyzed these presence-absence matrices for nestedness and modularity, arranging the matrix by island size, island isolation, and island habitat type. The nestedness and modularity corresponding to these three patterns were compared against each other, as well as against several null models. The goal was to understand the island characteristics that best correspond to nestedness and/or modularity among these islands, and to build the basis for knowledge that may enable more community-level conservation efforts across the Chesapeake and similar island systems. In Chapter 3, I present

and test a novel way of compensating for uneven sampling across a gradient of island characteristics. I calculate nestedness and modularity along gradients of island area and isolation once again, this time with the islands weighted by the amount of variable-space they represent, to correct for the naturally uneven distribution of island characteristics that may lead to some types of islands being over- or under-sampled. In Chapter 4, I summarize the information discussed in the previous chapters and paint a picture of the way these results (and the methods used to obtain them) fit into the broader landscape of community ecology.

CHAPTER 2

NESTEDNESS AND MODULARITY OF THE CHESAPEAKE BAY

AVIFAUNA

INTRODUCTION

In recent decades, ecologists have been exploring how similar communities are linked by the dispersal of their members, forming a metacommunity (Leibold et al. 2004). The species distributions across different communities within a metacommunity are often represented by a presence-absence matrix, in which the rows represent species and the columns represent communities, and each cell marks the presence (1) or absence (0) of a particular species within a particular community (Leibold and Mikkelson 2002). An important property of a metacommunity is the nestedness of these matrices (Ulrich and Almeida-Neto 2012). High nestedness occurs when communities with lower species richness have compositions that are proper subsets of the compositions of all richer communities and the most species-rich communities contain representatives of all species found in the metacommunity. It follows that less-rich communities contain no unique species that are absent from richer communities (Patterson and Atmar 1986). Nestedness is typically quantified by gap, overlap, or temperature metrics (Ulrich et al. 2009). Gap metrics often include a count of the number of unexpected species absences, unexpected species presences, the sum of unexpected absences and presences (Cutler 1991), or the presence/absence of changes needed to create a perfectly nested matrix (Brualdi and Sanderson 1999). Such gap metrics are simple metrics, and are biased by matrix size and shape, requiring standardization of some kind to compare among different matrix types (Ulrich et al. 2009). Overlap metrics count the number of species sets that contain other species

sets within the matrix, which in a perfectly nested system would be every set but the smallest (Hausdorf and Hennig 2003). Temperature metrics are the most complex analyses, assuming a perfectly nested system contains no presences to the outside of (and no absences to the inside of) an isocline that runs through the matrix (Atmar and Patterson 1993). The isocline is a line or simple curve that is drawn across the matrix to minimize the number of absences on one side and minimize the number of presences on the other. Temperature is calculated by weighting the deviations from perfect nestedness by their distance from the isocline (Greve and Chown 2006).

A different pattern of species distribution, known as modularity, arises when a group of species that co-occur are rarely found in communities with species outside that group (Borthagaray et al. 2014). These groups of co-occurring species are known as modules. Modularity is more computationally complex to quantify than nestedness, since it depends on the number of modules that the matrix is divided into, and the specific range of communities these modules contain (Fortuna et al. 2010). Modularity can be quantified using a Q metric: the difference between the observed number of connections (e.g., ecological interactions, spatial co-occurrence) within the module and the expected number of connections within the module, divided by the total number of connections in the system (Grilli et al. 2016). However, modularity could conceivably be quantified similarly to nestedness metrics by counting deviations from a perfectly-modular system—one in which every species belongs to a module and is not found outside of that module (Figure 1) (Borthagaray et al. 2014).

Once nestedness and modularity of species distributions are determined, one can determine the best environmental predictors, and degree, of nestedness and modularity of species distributions. For example, nestedness of the avifauna found across the Thousand Island Lake in China is most correlated with area of island, area requirement of each bird species, and habitat specificity of

each species (Wang et al. 2010). Studies that evaluate the nestedness or modularity of communities usually only incorporate one or the other, even though both nestedness and modularity are both relevant to community structure (Leibold and Mikkelson 2002; Fortuna et al. 2010). Studies that only examine one could be missing key environmental determinants of the biogeography of metacommunities.

The numerous small islands of the Chesapeake Bay, USA, represent a complex metacommunity that is, unfortunately, in danger of sinking below the water from a combination of natural and anthropogenic causes (Boon et al. 2010). Since the islands are well-known for their important role as bird habitat (Erwin et al. 2007), it is important to know how nested or modular bird distributions are, and whether these patterns are associated most with gradients in isolation, island area, and/or habitat type. Nestedness seems most likely to be strongest along gradients of isolation (based on the greater difficulty of reaching farther islands) and area (Wang et al. 2010), whereas modularity would likely be strongest across gradients of habitat type (where birds are presumably specialized for certain habitat types). The study proposed here aims to test these hypotheses to guide land managers as they attempt to prioritize conservation of island bird habitat to ensure long-term viability of local avifaunal populations.

METHODS

Island Selection

The geographic extent of the Chesapeake Bay is such that islands at the northern and southern ends are likely drawing from substantially different species pools, especially considering the mainland habitats at the northern and southern extents differ in habitat (deciduous forest vs

saltmarshes, respectively) (pers obs.). Because a number of northward islands are inaccessible

due to military testing, this led to an exclusive focus on islands south of South Marsh Island.

Figure 2: A map showing the locations of the 13 islands used for this study within the southern end of the Chesapeake Bay. One can see that they represent a variety of distances from the mainland and from other islands. Modified from the Chesapeake Bay Program (2021) (inset modified from Erwin and Beck [2007]).

I defined an "island" to be an area of land separated by a minimum distance of 200 m from any other land, to minimize the possibility of contaminating the sound recordings with calls from other islands, as well as to address the concern that birds may easily hop between islands if they are too close together. If two islands were within 200 m of one another, they were considered one island. My focus was on small islands, since islands like Tangier and Smith were large enough to have similar species richnesses to mainland sites (eBird 2021), and their size would require a representative sampling approach rather than the exhaustive survey approach I used for smaller islands. As a result, 100 ha was the cutoff for island size used in this study. Any islands < 0.5 ha were considered too small to support consistent bird use and were not used in this study. Given these considerations, there were 19 islands that were candidates for visitation. Of those, access was granted for 13 (Figures 2, 3).

Sampling Methods

I surveyed each island twice for all avian taxa from 19 June to 11 August 2021. Exhaustive sampling was achieved by a combination of audio recorders and transects. Anywhere from one to 11 audio recorders (Olympus VN-541PC recorders fitted with mattress foam to reduce wind noise) were placed the night before the surveys, except in a few cases when the logistics precluded such timing and the recorders were instead deployed the morning of the survey. The recorders were positioned such that at least 75% of the island was within 100 m of an audio recorder to ensure that every unit of island area received relatively equal sampling effort irrespective of island size. Only audio from the hours of 0500 to 0800 (EST) was used.

Visual identifications were performed along a "loose" transect (Watson 2004) and were supplemented by images taken with a Nikon D90 DSLR camera (for the purpose of better identifying species later). An additional Olympus audio recorder was also carried during these
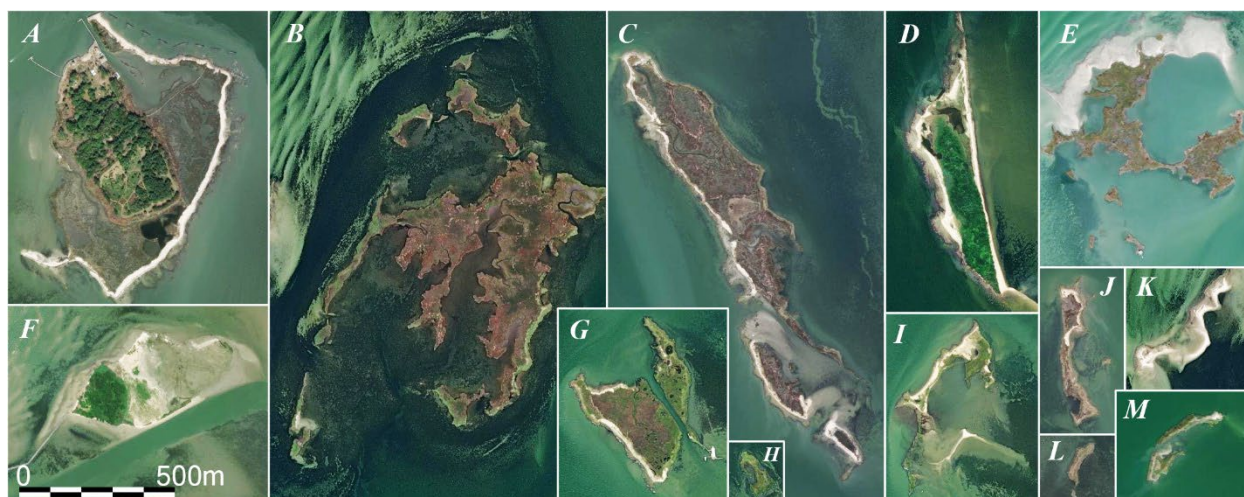
Figure 3: Satellite photographs (to scale with one another) of A) Port Isobel, B) Finney's Island, C) Goose Island, D) Watts Island, E) Parker's Island, F) Swan Island, G) Great Fox, H) Does Hammock, I) Clump Island, J) Fishbone Island, K) Scarborough Island, L) Upper Tump, and M) Lower Bernard. The islands show a wide range of sizes and habitat types. Images courtesy of Maxar via Bing Maps Aerial and ArcGIS (https://www.arcgis.com/home/webmap/viewer.html?webmap=8651e4d585654f6b955564efe4

transects. The main deviation I made from Watson's loose transect was that I focused on making sure I had reasonably covered the entire island at least once, which naturally took different lengths of time for different islands. Transects were conducted at sunrise, and sometimes continued until approximately noon, depending on island size and transportation constraints. In cases where several islands were near each other, the transect was split between the islands.

After all of the islands had each been sampled once from 19 June to 15 July, a second round of visits occurred from 22 July to 11 August in as close to the original order as possible, although some changes to the order were made to facilitate completion of sampling. Any migrant taxa were removed from the analysis, including those that appeared or disappeared midway through the season. The remaining species were used to generate a presence-absence matrix across the various islands.

Quantification of Island Characteristics

Island area was measured using high-resolution satellite photographs (Figure 3) publicly available through ArcGIS. Due to the lack of photographs from all points in the tidal cycle, the minor influence of tides on an island's area could not be addressed.

Because birds are active rather than passive dispersers (Salewski and Bruderer 2007), more complex inverse-square metrics of isolation were ruled out in favor of linear distance from the source population. Since many of these small islands were nearest to large islands like Smith and Tangier, and these large islands had a species count similar to the mainland (eBird 2021), they were deemed possible sources of immigration. As a result, linear distance from either the mainland, Smith Island, or Tangier was used as the isolation metric.

When evaluating habitat type, the islands each fell into distinct categories: 1) dominated by sand dunes with little vegetation, 2) dominated by saltmarshes, 3) dominated by grasses and shrubs
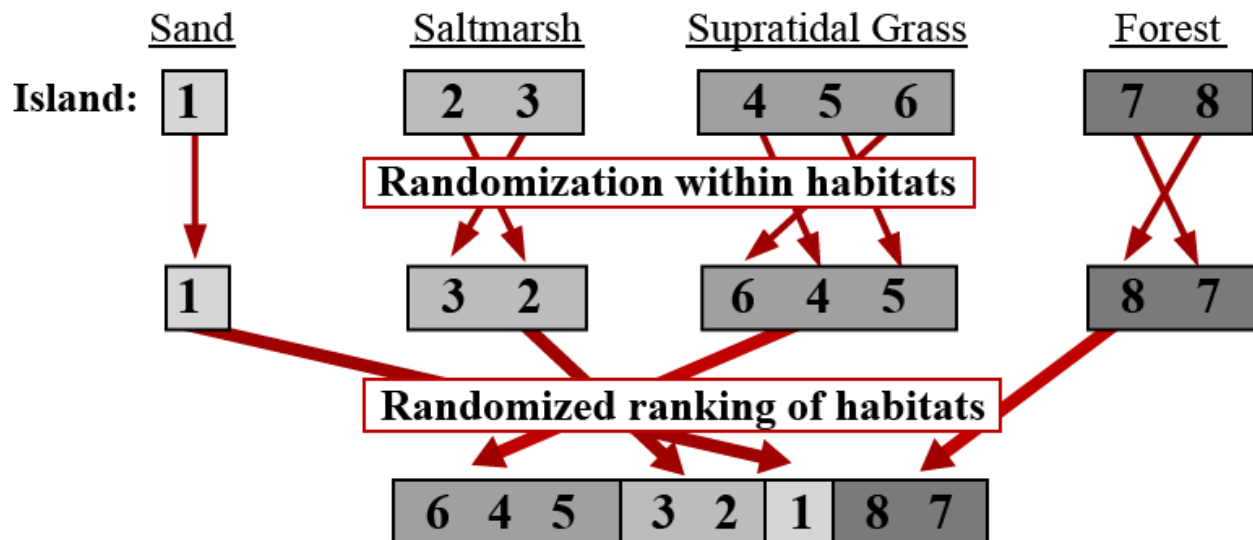
Figure 4: Visual demonstration of the way that a random set of rankings was generated to keep islands of the same habitat type (sand, saltmarsh, supratidal grass, or forest islands) clustered together, while randomizing the order of islands within each habitat and the order of the habitats.

growing above high tide, and 4) containing forests. The islands did not vary in an ordinal way

such that I was unable to determine a singular method of ranking islands based on habitat type.

Thus, I created a set of 1000 matrices in which islands of the same habitat type (be it sand dunes,

saltmarsh, supratidal grasses/shrubs, or forest) where kept adjacent to one another in the matrix,

while the order of the islands within the clusters and the order of the clusters within the matrix

was randomized (Figure 4).

Quantification of Nestedness

Of the many methods that have been used to quantify nestedness (Ulrich et al. 2009), a particular

gap metric dubbed the "discrepancy measure" (Brualdi and Sanderson 1999) was chosen for this

analysis. This metric counts the least number of presences/absences that must be changed to
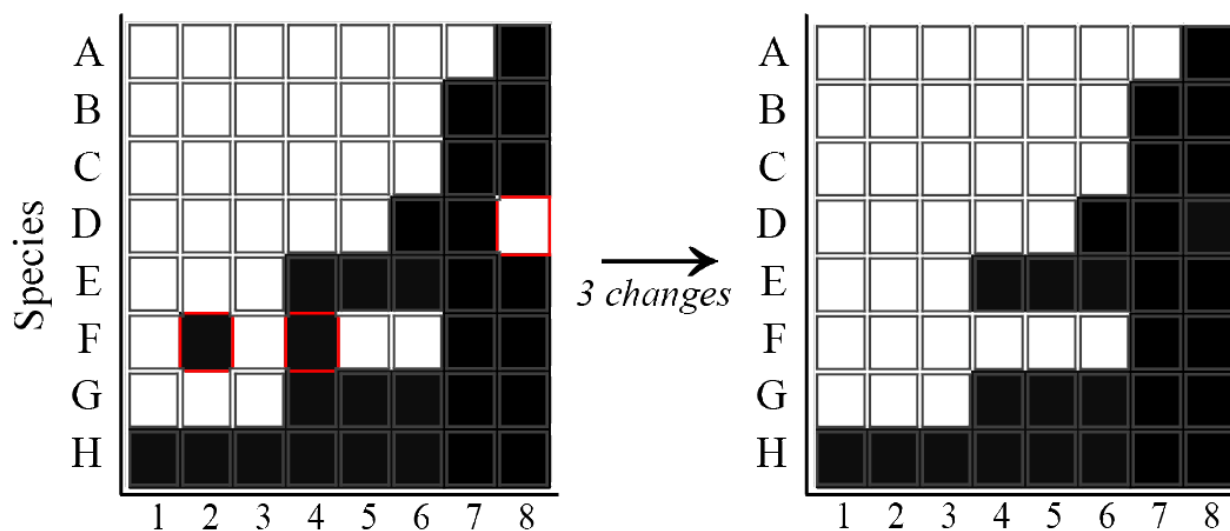
Figure 5: Demonstration of the "discrepancy" metric used to evaluate matrices for nestedness by counting the fewest number of changes needed to make a perfectly nested distribution. For Species D, the aberrant absence required fewer changes to fix (1) than would be required to consider the two prior presences aberrant (2). Meanwhile, species F's two aberrant presences bring the total number of changes necessary to 3. A similar approach was used to quantify modularity.

transform the observed matrix into a perfectly nested one (Figure 5). In other words, it is the number of deviations from perfect nestedness (Brualdi and Sanderson 1999; Ulrich et al. 2009). All gap metrics (including discrepancy measure) are skewed higher by increasing the size of the matrix or by changing the number of presences in the matrix (known as the matrix "fill"), but since the matrices compared in this study had the same dimensions and fill, this was not a concern (Ulrich et al. 2009). For each matrix evaluated, nestedness was calculated for both possible orientations of the island characteristic rankings (least to greatest and greatest to least), and the more nested of the two orientations is reported.

Quantification of Modularity

Modularity was quantified in a novel way that is similar in methods (and underlying assumptions) to the discrepancy measure metric of nestedness (Brualdi and Sanderson 1999). Modularity was considered the number of presence-absence changes required to turn the observed matrix into a perfectly modular system, in which a species belonging to a module was present on all islands within the module and absent from all islands outside the module. Similarly to how I determined the most nested orientation of a given matrix, modularity was based on my evaluation of all possible numbers of modules (from two to 13, the latter being the number of islands), and all possible ways that the 13 islands could be split into each number of modules (e.g., if there were two modules, the first module could incorporate the 1st, 2nd, and 3rd islands in the ranking, while the second module included the rest). Within each of these possible module numbers and arrangements, each species was assigned to the module that required the fewest number of presence/absence changes to make the species present on only islands within the module and absent on every island outside the module. The total number of these changes across

all species was summed, and the combination of module number and boundary position(s) that produced the fewest of these changes was reported.

Null Models and Bootstrapping

Before testing the nestedness and modularity of matrices ranked by area, isolation, and habitat type, the overall nestedness and modularity of the system was evaluated. I compared a set of 1000 randomly ranked versions of the presence-absence matrix produced from the observed data to a set of 1000 randomly scrambled matrices that had the same dimension (i.e. number of islands and species) and the same fill, but with the species presences and absences on each island
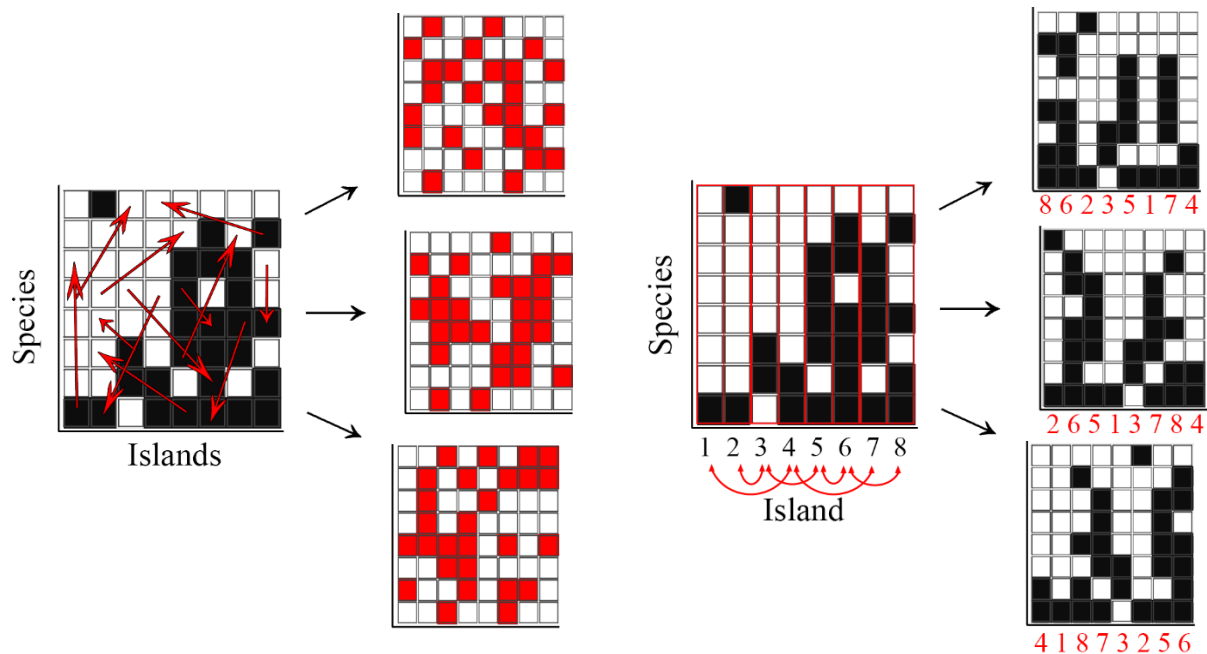
Figure 6: The creation of the two null distributions: the randomly scrambled matrices with the overall number of presences kept constant (left), and the randomly-ranked matrices (right). The former will be tested against the latter to determine whether the islands show more nestedness and/or modularity than expected by chance, regardless of ranking. Then, the latter will serve as the null model against which the rankings based on island area, isolation, and habitat type will be compared.

completely randomized (Figure 6). The latter served as a null model and was used to test whether these islands showed a stronger pattern of nestedness/modularity than expected by chance.

For evaluating the nestedness/modularity associated with the rankings of island characteristics, the randomly ranked matrix served as a null distribution. The threshold for a statistically significant difference between the null and the matrix ranked by an island characteristic was $p<0.05$. In other words, if ranking by a particular island characteristic produced a stronger pattern of nestedness/modularity than >95% of the random rankings, then that island characteristic was deemed useful in predicting nestedness and/or modularity.

RESULTS

Across the 13 islands sampled, more than 50 species were observed, 45 of which remained after the removal of species deemed to have migrated during the survey period. From these 45 species, the presence-absence matrix was generated. Even after accounting for migratory taxa, islands varied greatly in species richness, ranging from 8 to 35. Irrespective of the way the islands were ranked, randomly ranked matrices produced from the observed data showed higher degrees of nestedness and modularity than matrices with the same fill generated by random chance. In the case of nestedness, between the 1000 randomly scrambled matrices and 1000 randomly ranked versions of the observed matrix, there was no overlap (Figure 7), and the mean randomly ranked matrix produced less than half as many deviations as the randomly scrambled matrix.

In the case of modularity, the randomly scrambled and randomly ranked observed matrices also showed no overlap (Figure 7), with the mean random ranking producing about 75% of the

deviations produced by the mean scrambled matrix. In both cases, the patterns were stronger than one would expect from a matrix of this size and fill in which the species were spread randomly.
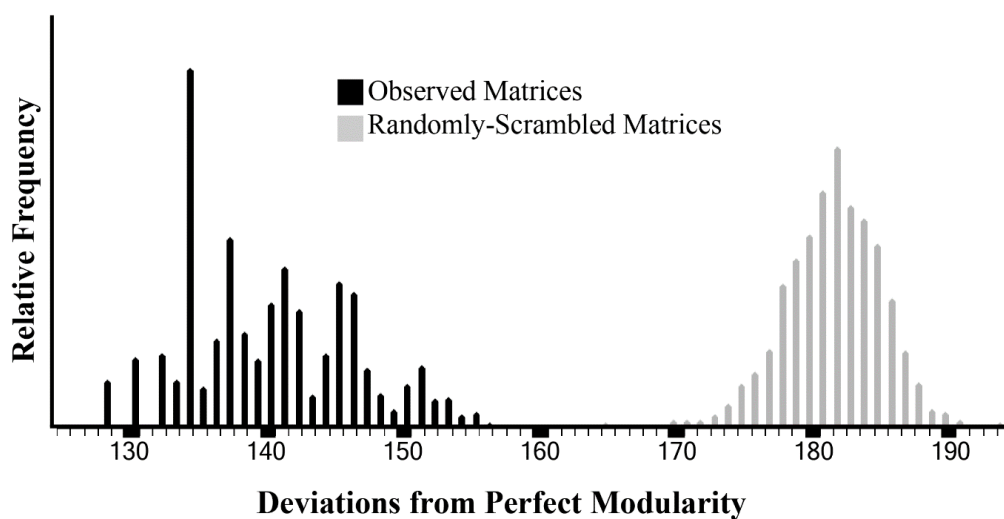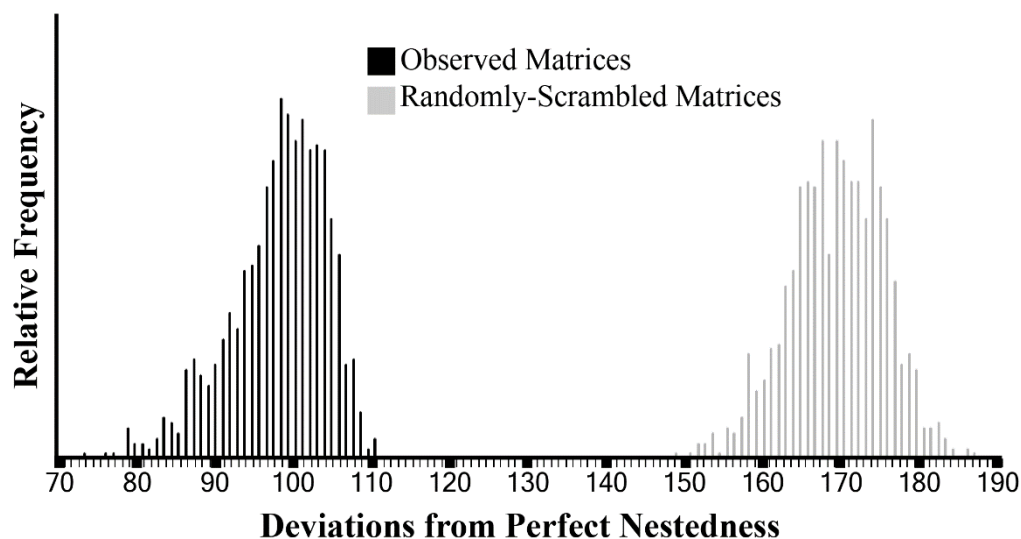
Figure 7: Comparisons between randomly ranked matrices of the observed data and the randomly scrambled matrices generated by assigning presences and absences at random. All 1000 randomly ranked matrices show fewer deviations from perfect nestedness and perfect modularity than all 1000 randomly scrambled matrices, indicating that regardless of the way the islands are ranked, there are fewer deviations from perfect nestedness and modularity than one would expect by chance. This implies that there is some degree of nestedness and modularity in the observed system as a whole.
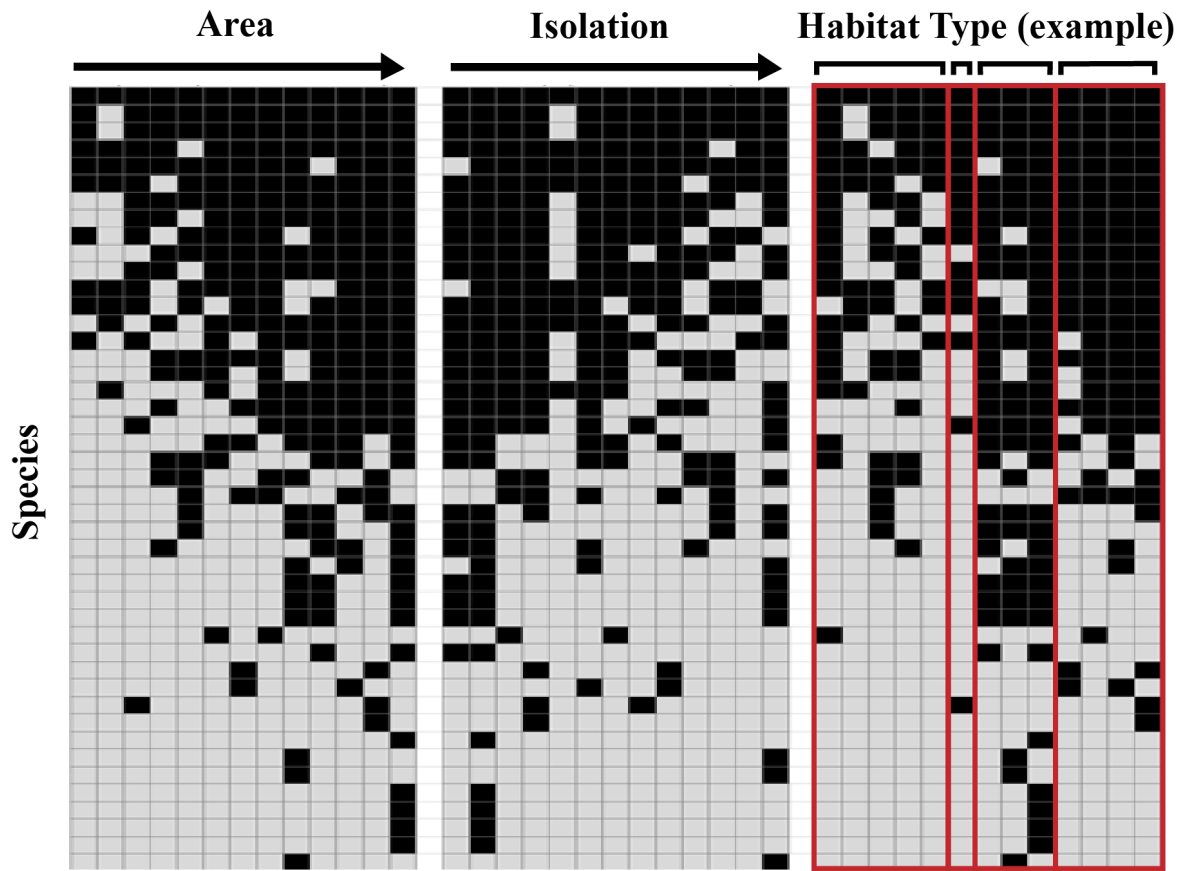
Figure 8: Three presence-absence matrices that rank the islands (columns) by the three island characteristics: area, isolation, and habitat type (which is represented here by just one example of such a ranking). All three cases appear visibly nested at a glance, although this habitat ranking example happens to appear more nested than most of the other possible habitat rankings.

Table 1. Comparison of the matrices as ranked by Area, Isolation, and Habitat Type with the Randomly Ranked matrix, which served as the null. In the case of habitat type, overlap included both the portion of the null distribution with as few deviations as the Habitat Type distribution's mean.

Ranked by:	Nestedness				Modularity			
	Random	Area	Isolation	Habitat Type	Random	Area	Isolation	Habitat Type
Mean	99.641	71	86	87.551	139.795	132	134	140.146
Median	101			89	139.5			139
Maximum	113			105	156			151
Minimum	73			61	128			128
# Matrices Generated	1000	1	1	1000	1000	1	1	1000
Difference from Null Mean		-28.641	-13.641	-12.090		-7.795	-5.795	0.351
Overlap with Null Distribution		0/1000	41/1000	58/1000 (mean)		87/1000	277/1000	558/1000 (mean)

Ranking islands by their characteristics

Area was significantly nested with decreasing island area (P<0.001), with 71 deviations from perfect nestedness compared to the mean of 99.641 deviations obtained within the randomly ranked bootstrapped sample of 1000 matrices (Table 1, Figures 8 and 9). Of the deviation values obtained from the 1000 matrices, none yielded a value <71. Island isolation was also significantly nested (P=0.041) with increasing island isolation, with only 86 deviations. The mean of the habitat-ranked matrices (87.551 deviations) did not differ significantly (P=0.058)
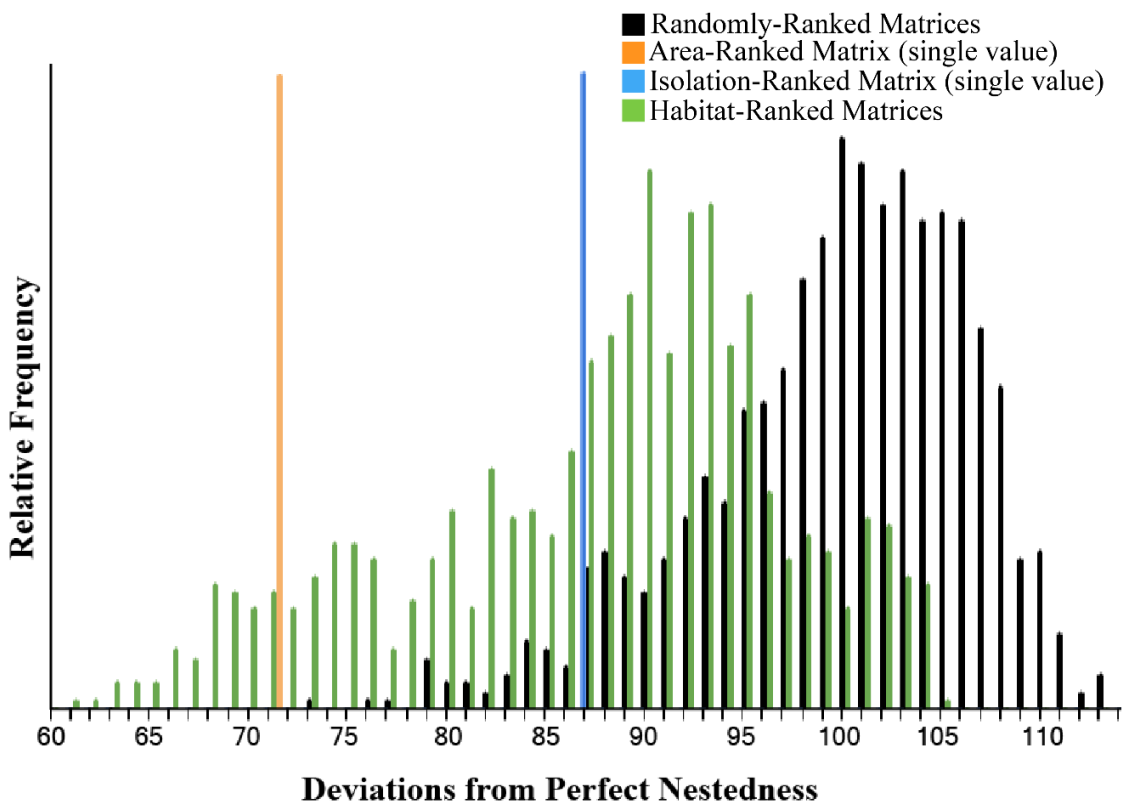
Figure 9: A histogram showing the numbers of deviations from perfect nestedness produced by the different ranking methods (Random, Area, Isolation, and Habitat Type). Like the random ranking, habitat type is presented as a distribution. The data shows a significant degree of nestedness when ranking the islands by both area (P<0.001) and isolation (P=0.41). Ranking by area produces the most nested pattern.
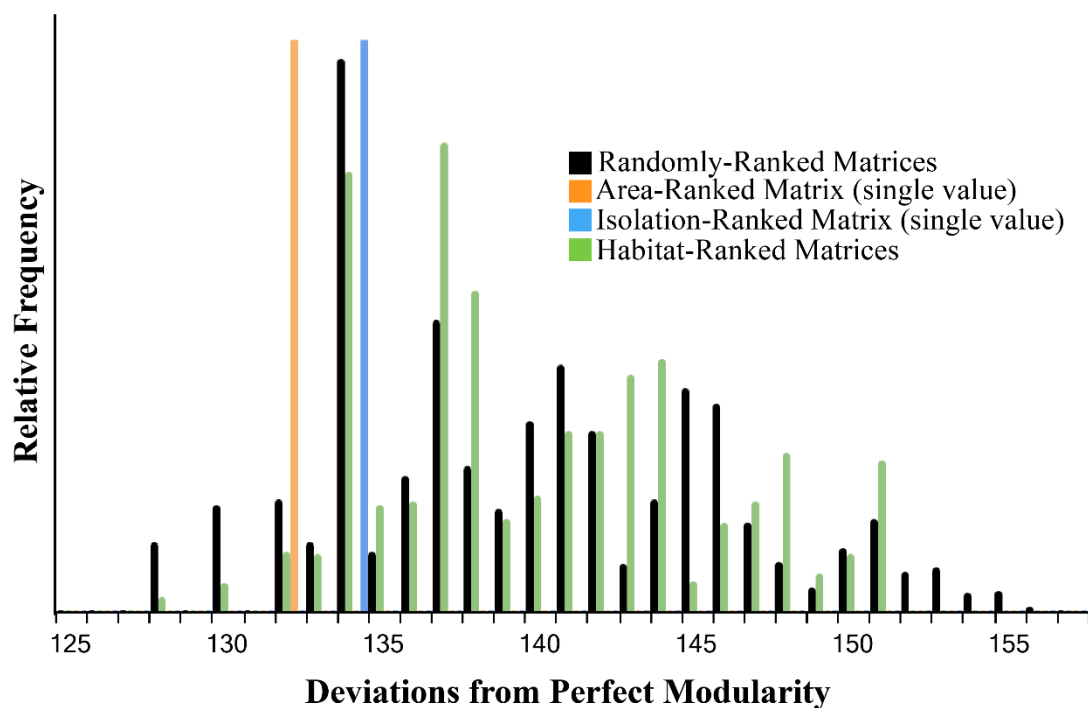
Figure 10: A histogram showing the numbers of deviations from perfect modularity produced by the different ranking methods (Area, Isolation, and Habitat Type). None of the three variables show any significant degree of modularity.

from matrices obtained with the 1000 bootstrapped samples. None of the rankings produced a

significantly stronger pattern of modularity than did the bootstrapped sample of 1000 randomly

ranked matrices (area, P=0.053; isolation, P=0.108; habitat type, P=0.558) (Figure 10). Taken as

a whole, the results show that nestedness was best predicted by island area.

DISCUSSION

The strengths of the patterns of nestedness observed across each island characteristic (island

area, island isolation, and island habitat type) did not necessarily correspond to the amount that

each island characteristic contributed to producing the pattern. These three characteristics may

all directly affect the nestedness and modularity of the system, or they may simply be correlated

with such patterns. Even if one were to assume that the gradient of island areas was the cause of the nested pattern, the nestedness exhibited across the gradient of island isolation could be entirely due to an unseen correlation between isolation and area in this particular system. It is also important to keep in mind that these results only necessarily reflect the avian metacommunity as it existed during the Summer of 2021, which not only means that year-to-year variation is unaccounted for, but that these patterns do not necessarily reflect the metacommunity during other seasons.

It is not surprising that of the three island characteristics examined, ranking by island area showed the most nested pattern. Similarly, Wang et al. (2010), showed that nestedness was significantly correlated with area within an island bird metacommunity. Isolation, habitat diversity, and plant species richness were also evaluated by Wang et al. (2010) but none of these variables showed as large an effect size, nor were they statistically significant in their system.

There were two probable contributors to the nestedness associated with gradients in island size seen in this study. Firstly, there is a well-known relationship between island area and species richness (Lomolino 2000b). Larger islands contain more resources, which allows for more individuals, which allows for more species by the sampling effect alone, even without invoking differences among species (MacArthur and Wilson 1963). Variation in species richness among islands alone can produce a degree of nestedness (Cutler 1991). Secondly, nestedness can be the result of differing species characteristics, namely the fact that some species are generalists that can exist on any sized island and others are specialists that require a large enough island (Wang et al. 2010). While the sampling effect creates some nestedness in virtually any island metacommunity that exhibits varying species richnesses, the nestedness seen in my study is likely due to the presence of generalists and specialists as well. A post-hoc examination of

different bootstrapping methods showed that randomly scrambling the observed matrix but keeping the number of islands occupied by each species intact produced a more nested set of matrices than a scrambled matrix that kept the species richnesses of each island intact (P<0.001) (unpublished data). This was the case not only when the islands were ranked randomly, but also when they were ranked by area. The generalist species that were present on almost every island were mostly larger birds with greater long-distance flying ability, such as gulls and terns. Passive sampling by an observer can produce an artificial appearance of nestedness due to differences in species abundance and detectability even among islands with identical species compositions (Andrén 1994), but the fact that the islands were exhaustively sampled in my study should largely dispel this concern.

While varying dispersal ability is usually an explanation for nestedness along an isolation gradient (Darlington 1957), in this case it may instead be responsible for some degree of nestedness along the size gradient. Better fliers can more easily reach any island in Chesapeake Bay, meaning they can depart islands more readily as well. This might make long-distance fliers more likely than small, less vagile birds to be found on small islands with few resources, since they can more readily travel among islands, making the trips to those islands worth the energy investment. A bird with less dispersal ability, meanwhile, would presumably not venture to an island unless it was large and resource-rich enough to be worth expending the resources to get there. Whether this is due to birds foraging optimally (Charnov 1976) or merely the fact that small birds that reach small islands do not have the energy to leave and quickly starve to death—a process known as selective extinction (Patterson and Atmar, 1986)—the inability of some species to readily arrive at or leave an island is one possible explanation for the nestedness associated with island area.

Contrary to the results seen in this study, Wang et al. (2010) did not find a significant correlation between isolation and nestedness, and this result suggested that the spatial scale at which Wang et al.'s fieldwork was conducted (the islands' distances from the mainland ranged from 21 to 3712 m) was smaller than the scale needed to segregate birds by dispersal ability. The Chesapeake Bay islands are more isolated than the islands examined by Wang et al. (with Watts Island being over 6 km from the mainland, with the islands near Tangier being even more remote). The significant nestedness associated with the second-best predictor (i.e., isolation) could simply be the result of a correlation between the best (i.e., area) and second-best predictors. Anecdotally, it appears that the least-isolated islands were also the largest in area. It is clear from the presence of small passerines on Watts Island (i.e., the most isolated island) that virtually any bird has the ability to reach any island in the system, and perhaps this negates the influence of distance and allows for island suitability to be the determining factor. The isolation metric itself was designed to be a compromise between a measurement of distance from the mainland that ignores other islands, and a more holistic measurement that incorporates nearby islands that ignores the fact that many nearby islands are too species-poor to be considered viable as sources of colonization. Although no single metric will address every concern, it may be possible to design a metric that is more sophisticated—perhaps one that takes into account the fact that small islands may be used as "stepping stones" to colonize other small islands.

When designing a method for ranking habitat type, I decided to opt for a partially random ranking that merely clustered habitat types together, rather than creating a single ranking (e.g., mean vegetation height or percent vegetation cover) that may have introduced confounding variables and ignored important components of the habitat types. It is now clear that this low level of specificity is not strong enough to detect a pattern. It is obvious that some form of

habitat-related pattern exists, especially modularity. For example, many birds are only found on forested islands, and some of them are found on *all* forested islands without exception (e.g., Northern Cardinal *Cardinalis cardinalis*, Gray Catbird *Dumetella carolinensis*, and Common Yellowthroat *Geothlypis trichas*). The confounding factor is likely that some habitats on the islands are physically nested within other habitats. For example, the islands all have some form of wetland component, and all of them are surrounded by shallow brackish water, meaning that they are all suitable habitat for a wide range of wetland birds, seabirds, and shorebirds. This fact may be what overrides the modular nature of habitat itself in this particular system. If one wants to understand the true relationship between habitat type and patterns of biogeography within island systems such as this, viewing the island communities as a hierarchical continuum (sensu Collins et al. 1993), in which distinct communities (e.g. forest birds, marsh birds, etc.) are nested within communities of generalists that exist across all the communities (i.e. gulls and other sea-going birds) may be the best way forward. Perhaps this pattern could be quantified and evaluated against different island characteristics in a similar way to nestedness and modularity.

Although Logue et al.'s (2011) idea of metacommunities as points within a three-dimensional space defined by habitat heterogeneity, dispersal, and species similarity was not meant to be a complete description of all relevant metacommunity characteristics, exploring real-world metacommunities from different corners of this space would be a good start to understand the range of metacommunity structures possible, and how characteristics of the species and the environments found in a metacommunity produce these structures.

The present study and that of Wang et al (2010) shows that when examining birds, a group with high dispersal ability but exhibiting low overall species similarity, living on small islands of various habitat types that vary in habitat heterogeneity, area is related to a large and significant

degree of nestedness within the metacommunity. My study, in particular, shows that modularity (according to this novel metric) may exist but is not predicted well by area, or any other variables. Do different combinations of metacommunity characteristics (e.g. dispersal ability, habitat heterogeneity) produce different patterns of nestedness and modularity?

Patterson and Atmar (1986) focused on small mountain-dwelling mammals, which are much less vagile than birds, in the southwestern United States, and found a pattern of nestedness stronger than expected by chance, even when accounting for uneven species richnesses among patches. They found similar patterns among small mammal data collected by other authors on the islands off Maine and Baja California and posited that this pattern was the result of selective extinction of all but the species generalized enough to survive on a given island. In doing so, they invoke an interesting historical factor: some patchy habitats are the result of fragmentation of a larger habitat and progressively lose species, while others are the results of new patches being created where no such habitat existed before (such as oceanic islands), which then gain species by colonization (Cutler 1991). Since the Chesapeake Bay was mostly above sea level during the last glacial period (Hobbs 2004), the islands that exist today are likely the result of fragmentation rather than habitat generation, implying that selective extinction would play a larger role in shaping the nestedness of island communities. However, just because a patch was the result of fragmentation of a habitat that already contained its own species does not mean that subsequent colonization could not have occurred, especially if the focal taxon had high dispersal ability. Wang et al. (2010) suggests that since the islands of the Thousand-Island Lake are fragments of what was formerly dry land, that selective extinction was the driver of the nestedness of the islands' lizard and mammal populations, but that the high vagility of birds means that selective colonization is the likely driver of avifaunal nestedness. It seems likely that this is also true of the

Chesapeake Bay islands' avifauna. Despite these possible differences in the mechanisms driving nestedness between the Chesapeake Bay avifauna and the mammals studied by Patterson and Atmar (1986), selective extinction and selective colonization have been shown to produce similar patterns, despite differing in whether the outliers come primarily in the form of unexpected absences or of unexpected presences (Cutler 1991).

Even lower on the dispersal ability spectrum, Angeler (2013) examined invertebrate and phytoplankton communities of multiple lakes in Sweden. This metacommunity was found to exhibit little nestedness, and that its nestedness decreased throughout the study period, with each lake contributing to the total diversity of the system rather than only the most speciose doing so. This may have been the result of the changes in the lakes' acidity and water clarity, creating greater heterogeneity among lakes. Despite the heavy turnover among lakes, the study does not comment on whether these lakes formed modules or not. If the turnover was gradual rather than clumped, it would not be very modular (Leibold and Mikkelson 2002).

Hill et al. (2017) found a similarly strong pattern of turnover compared to nestedness when examining species composition among ponds. In this case, dispersal ability varied among species, and the distributions of passive dispersers were unsurprisingly more influenced by spatial processes than active dispersers. If this reasoning is applied to the Chesapeake Bay islands, it would suggest that plants, and perhaps some small animals, are more likely to show patterns of nestedness along gradients of isolation than birds, which can actively fly to islands they intend to visit. However, this pattern would not be seen if the plant communities on the islands were the direct descendants of the plant communities present when the islands split from the mainland.

As for modularity, Presley et al. (2009) found that bat metacommunities of Paraguay formed a Clementsian (essentially, modular) distribution pattern, and that this pattern best corresponded to a gradient of temperature and precipitation. Bats, like birds, are good dispersers because of their ability to fly, and since bats as a whole show far less niche breadth than birds, the fact that modularity is visible in these bats but not in the Chesapeake Bay birds could be due to the bats' habitat being more continuous and not obstructing the underlying modular pattern surrounding habitat type with confounding factors such as patch size and isolation.

However, it can be difficult to directly compare findings among studies, since authors use a variety of subtly different definitions of nestedness and statistical techniques. Rather than ranking patches by a characteristic and quantifying the degree of nestedness or modularity it creates, studies will more often rank islands by species richness or optimize the ranking for the greatest nestedness. They will then test for a correlation between the order of islands in this ranking and the order of the islands when ranked by a particular characteristic (Wang et al. 2010). Alternatively, some will look for nestedness and turnover by testing whether the arrival/departure of one species correlates positively or negatively with the arrival/departure of another, and whether these changes are clumped, random, or overdispersed (Presley et al. 2010, 2012). Perhaps if each of these studies had used different metrics, they would have produced different results, making direct comparison between the studies potentially misleading. In addition, many authors have used techniques that have since undergone extensive criticism. Matthews et al. (2015) highlights this issue by pointing out many questionable methodological choices of earlier studies—namely the use of a randomly filled matrix as the null model rather than a randomized matrix of the same fill, which led to type I errors in an earlier summary by Watling and Donnelly (2006). When Matthews et al. re-evaluated Watling and Donnelly's data,

they found that only 9% of the datasets examined showed a significant pattern of nestedness. By contrast, they found that 16% of the datasets showed significant antinestedness, in which a system shows significantly less nestedness than would be expected even by chance. This highlights the importance of choosing the appropriate mathematical methodology when studying such patterns.

Conservation Implications

One of the aims of this study was to understand how environmental gradients could be used to predict specific biogeographic patterns across a particular kind of metacommunity. These different patterns have different conservation implications. Nestedness across a gradient of island size is an indication that smaller islands are redundant in terms of the species richness of the broader metacommunity, and that effort should be focused on larger islands, which not only contain all species found on small islands, but species unique to larger islands as well (Patterson and Atmar 1986). The debate over whether conservation resources should be put to preserving single large patches of the habitat of interest versus a greater number of small patches (known as the "single-large or several-small" debate, or "SLOSS") is very context-specific (Tjørve 2010), but perhaps island bird communities lean towards the "single-large" side of that debate. However, the arguments against the "single-large" approach often involve factors (such as disease outbreaks) that are not accounted for in a simple presence-absence matrix (Tjørve 2010).

While a presence-absence survey of all bird species across the islands of the southern Chesapeake Bay represents a uniquely broad look at the system that has implications for the conservation of both the Bay's species and those of similar systems, a presence-absence matrix such as the one created for this study does not incorporate certain conservation-relevant details. Most obvious is the fact that not all species have equal conservation relevance, and their

dependency on these islands varies greatly. Forest birds like the Northern Cardinal are rare in the

context of the Bay but have extensive populations on the mainland (BirdLife International 2018).

In the specific context of the Chesapeake Bay, their presence should not be weighted as heavily

as that of the endangered Saltmarsh Sparrow (*Ammospiza caudacuta*) (BirdLife International

2020), or the many seagoing birds from across the eastern seaboard that rely on the predator-free

islands to raise their young (Erwin and Beck 2007). This highlights another nuance not

accounted for by presence-absence; even within a single species, presences on different islands

should not be weighted the same. A great example is the Great Black-backed Gull (*Larus

marinus*), which was found on nearly every island, but only were seen to nest on relatively small,

isolated ones: the type of island that the presence-absence data would imply have the least

conservation value. Some other birds, including the Laughing Gull (*Leucophaeus atricilla*),

seemed to follow this pattern too. Boiling down the many ways a bird can use a habitat into a

single "1" in a matrix masks this pattern entirely. This is presumably why conservationists in the

Chesapeake Bay have focused primarily on breeding seabirds, which congregate from across the

region to nest on these small islands (Erwin et al. 2007).

However, the conservation implications of the current study expand beyond the Chesapeake Bay.

In island metacommunities where *all* species may be of conservation relevance, or if species-

specific data are not yet known, it is important to have a more holistic understanding of the entire

system before more species-specific conservation plans can be designed. Including all individual

species at the outset allows for greater flexibility later on, when new analyses are attempted.

While this particular study focused on the total avifauna of the islands, this same analysis could

be done on breeding birds, migrating birds, or any other subset of birds that has particular

conservation relevance, simply by paring down the matrix to contain particular taxa of interest.

However, to fully address many of the oversights of a presence-absence matrix, it may be necessary to introduce additional methods, such as weighting the presences and absences within the matrix (as presented in the next chapter, Chapter 3).

CHAPTER 3

WEIGHTING MATRICES TO OFFSET UNEVEN SAMPLING

INTRODUCTION

When analyzing the species compositions of different habitat patches within a metacommunity, a presence-absence matrix is commonly used (Leibold and Mikkelson 2002), despite several limitations. There has been much discussion over the "presence-absence" aspect of this technique, especially its advantages and disadvantages when compared to abundance data (Kirichenko-Babko et al. 2021), but I am not aware of many authors that have addressed the limitations of the "matrix" itself. In the context of biogeography, a presence-absence matrix is usually a bipartite matrix with the rows representing species and the columns representing sites, patches, communities, or other units of location (Leibold and Mikkelson 2002). The way in which the columns are arranged within the matrix is dependent on the intent of the author. If, for example, the columns are simply unranked communities that are being compared to find a pattern (e.g., nestedness), columns are usually ranked in the order that produces the strongest example of the pattern of interest (Wang et al. 2010). In other studies, the ranking of columns often corresponds to particular continuous variables, such as elevation (Presley et al. 2012). This presents a problem for a matrix; the only information contained by the arrangement of the columns is their ranking, but the amount of variable-space between them is ignored and functionally assumed to be equal. For example, if Sites A, B, and C were 100, 200, and 600 m in elevation, respectively; the matrix would be simply ranked ABC as if they were evenly spaced. If the intention of the study were to see how communities respond to changes in a continuous variable, the lower-elevation communities (A and B) would be disproportionately represented in

the matrix, and they would have a greater influence on the appearance of the overall pattern than they should. The easiest solution is to evenly sample the gradient so that this bias does not occur. This is possible for some continuous gradients like elevation in which almost any given elevation can be found in the field and sampled. However, other continuous variables cannot realistically be sampled for every point along a continuum, since only a limited number of values along that continuum exist in the field.

Patchy habitats present a problem because sampling a gradient of patch characteristics at even intervals may be difficult. If, for example, one wanted to sample different patches by even intervals of patch size, the patch sizes observed in the field would not represent these even intervals of size. Thus, one would be forced to use values of uneven interval. A potential solution is to incorporate enough patches into the dataset so that one can either choose patches that are close to being evenly-spaced (i.e. stratified sampling as described by Parsons [2017]) or bin patches into evenly sized groups that represent a range of values (e.g., 600–700 m^2, 700–800 m^2) (Presley et al. 2012). However, if the system under study does not have an adequate number of patches to choose from, one would presumably either have to supplement their study with data from other systems, or simply ignore the unevenness of the gradients being examined.

The islands of the southern Chesapeake Bay represent a system in which an even sampling of island size is not possible. This area contains approximately 20 small islands representing irregular intervals of size, shape, and distance from the mainland (pers. obs), making it difficult to sample any of these gradients evenly. One method to address this uneven distribution of island characteristics is by weighting the presences and absences on each island in the matrix to account for the amount of unsampled variable-space surrounding them. In this chapter, I have weighted ecological presence-absence matrices using this technique.

The goal of creating a weighted matrix was to compare and contrast with unweighted results from Chapter 2, which sought to rank islands by three variables—area, isolation from large landmasses, and habitat type—to determine which variable produced the greatest patterns of nestedness and modularity. Nestedness is the degree to which the species compositions of communities form nested subsets of one another (Patterson and Atmar 1986), and modularity is the degree to which communities belong to distinct "modules" containing communities of identical species composition that do not overlap in composition with communities belonging to other modules (Borthargaray et al. 2014). In this chapter, I create weighted matrices for area and isolation—the two continuous variables from Chapter 2.

Methodological fixes to faulty assumptions are important to explore. The conclusions of many studies of nestedness in metacommunities have been shown to be dependent on the particular methodology used (Matthews et al. 2015). I introduce the use of weighted matrices to reveal potential patterns and conclusions that are less evident with unweighted matrices, opening up the possibility that weighted matrices may be a more accurate representation of the patterns seen across a continuous variable-space. The advantages and disadvantages of a weighted approach will be presented in the hopes of providing a new analytic tool that could be used by investigators studying metacommunity patterns.

METHODS

I used a presence-absence matrix representing 45 species and 13 islands constructed from data collected from 19 June to 11 August of 2021 (see Chapter 2 for more details). Rather than simply ranking the islands, as was done in Chapter 2, the islands were weighted by the amount of variable-space they represented (W_c) along continua of area (size of the island) and isolation (i.e., linear distance from any landmass of area >100 ha). For these continua, a logarithmic scale was

chosen over a linear scalar, because the proportional impact of a given amount area or distance diminishes as these metrics increase, and the scale should reflect this (MacArthur and Wilson 1963).

A given island (island c such that $1 \leq c \leq 13$) with an area or isolation of value x_c was assumed to represent the variable space to either side of itself on the continuum of said variable, up until the midway point between the island's value (x_c) and the values x_{c+1} and x_{c-1} of the islands in adjacent positions along the continuum ($c+1$ and $c-1$). The midway points represented the arithmetic mean of the logarithms (in other words, the geometric mean) of two adjacent islands' areas or degrees of isolation (Equation 1, Table 2, Figure 11).

$$W_{c|1<c<13} = \frac{\log(x_{c+1})+\log(x_c)}{2} - \frac{\log(x_c)+\log(x_{c-1})}{2} = \frac{\log(x_{c+1})-\log(x_{c-1})}{2} \tag{1}$$

Unlike the other islands, the islands on the "ends" of the continuum ($c=1$ and $c=13$, the first and last columns) only had one adjacent island each ($c=2$ and $c=12$, respectively), instead of two. To account for this, the variable space between $c=1$ and the midpoint it shared with $c=2$ was assumed to be half the total variable-space occupied by $c=1$, so this number was simply doubled to represent the total variable space occupied by $c=1$. The same was done with the distance between $c=13$ and its midpoint shared with $c=12$ (Equations 2 and 3, Table 2).

$$W_1 = 2\left[\frac{\log(x_2)+\log(x_1)}{2} - \log(x_1)\right] = \log(x_2) - \log(x_1) \tag{2}$$

$$W_{13} = 2\left[\log(x_{13}) - \frac{\log(x_{13})+\log(x_{12})}{2}\right] = \log(x_{13}) - \log(x_{12}) \tag{3}$$
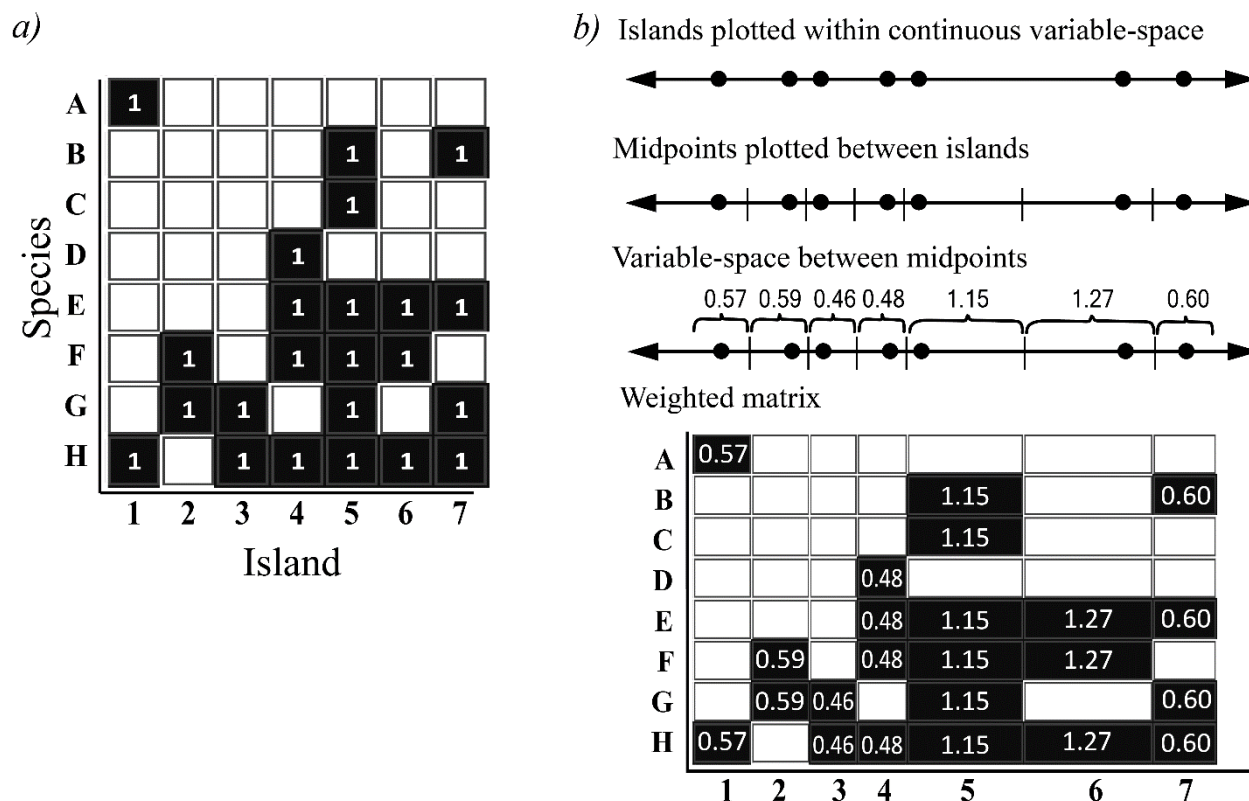
Figure 19: a) An unweighted matrix in which the islands are ranked by a characteristic and b) a visual demonstration of the mathematics behind creating a weighted matrix. Even visually, the second matrix appears much less nested than the first, raising the possibility that the high nestedness of the first is an illusion created by uneven spacing along the island characteristic gradient in question.

Quantification and Null Models

The methods for quantifying nestedness and modularity were the same as in Chapter 2. Both

metrics involved counting the number of deviations from a perfectly nested or modular matrix,

respectively (Brualdi and Sanderson 1999). The difference in the weighted approach is that these

deviations were weighted to represent the amount of variable space their respective islands

occupied. A presence on an island was assigned that island's weight *Wc*.

Table 2. The calculations associated with determining the weights assigned to each island in the area- and isolation-ranked matrices.

Island Ranked by Area	log(x in m²)	Variable Space Occupied (Wc)	Island Ranked by Isolation	log(x in m)	Variable Space Occupied (Wc)
Upper Tump	3.687	0.149	Swan	2.299	0.123
Midpoint	3.762		Midpoint	2.360	
Does Hammock	3.837	0.077	Port Isobel	2.422	0.128
Midpoint	3.839		Midpoint	2.489	
Scarborough	3.842	0.120	Parker	2.556	0.105
Midpoint	3.959		Midpoint	2.594	
Lower Bernard	4.077	0.223	Finney's	2.631	0.209
Midpoint	4.182		Midpoint	2.802	
Fishbone	4.287	0.161	Does Hammock	2.973	0.216
Midpoint	4.343		Midpoint	3.018	
Clump	4.398	0.316	Goose	3.064	0.070
Midpoint	4.659		Midpoint	3.089	
Great Fox	4.920	0.268	Clump	3.114	0.039
Midpoint	4.927		Midpoint	3.128	
Parker's	4.934	0.019	Scarborough	3.142	0.093
Midpoint	4.945		Midpoint	3.221	
Watts	4.957	0.036	Great Fox	3.300	0.124
Midpoint	4.981		Midpoint	3.344	
Swan	5.005	0.141	Lower Bernard	3.389	0.124
Midpoint	5.122		Midpoint	3.469	
Goose	5.239	0.204	Fish Bone	3.548	0.084
Midpoint	5.326		Midpoint	3.553	
Finney's	5.413	0.133	Upper Tump	3.558	0.143
Midpoint	5.459		Midpoint	3.696	
Port Isobel	5.504	0.091	Watts	3.834	0.277

Unlike in Chapter 2, in which the null models for both island area and habitat type were the same set of random rankings of the islands, the analysis presented here required separate null models for each, since the weights attached to each island were different between the two variables. The null distribution for area was a set of randomized rankings of the area matrix, including weights for area variable space. The null distribution for isolation was likewise that produced by randomized rankings of the isolation matrix. As in Chapter 2, $p < 0.05$ was used as the standard
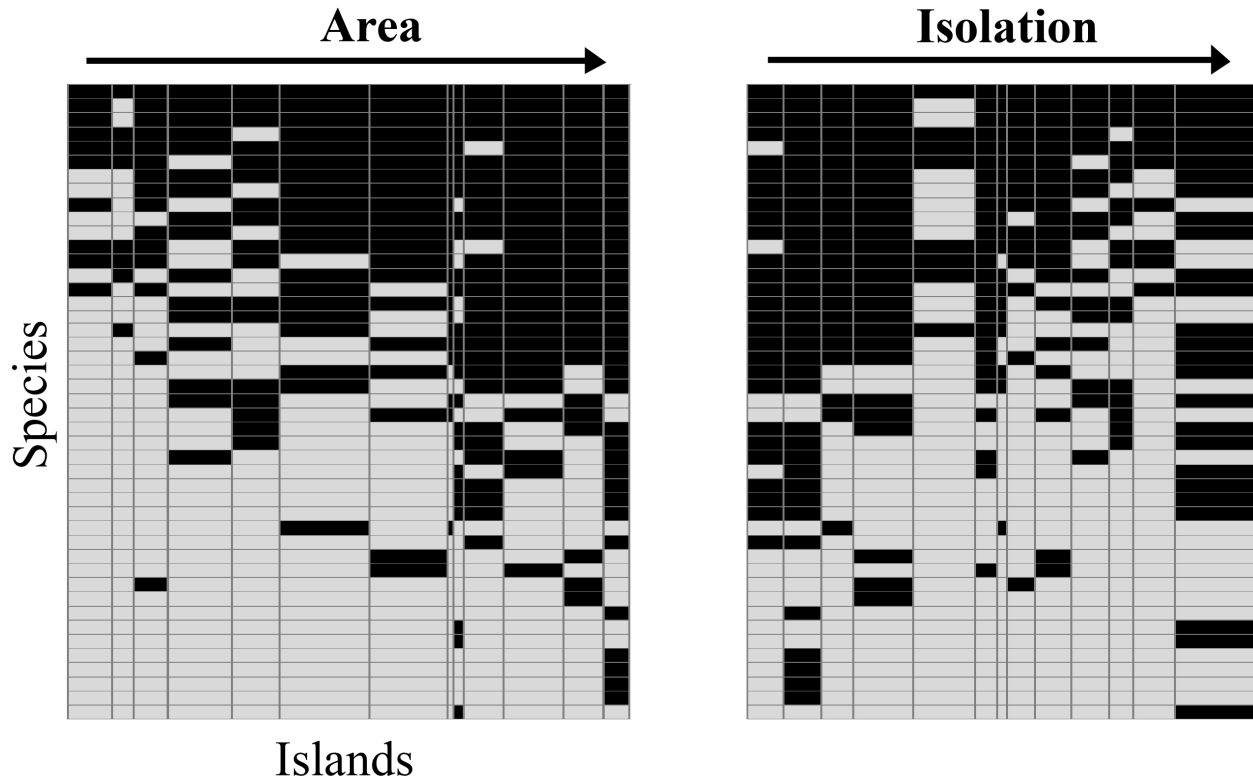
Figure 12: A visual representation of the weighted matrices, with the cell width corresponding to the weight assigned to each column based on the variable-space it represents. Isolation appears a great deal less nested when compared to both the weighted area-ranked matrix and the unweighted isolation-ranked matrix from Chapter 2.

for statistically significant differences between the area/isolation ranks and their respective null distribution values.

RESULTS

Area produced the strongest and the only statistically significant pattern of nestedness ($p<0.001$), while neither variable produced a strong pattern of modularity (Table 3, Figures 12 and 13). While area-ranked nestedness showed zero overlap with its null distribution, the isolation-ranked matrix was less nested (i.e., showed a higher number of deviations from perfect nestedness) than

32.8% of its null distribution. In the case of modularity, the area-ranked matrix showed 43.2%

overlap and ranking by isolation showed a 39.5% overlap.

Table 3. The results of the analyses and comparisons to their respective null distributions.

Nestedness:	Area-weighted Matrix			Isolation-weighted Matrix		
Ranked by:	**Random**	**Area**	**Difference**	**Random**	**Isolation**	**Difference**
Mean	12.567	9.005	-3.562	13.486	13.038	-0.447
Median	12.680	9.005	-3.676	13.629	13.038	-0.591
Maximum	14.125	9.005		15.959	13.038	
Minimum	9.345	9.005		8.797	13.038	
n=	1000	1		1000	1	
P value		<0.001			0.328	
Modularity:	**Area-weighted Matrix**			**Isolation-weighted Matrix**		
Ranked by:	**Random**	**Area**	**Difference**	**Random**	**Isolation**	**Difference**
Mean	17.542	17.063	-0.480	18.974	18.780	-0.194
Median	17.274	17.063	-0.212	19.037	18.780	-0.257
Maximum	21.483	17.063		21.479	18.780	
Minimum	16.081	17.063		17.466	18.780	
n=	1000	1		1000	1	
P value		0.432			0.395	

DISCUSSION

Broadly speaking, the results for the weighted analysis were similar to those found in Chapter 2

except that unlike in the previous chapter, ranking by isolation did not produce statistically

different nestedness values. These discrepancies raise the question of whether a weighted

approach of accounting for biases associated with ranking islands across particular

environmental gradients is necessarily a more accurate representation of the relationship between

those gradients and observed patterns of nestedness and modularity than a simple unweighted

matrix. In other words, in a world where there existed one Chesapeake Bay island for every

possible point on the area and isolation gradient, would the results of an investigation into the
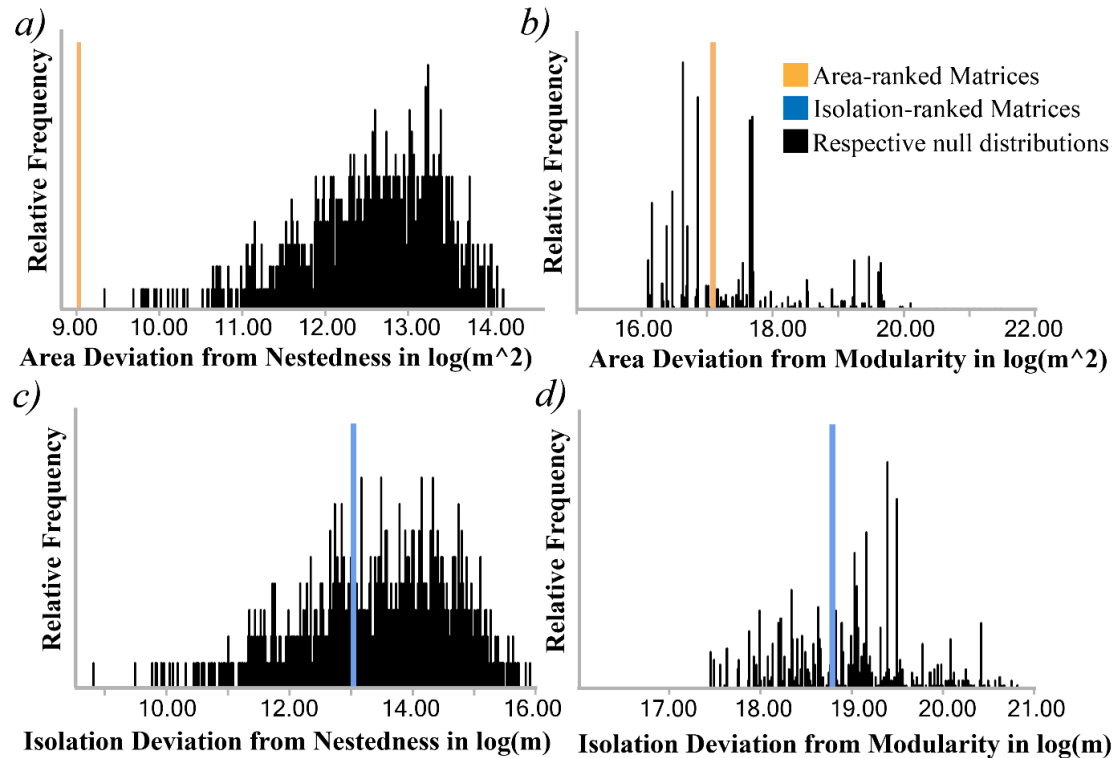
Figure 13: Four histograms showing a) the nestedness and b) the modularity when ranking by area, as well as c) the nestedness and d) the modularity when ranking by isolation, each with their respective null distributions (randomly ranked matrices). Only area and nestedness show a statistically significant relationship (p<0.001).

nestedness/modularity of the system agree more with a weighted analysis than it would with an

unweighted one? Despite this weighted method being designed to represent the effects of

different island characteristics on species distribution patterns in a more realistic way, the

particular mathematical approach used does have a few illogical implications, especially

involving the way that variable-space is "filled in" between islands. For example, if there is a

cluster of three islands close in area, but there is a large gap in the variable-space on one side of

the cluster, the island adjacent to this cluster would be assumed to occupy half of that large

variable-space, and be weighted accordingly, while the other two islands in the cluster would

only occupy a small variable space between themselves. Why should the one island adjacent to the large gap be so heavily weighted when the similarly sized islands in the cluster are lightly weighted? A solution to this problem might involve abandoning the need to "fill" the continuum with ranges of variable-space assigned to the islands, and instead simply weighting the islands by some metric of how over- or under-sampled their region of the continuum is.

A quantifiable answer to the question of which weighting technique more accurately represents a system would require simulations in which continuous species distributions are generated across a continuum of area or isolation, and random locations on the gradient are selected to represent the islands. These islands would then be used to create matrices with different weighting methods (no weighting, interpolating to midpoints, weighting by proximity to other islands, etc.), and if one method surpasses the others, it would suggest that it should be the method used going forward in these kinds of studies.

Alternatives to using weighted matrices at all include dividing up the continuum into even intervals and combining islands within their respective intervals. When looking for biogeographic patterns in presence-absence data across an elevational gradient Presley et al. (2012) did not sample the elevational gradient evenly, since it relied on previously collected specimens. The solution was to group specimens by interval (e.g., 1750–2000 m, 2000–2250 m, etc). Perhaps this would be a useful way to avoid the issue of naturally uneven sampling. It would also double as a way to smooth out the influence of confounding variables. For example, when ranking by isolation, the impact of area and habitat type on the patterns observed in the matrix might obfuscate any patterns associated with isolation. However, if the islands are combined into groups ("low isolation", "medium isolation", "high isolation"), each group could contain a variety of island areas and habitat types, allowing for the trend associated with the

variable of interest to be somewhat clearer. The main issue with this approach is that inevitably each grouping would be missing some combinations of island area and habitat type, allowing the confounding variables to continue bleeding through into the analysis of the focal variable. While this alone would be no worse than the unweighted one-island-per-column matrix, another more serious issue is that this interval-grouping method could result in uneven numbers of islands being assigned to each group, disproportionately increasing the species richness of some groups by the sampling effect alone.

If the weighted matrix method (or other methods such as grouping of islands) can be further developed, it may prove to be useful in correcting for the unevenly distributed characteristics of habitat patches across an environmental gradient to better understand how community composition changes along such gradients.

Although this chapter investigated the weighting of islands to correct for uneven sampling, these techniques can also be applied to species rather than only islands (i.e. rows rather than only columns). Perhaps the species could be weighted by probability of detection, with presence being weighted more heavily than absence for more cryptic species. The utility of weighting matrices may go beyond correcting sampling problems, extending into the weighting of species by conservation-relevant metrics like vulnerability to extinction (Minns 1987), dependence on the islands, or functional rarity (Violle et al. 2017). While many studies accomplish this focus on conservation-relevance by narrowing their studies to a few especially conservation-relevant bird species (Erwin et al. 2011), the use of weighted matrices can allow for a consideration of all the species in a community, without drowning out the most conservation-relevant ones (Minns 1987).

CHAPTER 4

CONCLUSION

The islands of the Chesapeake Bay represent an under-explored intersection between island biogeography, metacommunity structure, and conservation. While island biogeography is one of the oldest disciplines in all of ecology (Wallace 1863), the explicit idea that island systems—and to some degree, all patchy habitats—are linked by dispersal of their members, rather than being solely the product of random colonization events from the mainland, has only recently been examined in the context of metacommunity ecology (Leibold et al. 2004). Although many early forays into metacommunity theory were too eager to categorize their focal metacommunity composition as being dictated by either the neutral, patch dynamics, species sorting, or mass effects paradigm (Leibold et al. 2004, Brown et al. 2017), a more productive view of metacommunity dynamics is that of a multidimensional space defined by various characteristics of the environment and the biota (Logue et al. 2011). By exploring different regions of this space, perhaps one can map out the way that different metacommunities behave and interpolate the results to predict the behavior of less well-understood metacommunities, especially if these metacommunities also happen to be at conservation risk.

An important aspect of the behavior of metacommunities is the way that species compositions vary among communities, especially with respect to any consistent patterns within this variation. Two specific patterns are nestedness—the degree to which less-rich communities form nested subsets of the more-rich communities (Patterson and Atmar 1986)—and modularity—the degree to which species belong to modules of associated species that are never found without one another and never associate with other modules (Borthagaray et al. 2014). These patterns have

two very different conservation implications: nestedness implies that only the richest patches need be preserved to protect all species in the metacommunity (Patterson and Atmar 1986; Patterson 1987) while modularity implies that there are distinct clusters of species that each need to be given individual attention to preserve the metacommunity's biodiversity (Angeler 2013; Hill et al. 2017). If these patterns can be shown to correspond to gradients of particular patch characteristics, these characteristics can serve as predictive indicators for these patterns and serve as a guide to the types of patches one should prioritize for conservation prior to a complete survey of the biota (Wang et al. 2010).

Since the islands of the southern Chesapeake Bay exhibit a range of areas, degrees of isolation, and habitat types; they represent a great opportunity to conduct such a study. The fact that these islands are of such great conservation interest for their bird populations (Erwin et al. 2007) compounds the benefits of surveying and understanding them.

Ranking by island area showed the most nested pattern, while ranking by isolation proved to be more nested than chance. Habitat type rankings showed no particular nestedness compared to the random rankings. None of the variables were statistically significant predictors of modularity.

However, presence-absence matrices weight all islands equally. Since islands are ranked by continuous variables, an implicit assumption of this method is that the islands represent equal intervals within the variable-space in question. As a result, the assessment of patterns like nestedness and modularity using this matrix is biased towards regions of the variable-space that are oversampled. Since the islands themselves do not represent even intervals along any of the variables, one should not analyze matrices with such an assumption of equal intervals of variable-space between islands. For systems with unequal intervals, a weighted matrix can be

used such that each island is weighted according to the variable-space it represents, downplaying the importance of individual islands in over-sampled regions of the variable-space.

I created a matrix using the presence-absence data and weighted the presences and absences on each island by the amount of empty variable space that surrounded the island along a continuum of that variable. This produced similar results to the unweighted analysis, except that the strengths of the patterns when compared to their null distributions were observed to decrease.

The use of weighted matrices is worth developing further to evaluate its usefulness in the search for patterns of nestedness and modularity across patch characteristics. Not only is the weighting of islands potentially useful when accounting for uneven sampling, but the weighting of species by conservation relevance may allow for the problematic assumption of species equivalence seen in many presence absence matrices to be addressed (Minns 1987), while still maintaining the total-avifaunal perspective that has been overlooked in previous studies of the Bay.

Regardless of method, the data supports the idea that nestedness is greatest when islands are ranked by area. This is likely the result of the fact that unevenness in area produces uneven species richnesses (MacArthur and Wilson 1963) that in turn produce nestedness (Cutler 1991), and the fact that some species are more generalized or specialized (Patterson and Atmar 1986). In the case of modularity, if any modules exist within the system, it will take either a better quantification method or a more nuanced definition, perhaps invoking the hierarchical community structure described by Collins et al. (1993) in which there are overlapping metacommunities with different module boundaries.

The study reported here represents the first time, as far as I am aware, a standardized survey has been conducted across a multitude of Chesapeake Bay islands that incorporates all bird species

rather than a focal subset of the avifauna (Erwin et al. 2011), examining the patterns seen within

the Chesapeake Bay avian metacommunity as a whole. Furthermore, this study demonstrates

novel new approaches to the study of metacommunities and produces results that can be applied

to other systems.

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APPENDIX

COMPLETE PRESENCE-ABSENCE MATRIX

Species	Does Hammock	Upper Tump	Scarborough	Lower Bernard	Fishbone	Great Fox	Clump	Parker	Goose	Watts	Finney's	Swan	Port Isobel
American Oystercatcher (*Haematopus palliatus*)	■	■	■	■	■	■	■	■	■	■	■	■	■
Great/Lesser Black-Backed Gull (*Larus marinus/L. fuscus*)		■	■	■	■	■	■	■	■	■	■	■	■
Double-Crested Cormorant (*Nannopterum auritum*)		■	■	■	■	■	■	■	■	■	■	■	■
Great Egret (*Ardea alba*)	■	■	■		■	■	■	■	■	■	■	■	■
Laughing Gull (*Leucophaeus atricilla*)	■	■	■	■	■	■	■	■	■	■	■		■
Royal Tern/Caspian Tern (*Thalasseus maximus/Hydroprogne caspia*)	■	■	■			■	■	■	■	■	■	■	■
Brown Pelican (*Pelecanus occidentalis*)			■	■	■	■	■	■	■	■	■	■	■
Barn Swallow (*Hirundo rustica*)			■	■	■	■	■	■	■	■	■	■	■
Clapper Rail (*Rallus crepitans*)		■	■		■	■	■	■	■		■	■	■
Great Blue Heron (*Ardea herodias*)				■	■	■	■	■	■	■	■	■	■
Herring Gull (*Larus smithsonianus*)			■	■		■	■	■	■	■	■	■	■
Forster's Tern/Common Tern (*Sterna forsteri/S. hirundo*)	■	■			■		■		■	■		■	■
Mallard/American Black Duck (*Anas platyrhynchos/A. rubripes*)	■	■	■		■		■		■	■	■	■	
Snowy Egret (*Egretta thula*)	■			■		■	■	■	■	■	■	■	■
Osprey (*Pandion haliaetus*)		■	■				■	■	■	■	■	■	■
Seaside Sparrow (*Ammospiza maritima*)				■	■	■	■	■	■		■	■	■
Boat-Tailed Grackle/Common Grackle (*Quiscalus major/Q. quiscula*)				■	■		■	■	■	■	■	■	■
Canada Goose (*Branta canadensis*)	■						■	■	■	■	■	■	■
Tricolored Heron (*Egretta tricolor*)				■		■		■	■	■	■	■	■

Figure 14: The curated presence-absence matrix showing the bird species that were present on each island during at least one of the two visits each island received. Any species that migrated during the study window has been removed. For the sake of visual clarity, the species are ranked by the number of islands they occupy (although ultimately the ranking of species is irrelevant in this study), and the islands are ranked by their species richness.

Figure 14 (continued)

Species	Does Hammock	Upper Tump	Scarborough	Lower Bernard	Fishbone	Great Fox	Clump	Parker	Goose	Watts	Finney's	Swan	Port Isobel
Fish Crow (*Corvus ossifragus*)		■					■	■	■	■	■	■	■
Little Blue Heron (*Egretta caerulea*)					■	■		■	■			■	■
Song Sparrow (*Melospiza melodia*)			■	■		■		■				■	■
Black-Crowned Night Heron (*Nycticorax nycticorax*)			■	■				■		■	■		
Saltmarsh Sparrow/Nelson's Sparrow (*Ammospiza caudacuta/A. nelsoni*)				■	■			■	■		■		
Yellow-Crowned Night Heron (*Nyctanassa violacea*)				■						■	■	■	■
Carolina Wren (*Thryothorus ludovicianus*)				■						■		■	■
Glossy Ibis/White-faced Ibis (*Plegadis falcinellus/P. chihi*)			■					■				■	■
Bald Eagle (*Haliaeetus leucocephalus*)								■	■				■
Common Yellowthroat (*Geothlypis trichas*)										■		■	■
Gray Catbird (*Dumetella carolinensis*)										■		■	■
Northern Cardinal (*Cardinalis cardinalis*)										■		■	■
Black Skimmer (*Rynchops niger*)						■	■						
Brown-Headed Cowbird (*Molothrus ater*)												■	■
Least Bittern (*Ixobrychus exilis*)					■						■		
Marsh Wren (*Cistothorus palustris*)					■			■					
Peregrine Falcon (*Falco peregrinus*)		■									■		
American Bittern (*Botaurus lentiginosus*)											■		
Blue Jay (*Cyanocitta cristata*)													■
Cattle Egret (*Bubulcus ibis*)										■			
Downy Woodpecker (*Dryobates pubescens*)										■			
Great Crested Flycatcher (*Myiarchus crinitus*)													■
Green Heron (*Butorides virescens*)													■
House Sparrow (*Passer domesticus*)													■
Purple Martin (*Progne subis*)													■
White Ibis (*Eudocimus albus*)										■			
Island Species Richness	8	10	15	16	17	20	20	23	26	26	26	27	35

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SELECTED PRESENTATIONS

Bowers, G. W., E. L. Walters, and M. Leu. 2022. What kinds of islands host redundant versus unique bird communities? An analysis of the Chesapeake Bay's avian metacommunity structure. At the Association of Southeastern Biologists Conference, Little Rock, AR