The distribution and community ecology of breeding birds on the Antarctic Peninsula

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Abstract of the Dissertation

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Ecological communities are formed by the overlapping distributions of many species and can take on diverse patterns that depend on factors such as habitat suitability and species interactions. Much of the past development in the field has relied on the study of various model systems, the particulars of which demonstrate the diversity of different patterns and processes necessary to build consistent theories. In this dissertation, I lay the groundwork to develop the Antarctic Peninsula region as a new model system in which to examine community structure in an environment with unique properties. The Antarctic Peninsula has a number of features that make it an ideal system for fundamental community ecology, including a tractable number of bird species breeding on discrete rocky outcrops—an ideal setting to investigate metacommunity patterns. I collected data on the occupancy of all avian species using vessels of opportunity to access breeding sites, and aggregated abundance data for the four members of a particular guild of diving birds for which the survey history was extensive enough to allow a comprehensive analysis of population density. Results revealed that patterns in population density were dissimilar from those in occupancy, likely reflecting the influence of site-faithfulness. I also identify a novel habitat association for the occupancy of several species that was previously unrecognized as relevant to niche differentiation. The species distribution maps produced in this process are the most detailed ever prepared for most of the species in the region, and will be useful for conservation and management of Antarctic wildlife. This dissertation highlights the value of exploratory analysis and provides a new case study for the investigation of metacommunity ecology.

Dedication Page

To Emily, whose love and support has been with me every step of the way.

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CHAPTER 1: Introduction

Questions about species distribution patterns and the underlying causes for those patterns remain some of the most fundamental concerns of many ecologists. Where a species is found tells us much about its relationships to both biotic and abiotic aspects of its environment and, as anthropogenic change becomes faster and more pervasive (Steffen et al. 2011), understanding those relationships becomes increasingly important for conservation and ecosystem management. The field of community ecology has resulted in many theoretical frameworks for analyzing the distributions of multiple species occurring together, providing many useful insights into how and why species overlap in space and time (Mittelbach 2012).

The past century saw lively debates among community ecologists about the best way to measure the degree of overlap in species distributions, and how to identify those factors responsible for such patterns. One early debate centered on whether local assemblages of species had discrete boundaries and could be considered distinct "communities" (Clements 1916) or, alternatively, whether each species interacts with its environment more or less independently from other species, resulting in assemblages formed by many overlapping gradients (Gleason 1926). Clements' original notion of communities as highly discrete "superorganisms" was eventually abandoned, and Gleason's perspective was adapted by Hutchinson (1957) and MacArthur (1972) in the creation of the modern niche concept. This work, together with the competitive exclusion principle (Gause 1934), focused much of the field's attention on the role of interspecific competition in forming communities from overlap in species distributions. Bird distributions across South Pacific islands, for example, were described as evidence of so-called "checkerboard" distributions, in which species with similar niche-space seemed to exclude each other from habitat patches. The study of such checkerboard distributions emphasized the importance of competition (Diamond 1973, 1975, Gilpin and Diamond 1982) and precipitated a vigorous debate on how to adequately distinguish such patterns from those that could be generated by purely random processes (Connor and Simberloff 1979, Diamond and Gilpin 1982). Studying the distribution of trees in tropical forests, Hubbell (2001a) introduced the 'neutral' theory of biogeography by which community composition was explained by stochastic colonization and a lack of niche differentiation. In this way, Hubbell's neutral theory provided a null model against which to judge evidence for mechanistic processes such as competition. Though competition can play an important role in structuring communities, community ecologists have now begun to appreciate the role of additional deterministic forces; some communities, such as mammalian assemblages in montane habitats and island archipelagos, were found to have nested patterns, in which common species occur everywhere, but rare species are filtered out of some patches (Patterson and Atmar 2008). Recently, developments in metacommunity ecology have unified many of these points of view by highlighting how different patterns can emerge when spatial and temporal gradients interact with processes such as dispersal, extinction and colonization at both local and regional scales (Leibold and Mikkelson 2002, Henriques-Silva et al. 2013, Leibold and Chase 2018).

One fundamental difference in the way that many species assemblages have been studied relates to whether the underlying data represent measures of species occupancy (i.e., presence/absence, or detection/non-detection) or abundance. Abundance is more difficult to measure, but it has been shown that using abundance information can improve the accuracy of models to predict distributions (Estrada and Arroyo 2012, Yates et al. 2018). Using a meta-analysis, Weber et al. (2017) found that species distribution models based on occupancy data generally correlate with species abundance, however high environmental suitability did not always result in high abundance. Particularly relevant to this dissertation, Estrada and Arroyo (2012) implicated coloniality as one possible factor that may make occupancy models less predictive. For community ecologists, the utility of occupancy versus abundance data for understanding the relationships among different species remains unclear, and represents one of the motivations underlying my dissertation research.

As is often the case in other fields of science, crucial developments in community ecology often emerged from comprehensive data on species distributions from new study systems. Many of the well-known researchers in the field drew their inspiration from particular study systems, and the peculiarities of a single study system often serve to highlight only some of the ways in which process and pattern can be linked. Having a wide variety of case studies is important when documenting the diversity of ecological patterns for which empirical evidence exists (e.g., Logue et al. 2011). Similar to the many arguments made for reinvigorating the collection of basic natural history information (Futuyma 1998, Tewksbury et al. 2014), ecologists must have a diversity of examples with which to test and understand theories on the make-up and interaction of communities.

Polar environments like Antarctica provide a unique perspective, offering a useful contrast to many other systems. The poles represent the extreme ends of the well-established latitudinal species gradient, meaning that food webs and communities at high latitudes simply have fewer species (Willig et al. 2003). That simplicity makes it easier to comprehensively cover an entire functional or taxonomic group in a community analysis at larger spatial scales. For example, modeling all of the distributions or interactions among the birds of a tropical forest would be nearly impossible with the current state of knowledge, for two reasons: (1) too many species are so poorly studied that relevant data would be too sparse to draw reliable conclusions, and (2) the diversity of relevant factors, such as habitat requirements or species interactions, is so high that a truly comprehensive modelling approach would be paralyzingly complicated.

Breeding birds in the Antarctic Peninsula region offer a particularly valuable avenue for research. The emperor penguin (*Aptenodytes forsteri*), which is rare on the Antarctic Peninsula, breeds on sea-ice. Sixteen other species of birds (Table 1.1) require bare rock on which lay eggs, and because such rock generally exists in small patches surrounded by extensive glacial ice, breeding bird habitats in the region are discrete. The majority of the region's bird species are also colonial, tending to aggregate in space, beyond the natural aggregation due to habitat associations alone (McDowall and Lynch 2019). Many breeding bird sites host multiple species, often nesting in mixed aggregations. The discrete nature of habitat patches simplifies the problem of identifying the scale at which these species interact with the environment, making the network of multi-species Antarctic Peninsula breeding bird sites an almost textbook case of a metacommunity (Leibold and Chase 2018).

Compared with organisms in most other environments, Antarctic breeding birds also have relatively simple relationships to their habitat. With the exception of the snowy sheathbill (*Chionis albus*), a scavenger, all Antarctic birds are seabirds that derive all of their food resources from the ocean, supplemented in a few cases by predation or kleptoparasitism (i.e., theft of food) from other birds. The lack of extensive vegetation, or even deep soils in Antarctica, limits these seabirds to very simple nests; most nest on bare ground in simple nests of stones or in rocky crevices (Shirihai et al. 2007). Without complicated habitat requirements for the location of breeding sites, as might be common in forest or grassland environments, comprehensively modeling the distributions of Antarctic seabirds becomes more tractable. It is possible that competition for space at breeding sites may be important and some evidence suggests that direct interspecific competition may take place (Trivelpiece and Volkman 1979, Trivelpiece et al. 1984). However, the degree to which species interactions drive habitat use in these simple environments for the majority of the bird community remains unknown.

Variability in the Antarctic marine environment has the potential to impact breeding distributions of seabirds in a variety of ways, many of which remain poorly studied. Although many of the local marine communities are species rich, the Antarctic food web is dominated by the production of Antarctic krill (*Euphausia superba*) and many seabirds rely predominantly on krill as their main food source (Knox 2006). Seabirds are also central-place foragers, making repeated trips to and from their breeding colonies when nesting. This trait limits the geographic range in which many of the local species can forage during the breeding season with subsequent impacts of potential habitat associations (Rosenberg and McKelvey 1999). While much remains to be learned about marine habitat use among Antarctic breeding birds and differences in the way that foraging behavior may constrain the distribution of nesting sites, a few simple marine and terrestrial factors are likely sufficient to begin understanding the avian community structure in the region.

Another prominent feature the Antarctic is that until relatively recently the impact of human civilization on the region was much more limited than most other regions of world. The Antarctic was never settled by indigenous peoples and was not regularly visited by humans until the 19th century (National Research Council 1993). Although industrial-scale extraction of large marine mammals dramatically altered the populations of some species in the late 19th and 20th centuries, and areas around research bases may have been altered by anthropogenic activities, the basic structure of most terrestrial and marine habitats have remained virtually unchanged from pre-human states (National Research Council 1993). Of course, the area is now very much subject to the anthropogenic changes. Climate change has already altered air temperatures in some parts of the Antarctic almost as quickly as in the Arctic, the fastest-warming region on the planet (Mulvaney et al. 2012). Antarctic tourism has also dramatically increased in recent decades, and is highly concentrated in a few very small areas, raising the possibility of future direct impacts to terrestrial habitat such as invasive species and human disturbance (Bender et al. 2016). Most of the climate warming and virtually all of the tourism in the Antarctic have thus far been concentrated in the Antarctic Peninsula region, the roughly 1000 km mountainous peninsula and associated island groups that extend northward from the continent towards the southern tip of South America (Figure 1.1). Therefore, studies of the Antarctic Peninsula at this moment allow ecologists to document how an environment transitions from nearly undisturbed to heavily impacted by human activity.

1.1: Available data

Given the remoteness of the Antarctic Peninsula, a surprising amount of effort has been expended in establishing comprehensive occurrence and abundance data for many of the most common bird species. Over the past several decades, many authors have both mapped and documented population trends at many breeding bird sites, focusing primarily on the more easily surveyed, open-nesting species, such as penguins (e.g., Croxall and Kirkwood 1979, Poncet and Poncet 1987, Woehler 1993, Woehler and Croxall 1997, Naveen et al. 2000, Naveen 2003, Harris 2005, Harris et al. 2011, Naveen and Lynch 2011, Lynch et al. 2013). Many of the data in the past twenty years were collected from vessels of opportunity (e.g., commercial cruise ships) under the auspices of a project called the Antarctic Site Inventory (ASI), a private research partnership between several academic institutions and the non-profit organization Oceanites, Inc.

ASI surveys have permitted a more extensive exploration of the coastline than was possible when the scientific presence in the region was primarily restricted to staff located at research stations. Population estimates for some species are also now available from satellite imagery (Lynch et al. 2012b) and unmanned-aerial drone photography (Borowicz et al. 2018). The rapid expansion of data for the region has necessitated the development of an online data discovery tool (Humphries et al. 2017) for Antarctic seabird distribution and abundance. While many species have been surveyed quite extensively (Naveen and Lynch 2011), some are difficult to detect at nesting sites and have correspondingly less well-known distributions. Nevertheless, the wealth of data on breeding birds now makes it possible to start piecing together information on the distribution of all Antarctic seabirds throughout the Antarctic Peninsula region.

In this dissertation, I set out to use what is known about bird nesting locations in the Antarctic Peninsula region to first map breeding distributions, and then use those results to probe the structure of this metacommunity. My fundamental goal was to introduce a new example study system to the field of community ecology, taking advantage of the simple, discrete terrestrial habitat and relatively small number of species to allow careful examination of an entire community, free from the many complications present in other systems at lower latitudes. In many ways, the Antarctic Peninsula breeding bird community is a living ecological laboratory, offering great potential to examine patterns and processes. My first step (Chapter 2) was to build upon the well-established abundance data available for penguins to include a population analysis of the Antarctic shag (*Phalacrocorax* [*atriceps*] *bransfieldensis*), the only non-penguin member of the guild of pursuit-divers (i.e., seabirds that hunt prey by propelling themselves while underwater). The next step (Chapter 3) was to use presence/absence data collected on vessels of opportunity to construct a set of single-species occupancy models for the entire suite of species present in the region. Using the results from that occupancy model and the abundance data for the pursuit-divers, I then complete an analysis of the metacommunity structure for all of the region’s birds, exploring how observed patterns compare to predictions based on competing theories of community assembly (Chapter 4). Finally, the exploration of the pursuit-diver distributions revealed casual observations of a possible connection between the breeding distribution of the gentoo penguin (*Pygoscelis papua*) and a previously underappreciated habitat covariate, which I then explore (Chapter 5). Together these steps establish the Antarctic Peninsula breeding bird metacommunity as a model system for community ecology.

Common Name	**Species Name**	**Code**
Adélie penguin	*Pygoscelis adeliae*	ADPE
Antarctic shag	*Phalacrocorax* [*atriceps*] *bransfieldensis*	ANSH
Antarctic tern	*Sterna vittata*	ANTE
black-bellied storm-petrel	*Fregetta tropica*	BBSP
brown skua	*Stercorarius antarcticus*	BRSK
cape petrel	*Daption capense*	CAPE
chinstrap penguin	*Pygoscelis antarcticus*	CHPE
gentoo penguin	*Pygoscelis papua*	GEPE
kelp gull	*Larus dominicanus*	KEGU
macaroni penguin	*Eudyptes chrysolophus*	MACP
snow petrel	*Pagodroma nivea*	SNPE
snowy sheathbill	*Chionis albus*	SNSH
south polar skua	*Stercorarius maccormicki*	SPSK
southern fulmar	*Fulmarus glacialoides*	SOFU
southern giant petrel	*Macronectes giganteus*	SGPE
Wilson's storm-petrel	*Oceanites oceanicus*	WISP

Table 1.1: Breeding birds of the Antarctic Peninsula region, including four-letter codes used in figures.

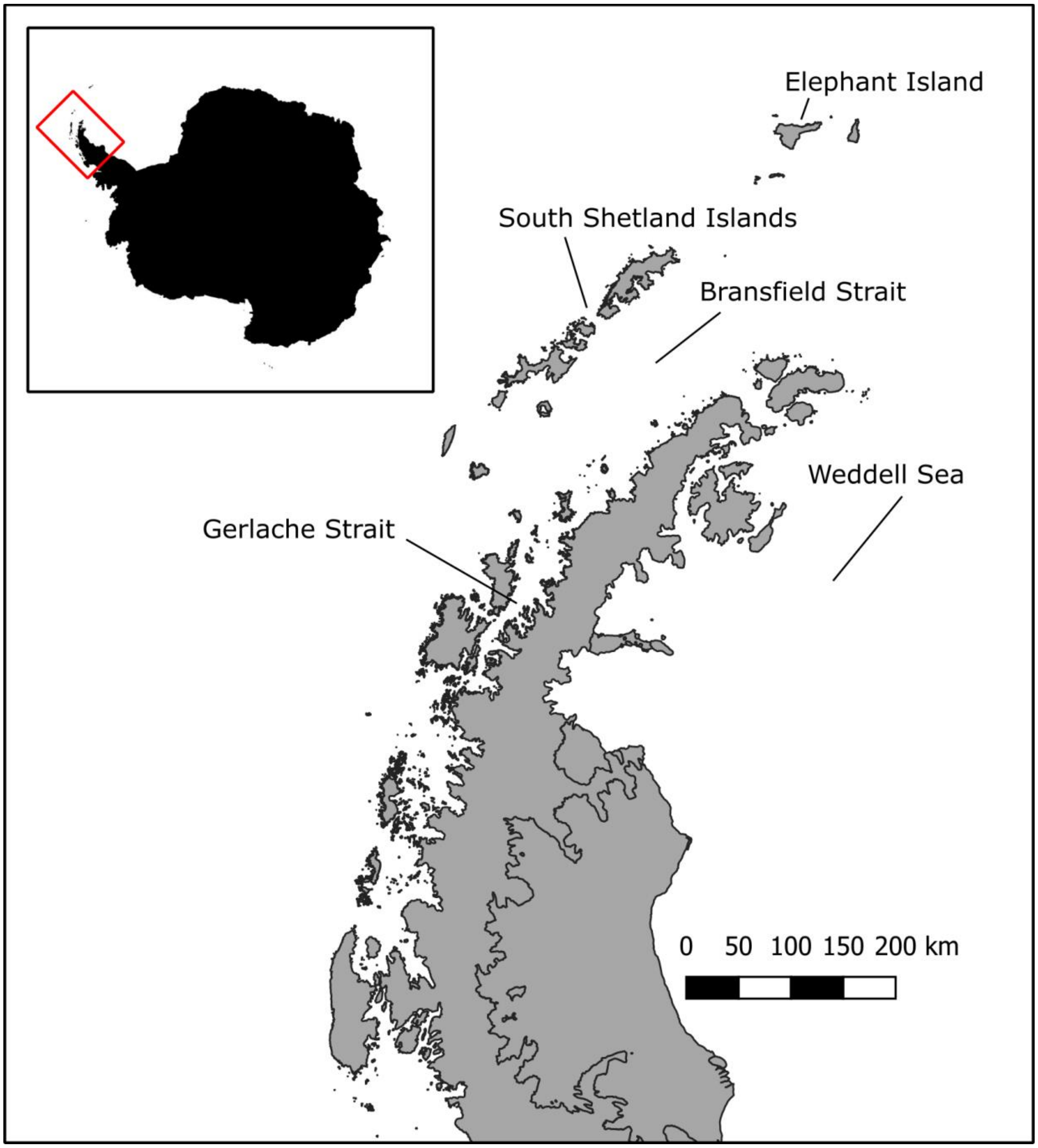

Figure 1.1: Map of the Antarctic Peninsula region.

CHAPTER 2: Population status of the Antarctic shag (*Phalacrocorax* [*atriceps*] *bransfieldensis*)

2.1: ABSTRACT

Antarctic shags (*Phalacrocorax* [*atriceps*] *bransfieldensis*) are the southernmost cormorants in the world, and assessment of their conservation status has been complicated by the logistical challenges of obtaining regular estimates of population size, as well as by taxonomic ambiguity of the blue-eyed shag complex. I review the available information on the taxonomy, distribution, and population size of Antarctic shags and present a refined estimate of the global population: 11,366 breeding pairs, plus an additional 1984 pairs of uncertain taxonomic status in the South Orkney Islands. The analysis suggests a possible spatial shift in the distribution of Antarctic shags similar to that reported for other Antarctic seabirds, which likely reflects a gradient in environmental changes along the western Antarctic Peninsula. This review will aid in future conservation and management assessments.

2.2: INTRODUCTION

Antarctic shags (*Phalacrocorax* [*atriceps*] *bransfieldensis*) inhabit the Antarctic Peninsula and surrounding island groups, making them the southernmost nesting members of the cormorant family (Phalacrocoracidae). While a considerable body of work has focused on Antarctic shag biology, particularly on diet and reproductive success (reviewed by Casaux and Barrera-Oro 2006), attempts to comprehensively assess their geographic distribution and total abundance have been relatively few. To address this information gap, I have compiled all publicly available information on Antarctic shag populations to identify what is known and, importantly, what remains unknown about their distribution, abundance, and any trends in abundance.

A comprehensive understanding of shag population distribution and abundance is required to quantify their role in the Antarctic food web and to identify breeding locations of particular importance to their conservation. Importantly, Antarctic shags differ from other diving seabirds of the region (e.g., most penguins) by predominantly consuming a variety of demersal fish rather than subsisting primarily upon krill (Casaux and Barrera-Oro 2006), making them potential indicators of fish populations that are themselves difficult to survey. The first step in developing shags as an indicator species would be an analysis of their population trends (Casaux and Barrera-Oro 2016). Several authors have found evidence of population declines at certain colonies or regions, suggesting that shags may be declining more generally (Naveen et al. 2000, Woehler et al. 2010, Coria et al. 2011, Casaux and Barrera-Oro 2016), but since the extent of interannual dispersal of Antarctic shags between colonies is unknown, it is difficult to draw conclusions about changes in population size without examining the entire population.

Despite being understudied relative to the region's penguins, the Antarctic shag plays a particularly important role in the designation of Important Bird Areas (IBAs) in the Antarctic Peninsula and surrounding island groups (Harris et al. 2011). Of the 43 IBAs identified by treating colony sites as points (as opposed to aggregating over larger areas), more than half (23) were triggered solely by shag congregations that exceeded 1% of the global population of the species. At the time of that report, many of those colony sites identified as IBAs had last been surveyed in the 1980s; population updates for these colonies, or for the global population, would likely refine the identification of bird 'hotspots' in the region. A comprehensive assessment of the global population size of Antarctic shags has been complicated by the uncertainty and debate surrounding the taxonomy of the blue-eyed shag complex, as past population estimates, including those available to Harris et al. (2011), have included colonies that may be appropriately treated as South Georgia shags (*P. georgianus*). For this reason, a complete analysis of shag populations in the Antarctic requires careful consideration of shag taxonomy.

2.2.1: Taxonomy

Throughout much of the 20th century, shags in the Antarctic Peninsula were considered conspecific with other shags throughout much of the Southern Ocean (e.g., Watson 1975, Harrison 1985), and usually named *P. atriceps*, with several English names that were primarily variants of blue-eyed shag or imperial cormorant. In Siegel-Causey's (1988) phylogeny of the Phalacrocoracidae, constructed using osteological characters, the blue-eyed shags were given their own genus (*Notocarbo*) within a subfamily (Leucocarboninae). The author described the Antarctic shag (*N. bransfieldensis*) as inhabiting "the Palmer Peninsula of Antarctica and islands along the Scotia Arc", and considered it distinct from the South Georgia shag (*N. georgianus*), which was described as "restricted to the Scotia Arc". In their widely-used taxonomy, Sibley and Monroe (1990) cited Siegel-Causey (1988) in their decision to keep these as separate species in the genus *Phalacrocorax*, though other authors continued to lump the blue-eyed shag complex together into *P. atriceps* (e.g., Johnsgard 1993). Most current taxonomies treat *georgianus* and *bransfieldensis* as separate taxa within a super-species that includes several other 'blue-eyed' shags around the Southern Hemisphere (Clements et al. 2016, Gill and Donsker 2017), though there remains disagreement about the genus name (*Phalacrocorax*, *Notocarbo*, or *Leucocarbo*). Other current taxonomies treat them as conspecific, retaining the names *georgianus* and *bransfieldensis* as subspecies, arguing that the differences between these taxa have never been rigorously documented (Orta et al. 2017). The current IUCN Red List still treats *georgianus* and *bransfieldensis* as subspecies of the imperial shag (*P. atriceps*).

All field-observable characters distinguishing *georgianus* and *bransfieldensis* from other blue-eyed shag forms, and especially from each other, are subtle and subject to much individual variation (Shirihai et al. 2007). The Antarctic shag (*bransfieldensis*) has more extensive white on the sides of the head, back, and perhaps outer scapulars than the South Georgia shag (*georgianus*), with small differences in average length (*georgianus*: 72-75 cm, *bransfieldensis*: 77 cm) and wingspan (*georgianus*: 27.0-30.4 cm, *bransfieldensis*: 32-33 cm). However, these differences are so slight that any field identification of live birds is based solely on range (Shirihai et al. 2007).

Regardless of whether the Antarctic and South Georgia shags are treated as distinct species or subspecies, all recent major taxonomies list the Antarctic shag as inhabiting the Antarctic Peninsula, South Shetland Islands, and Elephant Island, and the South Georgia shag as inhabiting South Georgia, Shag Rocks, South Sandwich Islands, and South Orkney Islands (Figure 2.1). Little information exists as to why the South Orkney Islands should be considered the southernmost extent of South Georgia shag, rather than the northernmost extent of Antarctic shag, and I have found no published evidence to support this boundary. The species/subspecies assignment of shags in the South Orkney Islands is important because that island group is traditionally managed together with the Antarctic Peninsula and South Shetland Islands. Previous summaries of shag populations, including those used in the designation of IBAs, have used the total population of shags from the South Orkneys together with those from the Antarctic Peninsula and South Shetland Islands (Harris et al. 2011). While management decisions could use either species or sub-species as taxonomic units, any thresholds based on a proportion of total population depend on the assignment of island group to either one or the other taxon.

For the purposes of this assessment of shag populations, I consider the Antarctic shag to be a distinct taxon from the South Georgia shag, and adopt the names *Phalacrocorax* [*atriceps*] *bransfieldensis* and *P*. [*atriceps*] *georgianus*, respectively, to reflect the continued ambiguity of their species status. I present summaries of known populations, and discuss the impact on IBA designations when the South Orkney Islands are and are not included in population totals.

2.3: METHODS

Shag population data were collected from as much of the published and 'gray' literature as could be obtained (Table 2.1 and the database located in the online supplemental material). This effort began with online searches of published literature using all forms of the common and scientific names of the species. For colonies at or near research stations, I attempted to fill in data gaps by contacting individuals who I believed may have knowledge about unpublished data. Any relevant studies or publications were searched for mentions of abundances, and any such data were associated with a location using either geographic coordinates or names of localities. The overarching strategy was to collect any abundance data on breeding aggregations from any location, and then standardize those data to a single metric by making reasonable assumptions about how different types of data could be compared.

One of the most challenging aspects of this process was determining whether data from different sources referred to the same or different breeding locations, as location names often vary among research groups. I was fortunate that a few research programs had maintained relatively comprehensive records of data collected at many different locations, reducing the time spent cross-validating sources. One such source contained archival data collected by S. and J. Poncet, which are referenced in Harris (2006) and Harris et al. (2011), and were provided directly by S. Poncet for this manuscript (pers. comm. 2017; hereafter referred to as ‘Poncet archival data’). Many data came from visits by the Antarctic Site Inventory (ASI; Naveen et al. 2000, Lynch et al. 2008, Lynch et al. 2013, Casanovas et al. 2015). Counts from any site with breeding shags visited by the ASI were taken from the most recent season available from surveys published by Lynch et al. (2013) and Casanovas et al. (2015), and then updated with any more recent ASI data (Lynch unpublished data). I note that there are likely to be additional unpublished datasets that I was unable to find and hope that my review highlights areas where additional existing data, were it published or otherwise made available, might be used to fill in gaps.

Methods for measuring population size differed among data sources, mostly relying on counts of physical nest sites (raised mounds of mud, excreta, and often plant material) that were judged active by the presence of eggs, incubating adults, or chicks. Occasionally counts were reported as the number of adults or chicks present. Antarctic shag nests situated on relatively flat rock outcrops are generally accessed on foot and can be observed either with the naked eye or from higher vantage points using binoculars. Nest sites on rock ledges or steep rocky slopes are generally counted from offshore vessels using binoculars.

The number of breeding pairs was used as the unit of choice for my population assessment, and I used the most recent count of breeding pairs available. This metric was chosen both because the majority of abundance records were measured in breeding pairs and because it is the measurement least likely to be influenced by intra-annual changes in phenology and attendance. When census numbers were reported as total number of adults (Shuford and Spear 1988) the total number of breeding pairs was estimated by dividing the count by 1.5, which is the median ratio of adults:nests visible in eight photographs of Antarctic Peninsula shag colonies (from various places and times available to the authors). Because nests are established within a phenological window and failed nests are abandoned, there can be significant intra-seasonal variation in the number of active nests at a site; repeated nest counts of the same population will fluctuate accordingly. In years with greater than two counts of the same type the maximum was used, in the interest of obtaining a population estimate as close to the true number of active breeding pairs during the peak of the nesting season. If counts of more than one type (i.e. nests and chicks) were available from a single season, priority was given to nest counts as the most direct measure of the number of breeding pairs. This is because some breeding pairs may have failed to hatch chicks, and because the number of surviving chicks at the colony at any one time requires additional assumptions regarding the number of chicks per nest (see below). Because the number of chicks decreases near the end of the breeding season due to fledging and chick mortality, I made the assumption that late-season chick counts were less reflective of the breeding population than nest counts from recent past breeding seasons. Four such late-season chick counts were discarded in favor of slightly older nest counts (Petermann Island: chick count on 25 Jan 2016 replaced by nest count on 20 Jan 2015; Andresen Island: chick count on 22 Jan 2016 replaced by nest count on 16 Jan 2013; Uruguay Islands: chick count on 24 Jan 2016 replaced by nest count on 21 Jan 2015; and Port Charcot: chick count on 17 Feb 2016 replaced by nest count on 21 Dec 2014). The remaining counts of chicks were converted to an approximate number of breeding pairs using a conversion factor of 1.7 chicks/pair. This value is the median ratio from all records (n=66) in the ASI database which counted both nests and chicks in the same visit.

Shag presence is confirmed at several colonies, but without an estimate of abundance, by Harris et al. (2011). In three such cases I was not able to find an alternative source for a population estimate. To estimate the number of shags that might therefore be unaccounted for in the global total, I imputed these missing abundances by sampling with replacement from the distribution of colony sizes and summing these three samples to represent the missing population; repeating this bootstrapping procedure 10,000 times yielded a probability distribution for the missing abundance.

Estimates of uncertainty were provided for some but not all of the counts reported in the literature, and were summarized by five categories: (I) < 5%, (II) 5-10%, (III) 10-25%, (IV) 25-50%, and (V) order of magnitude. Following the treatment of observation error by Che-Castaldo et al. (2017), I treated observation error as a log-normal process. A confidence interval (95%) for the estimate of shag population size was calculated using 10,000 random draws from a log-normal distribution for each colony, using the following scale parameters (see Che-Castaldo et al. (2017) Supplementary Data 2): (I) 0.025, (II) 0.050, (III) 0.120, (IV) 0.230, and (V) 0.510. Those counts with no uncertainty provided were assigned to category IV. While this method of measuring uncertainty is well suited to modeling observation error of counts, it does not include any error associated with other factors such as intra-annual changes in numbers of active nests or possible changes in population since the most recent count at many colonies.

Although long-term data on Antarctic shag populations are scarce, I attempted to document changes over time using two methods. First, for 46 colonies I had both a recent population estimate (≥2005-06) and a ‘historic’ population estimate (<1995-96), and used the difference in estimated abundance as a metric for long-term change in the population at that location. Second, time series of abundance at sites with at least 10 years of available population estimates were examined directly to assess temporal change. These time series are largely limited to the last twenty years, but provide a more nuanced picture of dynamics and interannual fluctuations than the simple decadal comparison.

2.4: RESULTS

I identified 185 active colonies of shags, representing a population of 13 230 breeding pairs, including 12 colonies of shags (1984 pairs) in the South Orkney Islands (online database) that might be considered South Georgia shags. The bootstrap procedure for the three populations with no abundance data (Cape Lindsey, Stinker Point, and Upper Island) suggested roughly 120 pairs (Appendix 1) might be missing from these known but unsurveyed colonies, which when added to the census total results in a total estimated population of 13,350 breeding pairs. Excluding the South Orkney Islands, the total population of Antarctic shags is estimated to be 11,366 breeding pairs distributed across 173 active colonies. Approximately 88% of the shag colonies (accounting for about 80% of the population) had some level of uncertainty reported with the most recent count. Using my lognormal model for observation error I calculated 95% confidence intervals of 12,788—15,018 for the entire population, and 10,846—12,926 for the population excluding the South Orkney Islands. Colony size is well described by a log-normal distribution (Appendix 2) and, accordingly, a relatively small number of large colonies represent the bulk of the total population. For example, there are only 11 colonies with more than 200 breeding pairs and collectively these colonies account for 41% of the total Antarctic shag population.

I identified 46 colonies for which recent and ‘historic’ population data were available (Figure 2.2A, colored diamonds), and discovered an unambiguous latitudinal boundary (in northern Marguerite Bay), north of which shag populations appear to have mostly declined or remained stable and south of which shag populations appear to have generally increased. Shags have also increased at a single large colony near the Weddell Sea (Cockburn Island), at the northeastern range edge. Data from Delaite Island, in the central Gerlache Strait, are difficult to interpret; while no nests were recorded in 1989-90, the population estimate of 115 from 2016 is broadly consistent with a count of 60 nests in 1983-84 (Poncet archival data), suggesting a small overall positive trend in a region otherwise characterized by declining populations.

Using data originally published by Casaux and Barrera-Oro (2016) and additional data from the ASI (Lynch et al. 2013 and Lynch, H. unpublished data) and S. Poncet (archival data), I was able to assemble reasonably comprehensive time-series for 10 colonies (Figure 2.2B-K). The two colonies described by Casaux and Barrera-Oro (2016), Harmony Point and Duthoit Point, exhibited declines (Figure 2.2B,C, respectively), as did the Orne Islands (Figure 2.2E). Seven other colonies showed no apparent trends (Figure 2.2D,F-K). Orne Islands, being the smallest of the ten colonies with extensive time series, had 13 breeding pairs in the 1994/95 season but declined to extinction five years later. It is notable that while there was no overall trend at the large Paulet Island colony (Figure 2.2D), there were large (2- to 3-fold) fluctuations in abundance during the mid- to late-2000's. At Petermann Island (Figure 2.2J) an abrupt increase in 2012/13 was the result of a new sub-colony that was established on the southern end of the island, ~0.5 km away from the original breeding colony. The birds around Petermann Island are not marked, making it impossible to say how many of the birds in the "new" colony may have relocated from the old colony, however the roughly three-fold increase in population in a single season at a new location is unlikely to have occurred without substantial immigration.

Site Name	**Lat**	**Long**	**Season**	**Pop Estimate**	**Source**
Emperor Island	-67.865	-68.710	2012	810	Casanovas et al. 2015
Cockburn Island	-64.201	-56.841	2006	800	Lynch et al. 2013
Paulet Island	-63.580	-55.788	2011	548	Lynch et al. 2013
Ginger Island	-67.749	-68.686	2012	504	Casanovas et al. 2015
Rocks near Andersson Island	-63.560	-56.486	2015	331	H. Lynch unpub. data
Avian Island	-67.773	-68.886	2016	321	W. Fraser unpub. data
Pearl Rocks	-63.590	-59.890	1986	310	Poncet archival data
Barcroft Islands area	-66.458	-67.140	2012	292	Casanovas et al. 2015
Lagotellerie Island	-67.890	-67.402	2012	270	Casanovas et al. 2015
Joubin Islands	-64.774	-64.399	1986	250	Poncet archival data
Islet E of Guepratte Island	-64.493	-62.955	1986	220	Poncet archival data

Table 2.1: List of major Antarctic shag breeding locations (greater than 200 breeding pairs). Abundance data are from the last available census.

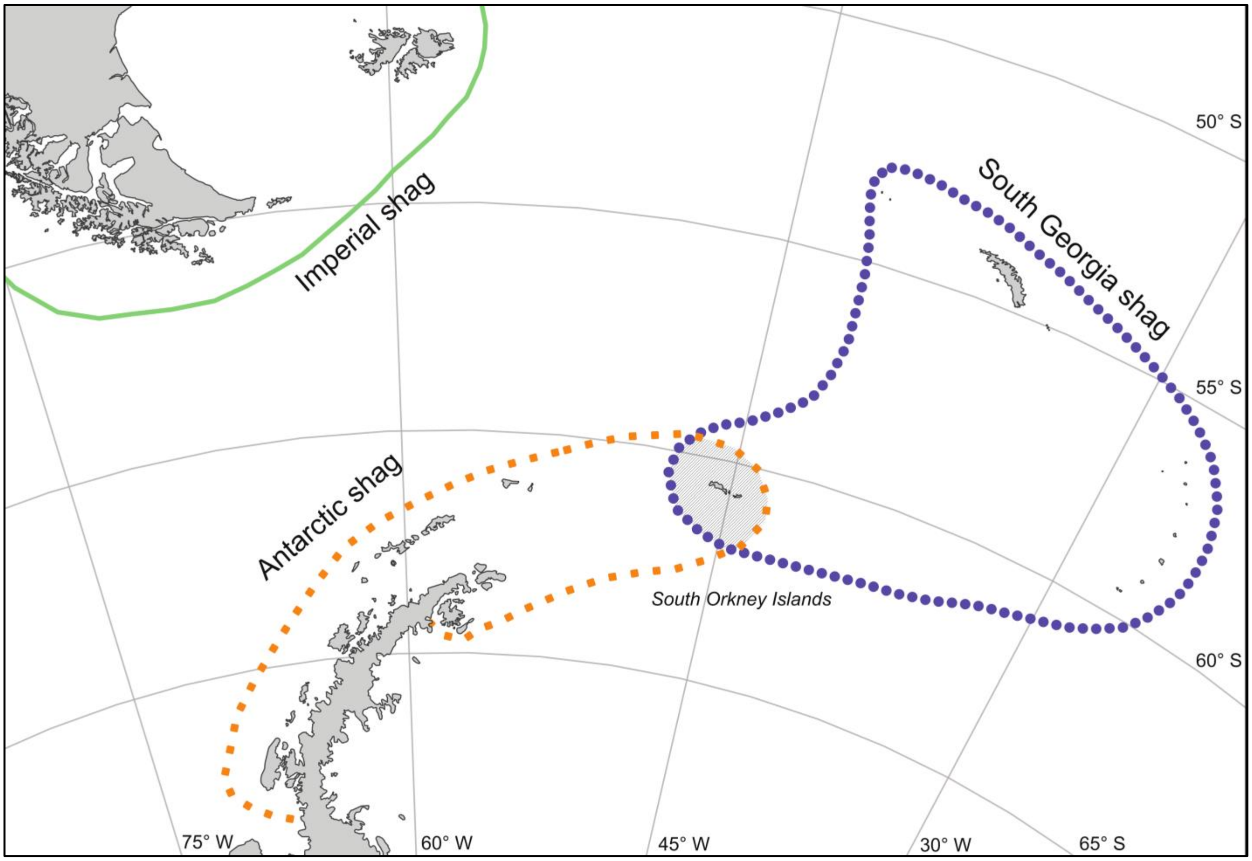

Figure 2.1: Ranges of the three generally recognized taxa of blue-eyed shags in the Scotia Sea region. Shags in the South Orkney Islands are most often described as South Georgia shags, however some sources have considered them Antarctic shags.

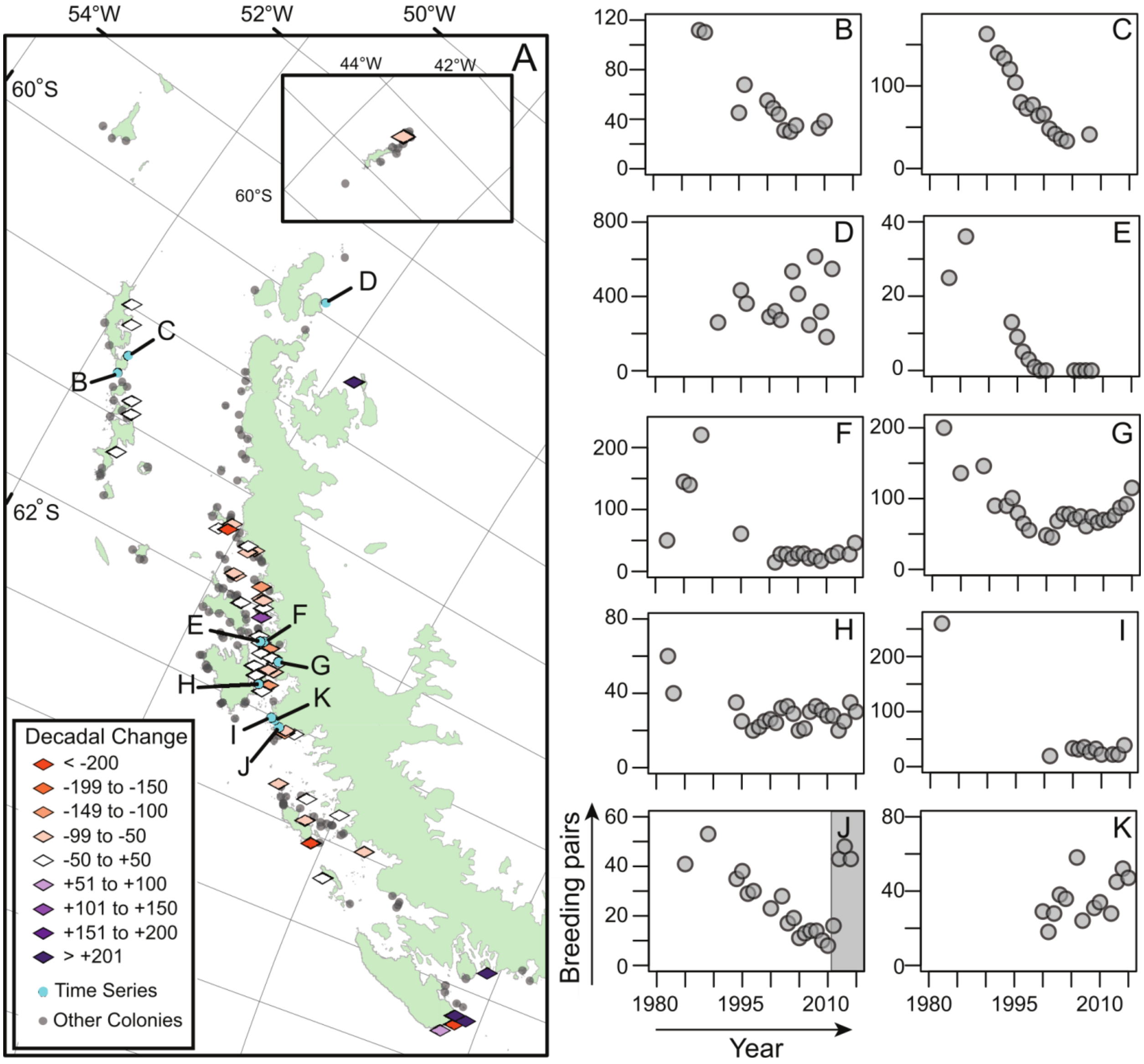

Figure 2.2: Map of known Antarctic shag breeding colonies, including colonies of shags (presumed South Georgia shag) in the South Orkney Islands (inset). Colonies with population estimates across decades are displayed as diamonds, color coded to indicate the apparent change from pre-1995 to post-2005. Side panels (B-K) display available population (number of breeding pairs) time series for B: Harmony Point[1], C: Duthoit Point[1], D: Paulet Island[2], E: Orne Islands[2], F: Cuverville Island[2], G: Brown Station[2], H: Jougla Point[2], I: Port Charcot[2], J: Petermann Island[2,3], K: Pleneau Island.

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[1] Data from Casaux and Barrera-Oro (2016).

[2] Data from pre-1994 come from Poncet archival data, including pers. comm. from J.J. Argoud (F: 1983) and C. Verheyden (I: 1991).

[3] Shaded region indicates the establishment of a new sub-colony elsewhere at the site.

2.5: DISCUSSION

Excluding the shags (arguably South Georgia shags) inhabiting the South Orkney Islands, I estimate the global population of Antarctic shags to be 11,366 breeding pairs, distributed across 173 active colonies. This is very close to the c.11,000 pairs usually cited (Shirihai et al. 2007, Orta et al. 2017). Including the twelve known colonies in the South Orkney Islands increases the total population size to 13,350 breeding pairs. This chapter is the most comprehensive review of the Antarctic shag population ever undertaken, and by describing in detail what is known and unknown about the distribution and abundance of Antarctic shags, I hope to establish a baseline of information that can be updated and corrected over time by the community.

It should be noted that 94 (54%) of the 173 active Antarctic shag colonies (accounting for about 45% of the total population) were last surveyed in or before the 1980's. The large span of time over which the most recent surveys were conducted, when combined with the apparent presence of both increasing and decreasing trends throughout the region, forces us to consider my estimate of the current population to be only approximate. In addition, the method of calculating confidence intervals does not incorporate uncertainty from outdated counts. The shag population at Astrolabe Island, along the northwestern Antarctic Peninsula, is one example of a site that needs to be resurveyed. A visit there in November 2015 noted the presence of many shags but was unable to obtain a population estimate (Foley, C. pers. comm. 2016). The observers noted that the number of nests may have been as high as 500, much higher than the January 1987 count of 154 cited by Harris et al. (2011). If true, this would make it the seventh largest colony known and increase the total population size by ~3%, to 11,661. It is not clear whether the apparent (but unverified) increase in shags at that location is due to a genuine increase in abundance (a notable exception to the north-south divide in population trends) or a failure of the original survey to adequately count shags nesting out of sight along the uppermost plateau. I suggest that seabird researchers prioritize the collection of shag census information from those larger colonies that have not been surveyed in several decades.

Although there are only a limited number of colonies that have been surveyed with high frequency, I find compelling evidence of a spatially explicit pattern of increases at the edges of the range (Marguerite Bay in the south and the Weddell Sea in the east) and a mix of both stable and declining colonies throughout the rest of the range. The best information on trends comes from the ten sites where it was possible to construct a detailed time series. The two colonies exhibiting clear population declines over the entire time series were those studied by Casaux and Barrera-Oro (2016), on Nelson Island, in the South Shetland Island group (Figure 2.2B-C). Most of the other colonies did not show clear trends over similar time scales, either because data for the 1980’s-90’s were lacking, or because of large variability in counts. This variability is observable on decadal scales, such as the large growth followed by large decline at Cuverville Island through the 1980’s-90’s, followed by a stable, smaller population in the 2000’s. A similar pattern could have occurred at Port Charcot (Figure 2.2I), but with only one count from the early 1980’s it is difficult to draw many conclusions.

The large number of relatively small shag colonies (i.e. < 50 nesting pairs) is in striking contrast to the distributions of the region’s other diving seabirds (i.e. penguins) that are rarely found breeding in such small groups. The persistence of small colony sizes may reflect weaker Allee effects in shags than in penguins. Connectivity and dispersal among colonies may also be relatively high in this species, compared to other seabirds in the region. It has been observed that the region’s shag colonies form and disappear more readily than penguin colonies (Poncet, S. pers. comm. 2017), and I identified ten locations that once had but no longer have, breeding shags. Two of those locations (Christine Island and Elephant Rocks) are in the Palmer Station area, and were impacted by the *Bahia Paraiso* oil spill in 1989. This event likely accounts for the disappearance of shags in these locations as well as the severe decline at nearby Cormorant Island (Fraser, W. pers. comm. 2017). With these exceptions, there are no obvious drivers for the other colony extirpations. Instead, this pattern of intermittent occupancy is consistent with a shag metapopulation defined by quasi-static populations connected by dispersal. Several of the smaller colonies not surveyed in recent decades may have subsequently gone extinct, and it is impossible to know how many of the colonies documented in recent years were not present in the past. Given the potential for adult dispersal among colonies, establishing a list of breeding locations for Antarctic shags may involve a catalog of suitable locations that fluctuate in occupancy status.

Where I had the opportunity to observe intra-seasonal dynamics, I found dramatic fluctuations in the number of active nests even within the span of a few weeks, particularly when nest abandonment causes a sharp drop in the number of occupied nests (Lynch, H. unpublished data). Very little is known about patterns of breeding phenology in Antarctic shags, making it very difficult to estimate how close any particular count is to the true number of pairs attempting breeding in any given year. As such, any given count represents a minimum number of actively breeding pairs in each year. This is one of several reasons why my estimates of uncertainty (based solely on observation error), should be considered a lower bound. Intra- and interannual variability in breeding phenology, reproductive success, and incidence of skipped breeding are poorly described in this species, making it difficult to extrapolate precisely how the total population is related to the number available for counting at the time of a survey. More data on these factors will likely be required to calculate a robust measure of uncertainty for the global population estimate.

In addition to intra-annual fluctuations in abundance, colonies appear to undergo substantial interannual fluctuations in abundance. Such interannual variability could reflect high rates of skipped breeding or movement among sites, and may explain the temporary disappearance of the Delaite Island population in 1989. Other species of cormorants also experience dramatic fluctuations in annual numbers of breeding pairs at colonies (Potts et al. 1980, Nur and Sydeman 1999, Bustnes et al. 2013), suggesting that such a pattern is not uncommon. A dedicated program of tagging individual shags so that they could be visually identified at other colonies (e.g. Barlow et al. 2013), while logistically challenging in the Antarctic, would be very helpful in interpreting these time series so that conservation-relevant declines may be separated from other dynamics.

Casaux and Barerra-Oro (2016) suggested that over-exploitation of some of the preferred prey (*Notothenia rossii* and *Gobionotothen gibberifrons*) could be the cause for declines in two additional long-term time series for populations of Antarctic shags at Harmony Point and Duthoit Point, South Shetland Islands. Their evidence for this alternative explanation came from diet data collected at those two colonies, compared with other diet information collected along the Danco Coast, outside of the region where these fish species had been exploited. The decreases in population exhibited by these two colonies (~120 pairs at Duthoit Point and ~70 pairs at Harmony Point between the late 1980's and late 2010's; Casaux and Barrera-Oro 2016) are similar to many of the patterns throughout much of the rest of the range described here (Figure 2.2). While it is certainly possible that interactions with fisheries are responsible for shag declines in some parts of the range, such as the South Shetlands, the absence of an inshore demersal fishery along most of the Antarctic Peninsula suggests that fisheries cannot be the only driver. More long-term time series data from different parts of the range will likely be required to fully understand the causes for the apparent shift in Antarctic shag distribution suggested by this analysis.

Given the unavoidable limitations in the available data, some notes of caution are appropriate. While the analysis of decadal shifts does identify several colonies that have undergone dramatic changes in numbers (Figure 2.2A), many of these decadal shifts are based on only two recorded counts, and in these cases long-term trends are unavoidably confounded with interannual variability. The decadal comparisons among colonies are also not standardized in time, meaning that population shifts at one colony may have been offset by increases or decreases at other nearby colonies. Despite these caveats, the overall geographic pattern in the decadal analysis is quite striking: all but one of the colonies suggesting dramatic increases in population since the 1980’s are at the southern and eastern range edges, while colonies with apparent decreases are scattered throughout the range. This pattern lends further support to the suggestion by Casanovas et al. (2015) of a gradient in shag population growth-rates similar to that observed in Adélie Penguins. Such a latitudinal gradient in shag distribution and abundance would be consistent with the impacts of climate change on other seabirds of the region (e.g., Cimino et al. 2016a).

This review is most directly useful to ongoing conservation efforts in the Antarctic, in particular the establishment of Important Bird Areas. Because a single colony that contains greater than 1% of a species’ global population is a threshold for identifying an IBA, refining the global population of shags by even several hundred birds can alter which colonies are or are not included. The most important update to consider in regard to the efforts by Harris et al. (2011)

would be to make a decision about whether the shags in the South Orkney Islands should be considered part of the global Antarctic shag population. Based on my results the threshold population value of 133 used by Harris et al. (2011) is appropriate if the South Orkney shags are to be included with those from the Antarctic Peninsula, however restricting the population to those usually described as *P.* [*atriceps*] *bransfieldensis* would reduce this threshold to 114. Alternatively, treating the entire blue-eyed shag complex as a single species, as is still favored by some taxonomies, would raise the threshold much higher (an exact number is beyond the scope of this review, but would likely be in the thousands, above the size of any Antarctic colony). Many of the colonies identified as IBAs on account of large shag populations have undergone apparent declines in recent years, and seven of them would no longer trigger IBA status. My results also identify several new candidate locations for IBA status, based on previously unreported colonies or recent population increases (e.g., Earle Island and Lagotellerie Island; see online database). Continued population declines in most of the range combined with increases at the extreme southern end of the range, have the potential to further change the status of additional IBAs in the same way. Finally, both intra- and interannual variability in abundance may make it difficult to identify IBAs based on a single year's census estimate. I believe that the designation of IBAs in the Antarctic is a valuable management objective, however its practical application to Antarctic shag colonies may require innovative methods that account for this species' apparent metapopulation structure.

2.5.1: Suggestions for Future Work

This review of Antarctic shags has identified where more information on the shags of this region is needed; here I identify four priorities for future work. (I) Updated surveys for colonies that have not been counted in the last two decades, particularly those with large populations, would improve the confidence of the global population size. (II) More time-series from individual colonies throughout the range would allow researchers to monitor whether a regional shift in distribution (from north to south) is actually occurring. (III) A mark-recapture study designed to estimate the rates of inter-colony dispersal rates and skipped breeding would allow better assessment of whether interannual variation in colony size is reflective of population growth rates, dispersal, or demographic patterns. (IV) A geographically comprehensive genetic analysis of shags from the Antarctic Peninsula and all major island groups in the region (including around Patagonia, the Falkland Islands (Malvinas), South Georgia, the South Sandwich Islands, the South Shetland Islands, and especially the South Orkney Islands) would allow the taxonomy of the *P. atriceps* complex to be resolved sufficiently to draw boundaries for conservation purposes.

Much of this information, particularly time-series, may already exist in unpublished records or gray-literature. Modeled probabilities of breeding are currently included in the online Mapping Application for Penguin Populations and Projected Dynamics (MAPPPD; Humphries et al. 2017), and it is possible that future efforts to model population of shags could be incorporated into that or similar database efforts. To facilitate data exchange for Antarctic shags, I have created a public GitHub repository to which I have added the population data reviewed in this manuscript (https://github.com/lynch-lab/Antarctic_shags). Other researchers are encouraged to add additional data and citations to that list. I believe that efforts such as this to collect and share survey data may be helpful for other species with discrete breeding locations, especially in places like the Antarctic where logistics make regular surveys difficult for any single research team.

CHAPTER 3: Regional breeding bird assessment of the Antarctic Peninsula

3.1: ABSTRACT

Conservation of seabirds in remote polar regions requires accurate information on the location of breeding sites, which is often limited by logistical constraints of surveying large areas. On the Antarctic Peninsula, many seabird colonies are visited briefly but regularly by commercial cruise vessels, a platform from which presence/absence data on the entire community of seabirds was collected. I used a multi-state occupancy model, accounting for limited detection during surveys, to estimate the probability of presence and breeding of all 16 species native to the area. Results from this analysis provide a much clearer view than was previously available of how avian diversity is distributed across the region's network of multi-species colonies and reveals species-specific differences in the effect of sea-ice concentration and site-fidelity on breeding probability. Several breeding sites host an unusually large number of breeding species, but these known richness hotspots are scattered throughout the region and I was unable to identify any clear gradients in species richness that might explain why some sites are so species rich. While accounting for detection failure accelerates the pace of reliable inference on species occupancy, as many as ten years of repeated visits are often required to fully catalog seabird richness at bare rock sites along the Antarctic Peninsula. This work highlights the challenges of identifying high priority sites for special protection or management and the importance for continued surveys, even at nominally well-studied locations.

3.2: INTRODUCTION

Comprehensive knowledge of the extent and distribution of an ecological community can assist both in the study of fundamental ecological relationships and in designing effective conservation management. Polar regions are relatively species-poor in terms of avian biodiversity (Willig et al. 2003), but the logistical constraints of surveying these regions nevertheless limits the collection of such information and can make it difficult to identify patterns of richness or biodiversity hotspots that may warrant special protection (Kennicutt et al. 2015). In addition to fulfilling practical management needs, comprehensive biodiversity data allows us to understand the processes behind patterns of species richness and community assembly. Despite being fundamentally important to nearly all questions in population and community ecology, mapping species ranges is surprisingly difficult, even for species like birds, that are generally well-studied (Wauchope et al. 2019). Knowledge of Antarctic bird distribution is primarily focused on penguins and other easily-detectable species. For much of the rest of the bird community, any efforts to design effective conservation measures to address anthropogenic climate warming, such as expanding the system of Antarctic Specially Protected Areas (Coetzee et al. 2017) or the designation of Important Bird Areas (Dias et al. 2018, Donald et al. 2019), will be hampered without basic data on occurrence. Site-specific information on breeding birds is also necessary for the effective management of the region’s fisheries (Trathan et al. 2018), as well as the burgeoning Antarctic tourism industry, which has grown by more than 300% since the early 1990s, and is likely to continue that growth in the future (Bender et al. 2016).

Bird breeding sites on the Antarctic Peninsula are almost exclusively on small snow-free islands or rocky outcrops scattered along a glaciated coastline. This patchy landscape naturally limits breeding to discrete locations generally termed “sites,” and many (perhaps most) of these contain nesting habitat for multiple species, resulting in a network of multi-species colonies. Conservation management of birds in the region has generally focused on these multi-species sites as units of potential attention for management policies (e.g., Harris et al. 2011).

Traditional efforts to record and synthesize knowledge of breeding bird distribution in the Antarctic have taken the form of either coarse-grained range maps (in reviews and identification guides such as Croxall 1984 or Shirihai et al. 2007), or large compendiums of known breeding locations accompanied by data, where available, on abundance (e.g., Woehler 1993, Naveen and Lynch 2011, Humphries et al. 2017). While the former approach provides information on the whole seabird community, it does not provide the detailed information on discrete colonies and/or populations required to make effective management decisions for specific sites. The latter approach requires years of data collection, representing the collective effort of many international research groups, and is generally done for only a few of the most well-studied species, usually penguins. Satellite-based surveys alleviate some of these issues, but are also currently limited to species that form dense, easily observable surface nest aggregations (Lynch et al. 2012b). There has been little effort to comprehensively document the breeding locations of the non-penguin avifauna throughout the Antarctic Peninsula with the possible exception of Harris (2005), which was focused primarily on guiding safe helicopter operations and, as such, did not address many of the region's species.

I applied recently-developed occupancy modeling techniques to study presence and breeding occurrence at a large (n = 196) collection of seabird colonies throughout the entire Antarctic Peninsula, including the South Shetland and South Orkney Islands. Such models use repeat visits to a set of sites to model the probability of occurrence (MacKenzie et al. 2009, Kéry and Schaub 2012, Bailey et al. 2014). One important benefit of this method is that the occupancy models account for imperfect detection, meaning that presence/absence data collected during relatively short (usually 1-4 hour) visits to sites can be corrected to model the probability of occupancy for cryptic species. I also used sea-ice concentration and a term to represent site-fidelity as covariates, allowing the model to predict occupancy status for species that were not detected.

My first objective was to better understand the breeding distribution of birds throughout the Antarctic Peninsula. My second objective was to determine how much sampling effort is required to produce reliable estimates of species richness at a particular site, as this allows the identification of sites that are under-sampled. Finally, the model was used to confidently identify sites that have high species richness, as well as sites that may have high richness but are likely under-sampled. This allows the identification of locations that may warrant special protection under the Antarctic Treaty System.

3.3: METHODS

3.3.1: Data Collection

Data on bird occupancy used in this chapter were collected by the ASI throughout the Antarctic Peninsula since 1994. Most sites ranged in size from 1–100 hectares, but are always discrete areas where breeding birds can freely move among the available patches of suitable exposed rock for breeding. Presence and breeding status were recorded for all species during each site visit (Naveen and Lynch 2011). Here I restrict attention to sites that host at least one species of breeding bird, and use presence/absence data spanning a period of 22 years (Nov 1995 to Feb 2017; Lynch et al. 2013). Most visits were made from late November through early March, encompassing the incubation and chick-rearing periods for most species (Shirihai et al. 2007) and lasted three to four hours in duration. Visit frequency both within and among years varied widely; while the maximum number of visits to a site in a single year was 11, most sites (79%) did not have more than two visits in any year. Some sites were visited every year of the survey period, while others were only visited occasionally. During each site survey, observers noted the presence of any bird species, and breeding was confirmed when nests were observed for that species. In this context, “presence” was defined as any observation of any number of individuals physically located on or over land at the site. This likely included some birds which were actively breeding at the location, but for which detection of nests was very difficult (such as crevice-nesting species like storm-petrels), as well as individuals of some species that were not breeding at the site, but were simply loafing at or exploring the site. Any evidence of imminent or attempted breeding, including birds attending empty nests, was considered “breeding”. Most visits by researchers were focused on obtaining abundance data for several target species: Adélie (*Pygoscelis adeliae*), chinstrap (*P. antarcticus*), and gentoo (*P. papua*) penguins, as well as Antarctic shags, southern giant petrels (*Macronectes giganteus*), and kelp gulls. Detection probability of breeding for target species was predicted to be uniformly high with narrow confidence limits, while more variability in detection was expected among non-target species.

Since long-lived seabirds are most likely making decisions about breeding location suitability using long-term (multi-year) information, I chose to use a single, average value for sea-ice concentration at each site, to approximate the general environmental conditions encountered over time. It is unlikely that individual seabirds make choices about where to breed based solely on current information, and therefore even less likely that occupancy at the colony level relates to environment at that time scale. November mean sea-ice concentration (i.e., percent of sea surface covered by ice) was obtained from the satellite-based Nimbus 7 SMMR, and SSM/I-SSMIS passive microwave sensors from 1995-2016, processed by the NASA Team algorithm (Cavalieri et al. 1995) via the National Snow and Ice Data Center (Cavalieri et al. 1996). November was chosen because it represents the time when most of the species in the region are forming nests (Shirihai et al. 2007). The monthly concentrations were then averaged across the study period (1995-2016) to create the single site-specific habitat variable. This choice relies on the assumption that the information captured during this period is indicative of the long-term information available to birds about each site. I felt this assumption was reasonable, given that the range in average November sea-ice concentration over the entire study region (from completely ice-free to approximately 67%) was much larger than the inter-annual variation at most sites. Satellite sensor resolution over the period of the study limited the sea-ice concentration to a 25 km grid size. Mean sea-ice was calculated within a 100 km buffer of each site. The buffer radius was chosen to represent a reasonable limit to the regular foraging range of most breeding seabird species. Detailed information on exact foraging distance is lacking for most seabird species in the Antarctic Peninsula, but many likely forage in near-shore areas within tens of kilometers (Croxall 1984, Knox 2006).

3.3.2: Model

I used a series of single-species Bayesian multistate occupancy models to determine the probabilities of both occupancy and breeding at each site (Kéry and Schaub 2012). Each species at each site (s) had a probability of presence (ψ_s), and a probability of breeding conditional on the species being present at the site (r_s). These two parameters were used to specify the latent state-space probabilities of occupancy at site (s) in year (y) as:

$$z1_{s,y} \sim Bernoulli\left(\psi_{s,y}\right) \tag{3.1}$$

$$z2_{s,y} \sim Bernoulli\left(r_{s,y} * z1_{s,y}\right), \tag{3.2}$$

where each binary state represented whether each site was attended in a given year ($z1_{s,y}$), and whether there was breeding that year ($z2_{s,y}$). Note that unlike previous formulations of multistate models, in which state is drawn simultaneously from a categorical distribution (Kéry and Schaub 2012), this implementation used a sequential model (Equations 3.1-3.2). I chose parameterization of existing states rather than the colonization/extinction parameterization of dynamic (i.e., multi-season) models from MacKenzie et al. (2009) because the process of interest was how environment and prior state influenced the current state, rather than the dynamics of colonization (which is, for most of these species, rare). Having made this choice, two sequential draws from the Bernoulli distribution rather than a single draw from a Dirichlet distribution (which describes probabilities summing to one but divided among an arbitrary number of states) helped to better reflect the biological mechanism whereby birds determine whether to breed only once they have begun occupying a site. These two states could then be converted into a categorical multistate variable, similar to the more traditional multistate vector described by Kéry and Schaub (2012),

$$z_{s,y} = \boldsymbol{I}(z_{s,y}) \begin{bmatrix} 1 \\ 2 \\ 3 \end{bmatrix} = \begin{bmatrix} 1 - \max(z1_{s,y}, z2_{s,y}) & z1_{s,y} - z2_{s,y} & z2_{s,y} \end{bmatrix} \begin{bmatrix} 1 \\ 2 \\ 3 \end{bmatrix}, \tag{3.3}$$

where $\boldsymbol{I}(z_{s,y})$ is the indicator vector representing the true state and $z_{s,y} = 1$ represents ‘not occupied’, $z_{s,y} = 2$ represents ‘present but with no breeding’, and $z_{s,y} = 3$ represents ‘breeding’. Ecologically, the state of ‘present but with no breeding’ here simply means that the species may be found at the site at some point during the breeding season (of year y). This model cannot distinguish between birds that are regularly present during the season (perhaps for feeding ashore—i.e., predators—or prospecting for future nest sites) and those that may simply be present occasionally, such as a vagrant that happened to be detected.

The probabilities of presence and breeding were modeled as a function of sea-ice and prior state,

$$f\left(\alpha_{\psi}, \beta_{\psi}, \gamma_{\psi}, z1_{s,y-1}\right) = logit\left(\psi_{s,y}\right) = \alpha_{\psi} + \beta_{\psi} seaice_{s} + \gamma_{\psi} z1_{s,y-1} \tag{3.4}$$

$$g\left(\alpha_r, \beta_r, \gamma_r, z2_{s,y-1}\right) = logit\left(r_{s,y}\right) = \alpha_r + \beta_r seaice_s + \gamma_r z2_{s,y-1}, \tag{3.5}$$

where the intercepts (α) and slopes for sea-ice (β) were constant across all sites so that information from well-sampled sites could improve inference on occupancy state for poorly surveyed sites. The covariate γ allowed both the presence and breeding probabilities to be dependent on the state in year $y - 1$. This permitted the model to estimate the strength of site persistence, while allowing for site colonization and extinction. It was assumed that $z1_{s,0} = z2_{s,0} = 0$, however the results are insensitive to this assumption about occupancy prior to the survey period. I fit this same model to each species individually. This facilitates direct comparisons between the parameter posteriors (α, β, γ) across species.

To incorporate the probability of non-detection, the following state detection matrix was specified:

$$\boldsymbol{\pi} = \begin{bmatrix} 1 & 0 & 0 \\ 1 - p_2 & p_2 & 0 \\ p_{3,1} & p_{3,2} & p_{3,3} \end{bmatrix}, \tag{3.6}$$

where rows represent true state, and columns represent observed state ($1 =$ no presence detected, $2 =$ presence but not breeding detected, $3 =$ breeding detected). Note that rows (true states) must sum to 1, but columns do not share that requirement, meaning that detection probability for any particular true state is not constrained by the detection probability of other true states. I did not hierarchically model detection probability as a function of other covariates. Relevant variables either varied enough over the course of the history of visitation to each site (e.g., observer identity, weather conditions, duration of visit), or varied so little among sites (e.g., simplicity of the bare-rock habitat and the resultant uniformity of physical features), that any variation in detection would be accommodated within the width of the detection posterior probabilities.

While the detection probability allowed the model to accommodate false absences, it did not account for false positives. With the sole exception of the two congeneric and occasionally hybridizing skua species (*Stercorarius* spp.), Antarctic birds were all easily identified and distinguished from one another, and therefore false positives were assumed to be very rare. Field observers in doubt of a skua classification noted their presence in a separate ‘un-identified’ category. Data from that category were combined with those from the two species for a separate model of “any skua,” the results from which were used in a separate model to allow me to estimate the minimum number of skua species at a site.

The observed state ($x_{s,y,v}$) was modeled at site (s) during year (y) and visit (v) as a function of the parameters that describe detection probability ($p_2, \boldsymbol{p_3}$) and the true (latent) occupancy state from the previous year ($z_{s,y-1}$), the latter of which depends on the covariates (α, β, γ) for the probabilities of breeding and occupancy (ψ, r). The joint distribution for each species is:

$$\begin{aligned}
&\left[\,\alpha_\psi, \beta_\psi, \gamma_\psi, \alpha_r, \beta_r, \gamma_r, \boldsymbol{\pi}(p_2, \boldsymbol{p_3}), \boldsymbol{z1}, \boldsymbol{z2} | \boldsymbol{x}\right] \propto \\
&\qquad \prod_{s=1}^{197} \prod_{y \in Y} \prod_{v=1}^{V_{s,y}} \text{categorical}\big(x_{s,y,v} | \boldsymbol{I}(z_{s,y}) \cdot \boldsymbol{\pi}\big) \\
&\qquad \times \prod_{s=1}^{197} \prod_{y=1}^{22} \text{Bernoulli}\left(z1_{s,y} | f\left(\alpha_\psi, \beta_\psi, \gamma_\psi, z1_{s,y-1}\right)\right) \\
&\qquad \times \text{Bernoulli}\big(z2_{s,y} | g\big(\alpha_r, \beta_r, \gamma_r, z2_{s,y-1}\big), z1_{s,y}\big) \\
&\qquad \times \text{normal}\big(\alpha_\psi | 0, 2.59\big)\text{normal}\big(\beta_\psi | 0, 2.59\big)\text{normal}\big(\gamma_\psi | 0, 2.59\big) \\
&\qquad \times \text{normal}(\alpha_r | 0, 2.59)\text{normal}(\beta_r | 0, 2.59)\text{normal}(\gamma_r | 0, 2.59) \\
&\qquad \times \text{uniform}(p_2 | 0,1)\text{Dirichlet}(\boldsymbol{p_3} | 1,1,1),
\end{aligned} \tag{3.7}$$

where 196 is the total number of sites, and 22 is the total number of years for which data were collected. Because I assumed that state is fixed over the period of a single breeding season, replicate visits to a site ($v = 1, \ldots, v_{s,y}$) within a year allowed me to estimate species-specific detection probabilities. Non-informative prior distributions were chosen for the detection parameters, and priors for the logit-linked parameter covariates (α, β, γ) were each selected to approach a uniform distribution over the interval $(0, 1)$ when on the probability scale (following Lunn et al. 2012). This choice of prior is consistent with previous Bayesian multistate occupancy models and reflects an absence of prior information on the model coefficients.

3.3.3: Model Implementation

Posterior distributions for all parameters and states were estimated using Markov chain Monte Carlo (MCMC) methods implemented in JAGS 4.0.0 (Plummer 2015) with the 'R2jags' package (Su and Yajima 2015) in the R computing environment (R Development Core Team 2019). Source code for the entire modeling process and for managing and viewing results can be found at the following GitHub repository: https://github.com/lynch-lab/Schrimpf_etal_PolarBiology_Occupancy. Each single-species model was run with three chains, each with a burn-in of 250,000 iterations, and an additional 100,000 to use as the draw from the posterior distributions, keeping every 50th draw. Convergence was assessed visually and by calculating Gelman-Rubin diagnostic (Gelman et al. 2013). I report the medians and both 50% and 95% highest posterior density intervals (HDIs) for modeled coefficients. In addition to exploring the impact of the closure assumption, the model was used to create maps of presence and breeding for each species, many of which had never been comprehensively mapped at the site-level in this region before. For this purpose, I used the latent states ($z1$ and $z2$), which incorporated both available data and the probability of occupancy based on sea-ice concentration and persistence. Note that the interpretation of the three-state probability of occupancy (i.e., the probability of being either not present, present without breeding, or present with breeding) derived from the model is also possible, but when parameterized with independent prior probabilities of both presence and breeding in the manner here produces a counter-intuitive ternary probability weighted towards not present (Appendix 3). The net result of this effect is that these models are conservative when data are limited, requiring positive detection to raise the posterior probability of either presence or breeding, thus making the latent states ($z1$ and $z2$) a more reliable measure of true state in such cases. Finally, model fit was assessed with a posterior predictive check wherein a modified chi-squared test statistic was compared for observed versus predicted data (Gelman et al. 2013); see Appendix 4 for details.

3.3.4: Species Accumulation

Site- and species-specific breeding bird occupancy results were summarized by extracting the latent breeding ($z2$) state from each single species model to create site- and year-specific posterior distributions. Skuas were grouped into a “total skua” category, which summed the states of the individual species, and then used the state from the “any skua” model to determine the minimum number of skua species for each iteration. Therefore, the posterior for “total skuas” ranges between zero and two. To facilitate site-specific comparisons to a traditional species accumulation analysis I used only those years for which each site was visited, and then recorded which species had been modeled as breeding either during or prior to that year of visitation within each iteration of the posterior. The states of all species were summed to create a posterior distribution for richness, which was then summarized by reporting the median and 95% HDI.

Both the model-derived and raw species accumulation data were used to calculate estimates of species richness, using the function “specpool” from the R package: vegan (Oksanen et al. 2019). Of the various statistics available, I chose the Chao2 estimator, which is essentially a correction for the reported richness to include possible missing species, based on the frequencies of rare (i.e., difficult to detect) species that occur in only one or two of a series of replicated incidence samples (Chao 1987, Gotelli and Colwell 2011).

3.4: RESULTS

Between the 1995-96 and 2016-17 Antarctic field seasons, the ASI collected detection/non-detection data at 196 different sites during a total of 1565 visits. The maximum number of visits at any one site was 78, and the most visits within a single year at a single site was 11. Over the 22 total years since the beginning of the study, 87 (44%) of the sites were only visited in a single year, and 151 (77%) of the sites had visits in only five or fewer years. Several sites have a visitation history stretching throughout the entire time period, however, including two sites that were visited in each of the 22 years. Details on model fit may be found in Appendix 4).

3.4.1: Occupancy model parameters

Several species had measurable relationships with sea-ice concentration, either affecting their probability of presence or breeding, and very rarely both (Figure 3.1A-B). Only for the gentoo penguin did sea-ice impact both presence and breeding, negatively for the former and positively for the latter. The other two *Pygoscelis* penguins were the only other species for which sea-ice was important for breeding (positively for Adélies and negatively for chinstraps), however several of the more sub-Antarctic species (e.g., macaroni penguin, *Eudyptes chrysolophus,* and cape petrel, *Daption capense*) had negative associations between sea-ice and presence.

Detection probability of presence was generally fairly low (Figure 3.1C), reflecting the difficulty in determining whether a species does or does not occur at some point during the breeding season at any particular site. For some species, such as the crevice-nesting storm-petrels and solitary surface-nesting skuas, detection probability of breeding was also low, but for the dense surface-nesting *Pygoscelis* penguins it was very high (Figure 3.1D). Interestingly, it was for these three species only that the posteriors for the effect of sea-ice on breeding did not overlap zero. Species which were detected very infrequently, such as the black-bellied storm-petrel (*Fregetta tropica*), had covariates for detection probability and sea-ice that remained essentially unidentifiable, reflecting true uncertainty in these parameters.

The term for site fidelity was strongly positive for breeding in most species, while also positive for presence in several species as well (Appendix 5), as would be expected in philopatric seabirds. When I ran the occupancy models without including a term for site fidelity, many of the sea-ice coefficients became much more extreme, providing evidence that such models can be biased by not explicitly modeling the inertia imposed by a species' site faithful behavior (see Appendix 6 for more details).

3.4.2: Species-specific findings

The probability of breeding occupancy for each species was calculated by taking the proportion of ones to zeros from the latent state posterior distribution from each site ($z2_{s,y}$), using only years in which the site was visited. Maps of the site-specific probability suggested several interesting patterns, (e.g., cape petrel and snowy sheathbill, *Chionis albus*, described below and shown in Figure 3.2), and can be compared to range maps used by the International Union for Conservation of Nature (IUCN) as representative of standard distribution data readily available for most managers and policy-makers (BirdLife International and Handbook of the Birds of the World 2013, 2017). For example, the results suggest with high certainty that cape petrels breed at several sites throughout the South Orkney, South Shetland, and Elephant Islands, as well as at the northernmost tip of the Antarctic Peninsula (Figure 3.2A), but are less certain regarding several potential breeding locations further south along the western Antarctic Peninsula. This is broadly consistent with the IUCN's range map, though the IUCN range map does not include the northern peninsula region as within the cape petrel's breeding range. The small enclaves indicated on Joinville Island to the north and Anvers Island to the southwest are locations that are not well surveyed, and likely include additional breeding sites.

Snowy sheathbills were mapped with high confidence at sites throughout the Antarctic Peninsula and associated island groups (Figure 3.2B), as far south as (but not beyond) Grandidier Channel, and the strong negative association between sea-ice concentration and sheathbill presence resulted in very low probability of breeding further south. This also accords fairly well with the IUCN range map, though the exclusion of the Joinville Island area to the north of the Peninsula is unusual, as there were several breeding locations located there. Notably, the snowy sheathbill range is remarkably similar to that of the gentoo penguin, even though there is no *a priori* reason to suspect sheathbills interact more strongly with, or have more similar habitat requirements to, gentoo penguins, as compared with the other penguin species.

Site-specific breeding probabilities for all 16 species are presented in map form (Appendix 7) and are available in table form along with the results for the probability of presence at the GitHub repository online. These results are also available online via an interactive map at the Mapping Application for Penguin Populations and Projected Dynamics (penguinmap.com).

3.4.3: Species accumulation

Accumulation curves showed a variety of patterns among sites (Figure 3.3; see the GitHub repository for code to produce a curve for any site). At almost all sites the model results suggested higher diversity than had been confirmed in the field. For those sites with the longest history of visitation, both model- and raw data-based species accumulation curves reached fairly stable asymptotes after approximately 10-15 years of sampling (Figure 3.3A-D), though a few reached asymptotes after only roughly five years (Figure 3.3B). The occupancy model results often increased sooner than the raw data curves by several years (i.e., where the highest density interval of richness during a particular year was greater than the confirmed richness), indicating that in those cases the model correctly predicted the occurrence of breeding species based on sea-ice conditions or detection of presence-only. Because the occupancy model assumes there were no false positives, the modeled richness can never go below the uncorrected richness (dashed lines in Figure 3.3). The Chao2 estimated richness was generally much greater for the model results than for the raw data (Figure 3.3; closed and open points, respectively) though sometimes both estimates were very close (e.g., Figure 3.3A,B,D). At sites with the longest visitation history (Figure 3.3A-D), the median model richness at the end of the time series was equal to the Chao2 estimated richness (i.e., the species richness asymptote was reached).

Several species, most notably the Antarctic tern (*Sterna vittata*), Wilson’s storm-petrel (*Oceanites oceanicus*), and southern fulmar (*Fulmarus glacialoides*), despite being undetected at many sites, had low but non-zero occupancy probabilities. As a result, the model would often predict “breeding” in at least one year of the long time series, increasing accumulated species richness by one to two species (e.g., Figure 3.3A-B) over what was directly observed. This had little impact on the relative pattern of species richness across sites, however I recommend that readers interested in site- or species-specific results from the model refer primarily to the probabilities in the online table of results. In an effort to determine how reliable the Chao2 estimator was at predicting species accumulation early in a time series, I downsampled the results for the ten sites with the longest time-series, but the estimated richness simply reflected the median modeled richness in almost all cases. This indicates that adding a rarefaction-based step onto the occupancy modeling process did not lead to any increased ability to predict species richness (Appendix 8).

Sites with high species richness (median richness ≥10; Table 3.1) were distributed throughout the study region (Figure 3.4). Based on a visual assessment of species accumulation curves asymptotes, sites were grouped into three uncertainty categories, reflecting the confidence in model estimated richness as a function of years of data collection: Low (< 5 yrs); Medium (5-9 yrs); High (≥ 10 yrs). All of the lowest richness sites also had low confidence, while the upper end of the richness distribution contained a mix of medium and high confidence sites (Figure 3.5). While this pattern is exactly what one would expect with a method for modeling richness that accumulates more species over time, a large proportion of sites fell into the low confidence category. These sites may support higher species richness than my models would suggest and should be considered priorities for future surveys. I provide a recommended survey priority ranking for each site in the online table of results.

Site Name	Latitude	Longitude	Number of ASI visit years	Median Richness	95% HDI Richness
Barrientos Island	-62.4071°	-59.7517°	20	13	(13, 13)
Brown Bluff	-63.5222°	-56.9050°	17	13	(12, 13)
Hannah Point	-62.6545°	-60.6134°	13	13	(11, 13)
Britannia’s Figleaf	-61.2780°	-55.2130°	10	12	(10, 13)
Fort Point	-62.5420°	-59.5800°	5	12	(11, 12)
Paulet Island	-63.5801°	-55.7881°	15	11	(10, 12)
Port Charcot	-65.0670°	-64.0260°	14	11	(10, 12)
Petermann Island	-65.1760°	-64.1370°	17	11	(10, 12)
Bailey Head	-62.9650°	-60.5060°	19	10	(9, 11)
Cuverville Island	-64.6840°	-62.6260°	22	10	(9, 11)
Entrance Point	-62.9981°	-60.5533°	9	10	(9, 11)
Georges Point	-64.6694°	-62.6696°	18	10	(9, 11)
Gourdin Island	-63.1969°	-57.3074°	6	10	(9, 12)
Heroina Island	-63.3944°	-54.6083°	5	10	(9, 11)
Orne Islands	-64.6620°	-62.6730°	20	10	(9, 11)
Pleneau Island	-65.1040°	-64.0556°	17	10	(9, 11)
Robert Point	-62.4500°	-59.3830°	4	10	(8, 11)
Spigot Peak (Orne Harbour)	-64.6350°	-62.5540°	10	10	(8, 11)
Turret Point	-62.0875°	-57.9514°	6	10	(8, 12)
Useful Island	-64.7170°	-62.8640°	6	10	(9, 11)
Waterboat Point (Gonzáles Videla base)	-64.8236°	-62.8581°	10	10	(8, 11)
Point Wild	-61.0980°	-54.8610°	10	10	(8, 12)

Table 3.1: All sites with median model species richness ≥ 10, including the 95% highest density interval of richness and the number of years ASI researchers collected presence/absence data there between Nov 1995 and Feb 2017.

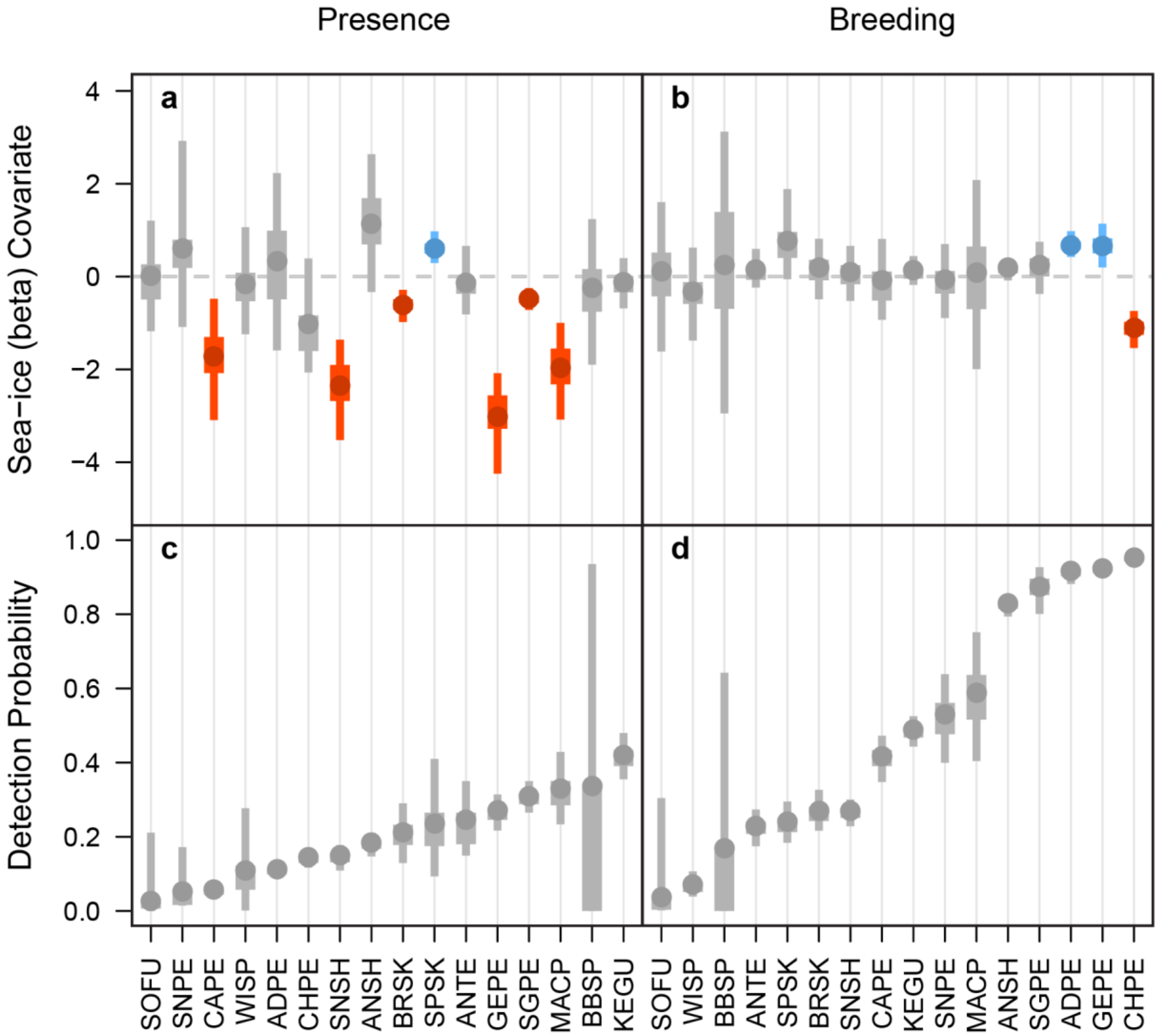

Figure 3.1: Posterior distributions for the coefficients for (**a-b**) sea-ice concentration, and (**c-d**) detection probability in both the models for presence (**a,c**) and breeding (**b,d**). Circles indicate medians, while wide and narrow bars indicate the 50% and 95% HDIs, respectively. Color denotes whether the 95% HDI overlaps (gray), is above (blue), or is below (orange) zero. See Table 1.1 for species codes.

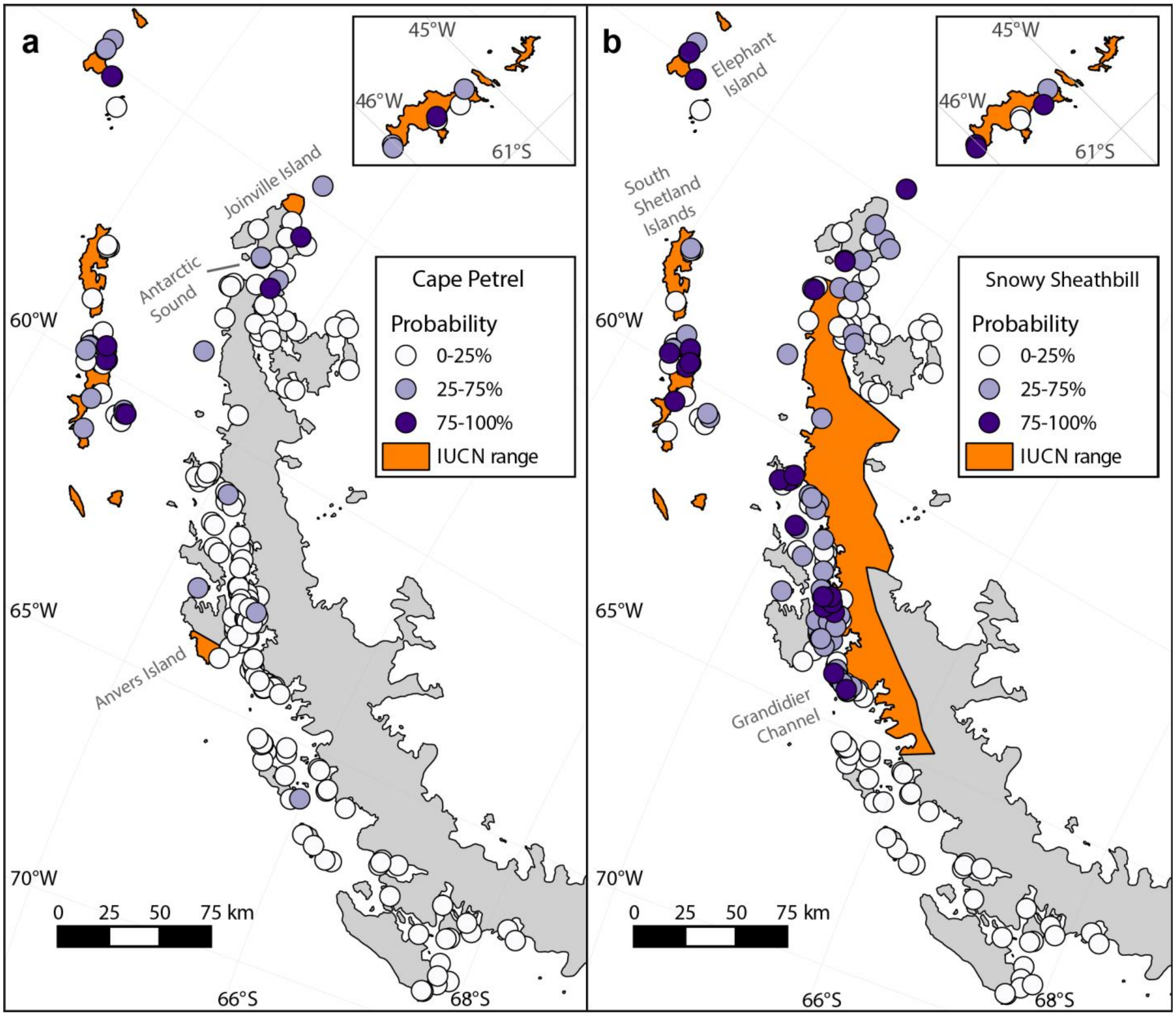

Figure 3.2: Breeding range maps of (a) cape petrel and (b) snowy sheathbill. Colored circles represent the proportion of the model's breeding state posterior for each site that indicated breeding (i.e., the modeled probability), including only those years for during which the site was visited by researchers. The current IUCN range map for the species in the region is displayed in orange. The inset boxes show the South Orkney Islands.

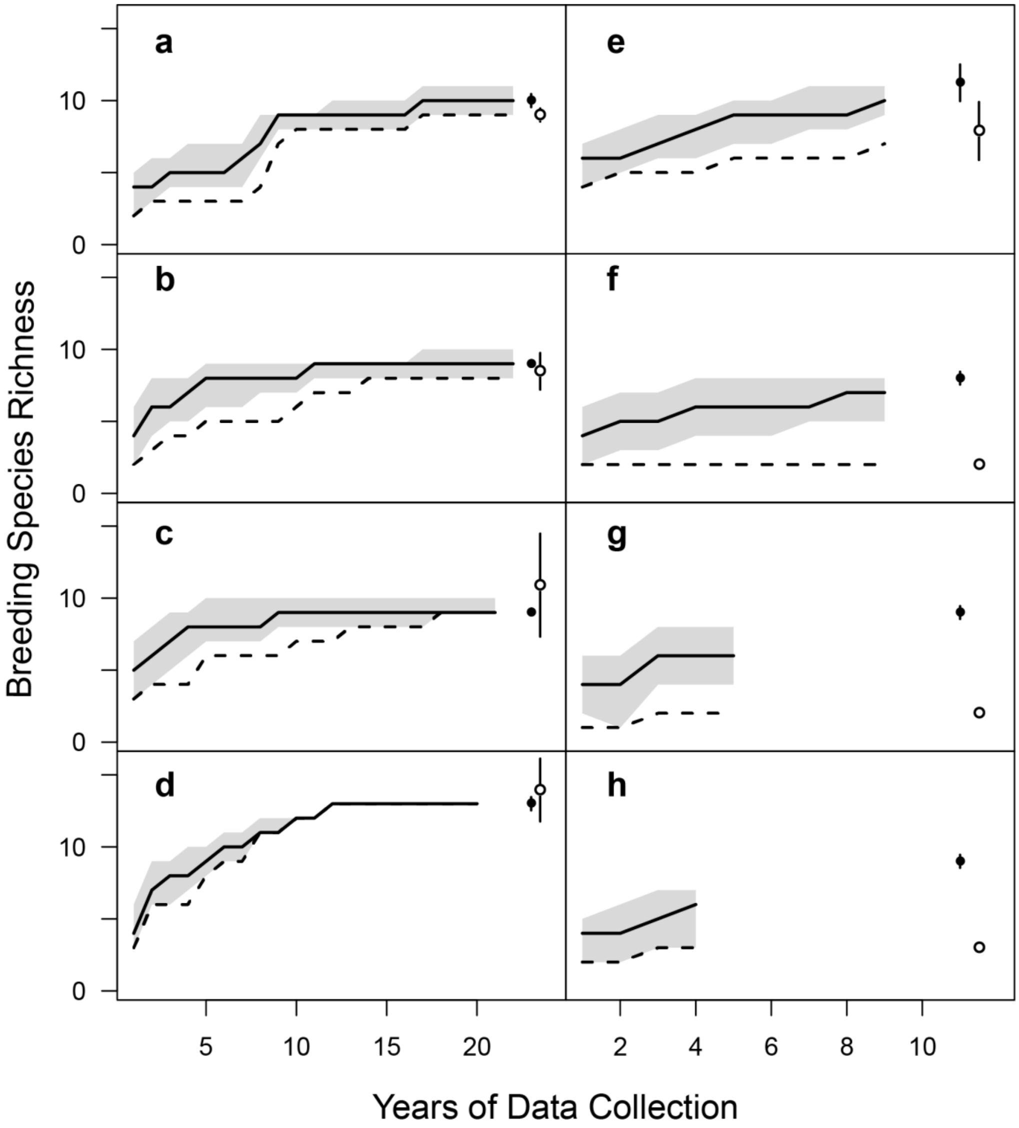

Figure 3.3: Species accumulation curves for raw data (dashed line) and model posterior results (solid line=median; shaded region=95% highest density interval). Points along the right-hand side represent Chao estimated richness (+/- 1SE) using the raw data (open circles) and model results (closed circles). Chao estimated parameters (richness and SE) were calculated for each iteration of the model posterior separately and the medians for both are displayed. Sites are: (a) Cuverville Island, (b) Jougla Point, (c) Brown Station, (d) Barrientos Island, (e) Entrance Point, Deception Island, (f) Bryde Island East, (g) Skottsberg Point, (h) Cape Tuxen, see GitHub repository for site metadata.

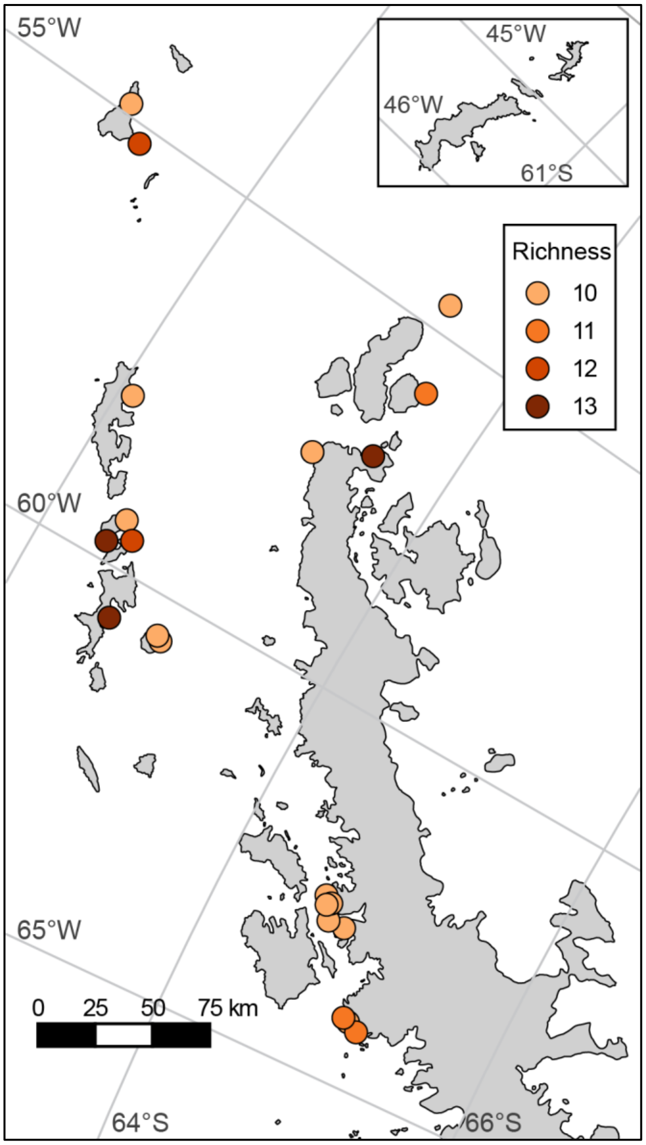

Figure 3.4: Those sites at which the stacked model results suggested ten or more breeding species are present.

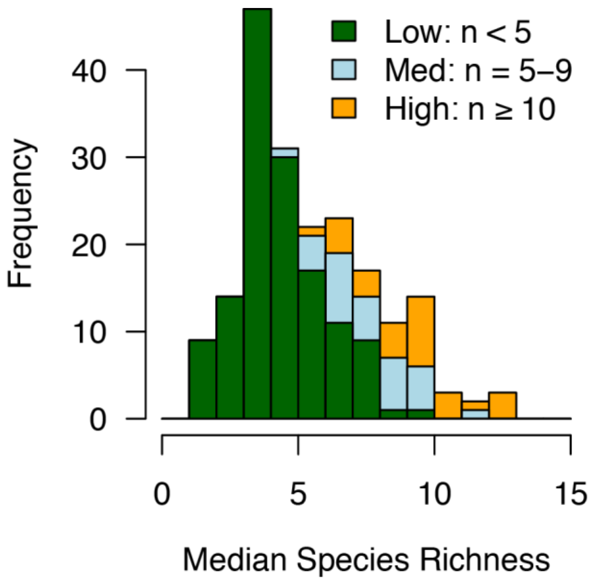

Figure 3.5: Distribution of median posterior species richness from stacked occupancy model results. Frequency is color-coded to indicate the confidence in the richness estimate, based on the number years of visitation (n) to each site.

3.5: DISCUSSION

By examining the occupancy of all species in the same modeling framework, this analysis provides a clearer picture of how breeding birds are distributed throughout the Antarctic Peninsula region. Although comprehensive catalogs of breeding species have been attempted for smaller regions in the vicinity, such as the South Sandwich Islands (Convey et al. 1999) or at specific locations or islands (e.g., Coria et al. 2011), to my knowledge this is the first attempt to document site-specific species richness patterns at such a large scale. Although opportunistic surveys are unable to visit every seabird breeding site along the coast, the large geographic scope of the project provides a more complete picture of colony distribution than was previously available for most species, excepting the highly charismatic and densely-packed surface nesting species, such as penguins (Woehler 1993, Humphries et al. 2017) and shags (Chapter 2). Having occurrence data on the entire community of birds will likely aid efforts to protect important concentrations of avian biodiversity in the region, such as the designation of Important Bird Areas (Harris et al. 2011, Donald et al. 2019). Moreover, this approach provides a quantitative measure of uncertainty, such that undetected species can have a probability of occurrence that reflects underlying site conditions and prior survey findings. Efforts to document biodiversity in remote regions like Antarctica, especially in places designated as protected areas, such as recent work by Wauchope et al. (2019) that relied on collections of species presence records only, will likely benefit from measures that can include uncertainty.

The maps of breeding distribution presented here accord well with previously known limits to species ranges, such as the southern limit to gentoo penguins (Lynch et al. 2012a), although my approach uncovers new information on less well-described patterns, such as the similar limit in snowy sheathbill range (Figure 3.2). In some cases, we've been able to identify additional breeding areas not reflected in earlier range maps, such as the cape petrel colonies in the northern Antarctic Peninsula (Antarctic Sound vicinity). By focusing on individual seabird breeding sites, this model provides a much more nuanced examination of the breeding distribution than is possible with coarse-grained range maps. For example while the central-west Antarctic Peninsula, in the vicinity of Anvers Island, provides good habitat for snowy sheathbills, breeding appears concentrated in several small clusters of sites, with other less probable sites scattered between those clusters. This type of site-specific knowledge is also helpful when examining maps of less-common species (Appendix 7), such as macaroni penguin or snow petrel (*Pagodroma nivea*), both of which are only breeding at a few of the 196 sites considered. A range map that includes the South Shetland Islands for macaroni penguins or the northern Antarctic Peninsula for snow petrels would be arguably correct, but would obscure the fact that the species in question only breeds at a tiny number of places scattered over hundreds of miles of coastline. Contrast this with species like the Wilson’s storm-petrel or Antarctic tern, which are much more wide-spread; my results suggest they have a reasonable probability of using many of the sites in that range, rather than a few specific locations.

It is important to have this site-specific distribution information for effective management and to verify where rare species are located. This study also raises questions about the mechanisms that produce such distribution patterns. Several hypotheses could explain why, for example, the snowy sheathbill (Figure 3.2B) might be absent from a site, including a lack of appropriate microhabitat for nesting sites, competition with other species (i.e., skuas) for penguin-derived food resources, or even simply a random assortment of which sites were colonized. Antarctic bird populations may best be described as metapopulations, with particular sites transitioning, albeit rarely, from occupied to unoccupied. As a consequence, they likely require monitoring across a network of sites for effective conservation (Mittelbach 2012).

The analysis of species accumulation curves using both the model results and raw data revealed that the model-based approach occasionally results in reaching a stable estimate of species richness faster for particular sites, but that even in such cases five to ten years of data are still required before I could have high confidence in the estimate. Downsampling the most well-sampled sites with each successive year of model results revealed that the diversity predicted by the model posterior closely mirrored the Chao estimator-based diversity. This suggests that there is no added benefit in attempting to use rarefaction in addition to the occupancy model prediction to evaluate site richness. The model did predict several breeding species at sites such as Bryde Island-East (Figure 3.3F), that are quite small and may not have room to host as many as five or six breeding bird species. However, the model is using all available evidence to account for species with low detection probability, which is unbiased on average, even if it over-predicts breeding richness for specific sites. Future efforts based on finer spatial-scale distribution data, as well as high-resolution datasets on terrain and other environmental covariates, will improve predictions of richness. Fitting occupancy data with a multi-species model may also improve the estimation of species richness (e.g., Dorazio and Royle 2005), though doing so greatly increases the computational requirements for model fitting.

The analysis identified 22 sites with “high” (≥10 breeding species) avian species richness (Table 3.1), of which, only Entrance Point (Deception Island) is designated an Antarctic Specially Protected Area (ASPA). Of that group, 13 were identified as potentially sensitive to anthropogenic disturbance by Naveen (2003), three as “highly” sensitive and the remainder as “moderately” sensitive, which were identified using the presence/absence data that had been collected to that point. Due to the large number of sites with low confidence, however, and the fact that this study only sampled 196 of the hundreds of breeding bird sites in the region, there could be many more locations on the Antarctic Peninsula with large concentrations of richness. Opportunistic visits using cruise ships are also unavoidably biased towards places that draw more tourists, which may themselves be biased towards high-diversity areas. To aid future survey efforts of the avian breeding locations examined by this study, I have included a column in the site metadata (see GitHub repository) that categorizes the highest priority sites for re-survey.

Many stretches of the Antarctic Peninsula are rarely visited and remain under-explored for aggregations of wildlife. Having methods of surveying biodiversity will become ever more important as climate change is projected to open up thousands of square kilometers of new ice-free area on the Antarctic Peninsula, with dramatic potential impacts to both native and non-native taxa (Lee et al. 2017). This approach provides a starting point for understanding avian biodiversity patterns on the Antarctic Peninsula and can be used to identify additional sites of high conservation value.

CHAPTER 4: Influence of stochastic and deterministic factors on metacommunity patterns in site-faithful avian breeding assemblages

4.1: ABSTRACT

Empirical examples of randomly structured metacommunities are rare, especially among vertebrates, which are often difficult to study in the wild. I explored the metacommunity structure of Antarctic Peninsula seabirds, which breed in a clearly defined patchwork of breeding sites located in a simple terrestrial environment. The system is well-suited to examining occupancy patterns. The arrangement of species among sites did not display any significantly coherent patterns, suggesting neither positive nor negative associations among species. Non-metric multidimensional scaling of the community composition at each site also showed no clustering of sites into distinct species assemblages, and what subtle variation in community structure did exist displayed no clear geographic patterns, supporting the hypothesis that stochastic colonization drives species incidence. However, the three members of the genus *Pygoscelis* and the Antarctic shag, which together constitute one of the region's foraging guilds, displayed strongly non-overlapping patterns in abundance concentration. These findings suggest that while neutral processes may determine occupancy patterns, growth of populations is likely dependent on more deterministic factors, although without clear indication of what those factors might be. This study highlights how factors such as site-fidelity and scale may impact niche differentiation and metacommunity structure, and introduces a new model system to community ecology with many possibilities for future exploration.

4.2: INTRODUCTION

Metacommunity theory is a useful framework for understanding patterns of spatial variation in community structure, but some patterns, especially those consistent with stochastic processes, have been supported by few empirical examples (Logue et al. 2011, Leibold and Chase 2018). The role of stochasticity in structuring ecological communities depends on how it is defined and measured (Vellend et al. 2014). In particular, some authors focus on patterns of occupancy (e.g., Leibold and Mikkelson 2002) and others on abundance (e.g., Vellend et al. 2014). Building from results of Chapter 3, this study was designed to explore a system not previously represented in the metacommunity literature, examining patterns in both occupancy and abundance.

Leibold and Mikkelson (2002) outlined a method (refined by Presley et al. 2010) by which site × species incidence matrices (created from presence/absence data—here also referred to as occupancy data) could be used to explore the structure of a metacommunity. In this approach, matrices consistent with random patterns (usually linked to neutral theory; Hubbell 2001a) can be distinguished from those consistent with other patterns, such as checkerboard matrices (Diamond 1975), nested subsets (Patterson and Atmar 2008), or gradients in species turnover, the last of which represents a continuum with assemblages of distinct sets of species at one extreme (Clements 1916) and systems in which species assemble independently with respect to environmental factors on the other (Gleason 1926). Empirical examples of Clementsian and Gleasonian patterns from site-by-species incidence data are well documented, however examples of random metacommunities are scarce, especially among vertebrates (see Table 4.1 in Leibold and Chase 2018). Although mechanisms for ‘random’ or ‘neutral’ patterns may vary (McPeek and Siepielski 2019), here I focus on whether the arrangement of a site × species incidence matrix is consistent with a pattern that could be generated by a random colonization process.

There are several reasons why random metacommunities might be rare or difficult to detect. First, it is possible that stochastic processes (generally, any mechanisms causing random turn-over in species composition, i.e., ecological drift) are less influential than deterministic factors such as habitat heterogeneity and competition. If true, ‘neutral’ metacommunities would be genuinely rare. Another possibility is that random processes influence community structure more often than is appreciated, due to the importance of the scale of investigation in measuring ecological patterns (Levin 1992). Viana and Chase (2019) found that deterministic processes, such as the impact of environmental heterogeneity, more strongly influenced the structure of a simulated metacommunity at larger spatial extent and smaller spatial grain. Still another possible cause for the paucity of metacommunities with random species incidence patterns is heterogeneity in abundance. A commonly observed pattern in ecology is that the most common species are generally the most widely distributed (Hanski 1982, Holt et al. 1997), but many factors, such as dispersal, can influence the effect size of that occupancy-abundance relationship (Gaston et al. 2000, Blackburn et al. 2006). Estrada and Arroyo (2012) showed how occurrence models may be insufficient to model the abundance patterns of semi-colonial species, leading me to suspect that patterns in abundance, particularly when coloniality impacts dispersal patterns, may not coincide with stochastic occupancy patterns. In other words, differences in species incidence distributions may be subtle, whereas differences in abundance may be much easier to detect.

I investigated the extent to which the distribution of the avian community on the Antarctic Peninsula was consistent with stochastic processes, made possible by the comprehensive occupancy information in Chapter 3 and the collection of abundance data for some species (Humphries et al. 2017, Chapter 2). Most seabird species are highly colonial and philopatric to their terrestrial breeding colonies (Pietz and Parmelee 1994, Hinke et al. 2007), which may contain multiple species breeding together (Wittenberger and Hunt 1985). Their habitat patches are devoid of most other biota and there is likely very little terrestrial variation among them from the birds' perspective. This suggests that the seabirds breeding there are functionally equivalent (sensu Hubbell 2005) with respect to their nesting site choices.

While the Antarctic Peninsula's terrestrial habitat is relatively uniform, its marine habitat contains geographic gradients, generally running north-south, in ocean temperature and sea-ice conditions (Cook et al. 2016). These gradients may deterministically cluster species into disparate communities, either in nested subsets or along a Clementsian-Gleasonian gradient. The relative importance of either such deterministic forces or random assembly in forming seabird communities along the gradient is currently unknown, providing the opportunity to explore a species incidence pattern in a system that was new to the metacommunity literature.

Although patterns of occupancy are now modeled for the entire suite of species in the community (Chapter 3), comprehensive information on abundance is only available for the four common members of the guild of pursuit-diving species, including the three penguins in the genus *Pygoscelis* (Humphries et al. 2017) and the Antarctic shag (Chapter 2). Despite being only a subset of the whole species pool, this guild is an interesting focal group because it comprises a substantial fraction of the seabird population in the region, and *Pygoscelis* is the only genus with more than two species breeding locally.

Here I examine the site × species incidence of all bird species (and consequently, all terrestrially-breeding vertebrates) on the Antarctic Peninsula, exploring the extent to which community structure is consistent with expectations of either stochastic or deterministic forces. Abundance data for one guild were then used to see whether the concentration of population size differed from patterns in incidence. The study was motivated by and interest to understand the underlying ‘rules’ by which bird communities were assembled from the regional species pool, and facilitated by access to uniquely comprehensive datasets on occupancy and abundance.

4.3: METHODS

Occupancy data were obtained from the results of single-species multi-state occupancy models (Chapter 3). For the analysis of the avian metacommunity I used the site-specific posterior probabilities of breeding from these models, and drew 1000 random matrices of binary species states (breeding/not-breeding) across all sites to create 1000 site × species matrices. These essentially represent a posterior distribution for the community at each site. This allowed me to summarize the most likely site × species matrix using the median state of each species at each site, or, alternatively, to use the full distribution of 1000 matrices to represent uncertainty around the metacommunity’s structure. In Chapter 3, I determined that the models could not confidently capture the full breeding diversity of a site with less than five years of data collection, so only the 56 sites for which at least five years of data were included. I included all of the species from those models (which represented the entirety of the Antarctic Peninsula breeding bird species pool); however, I combined results for the two species of skua (*Stercorarius maccormicki* and *S. antarcticus*) that are known to hybridize and are often difficult to distinguish in the field.

Metacommunity structure was evaluated using the framework outlined by Leibold and Mikkelson (2002) and refined by Presley et al. (2010), which uses the distribution patterns of species among sites to calculate the level of coherence, turnover, and boundary clumping. The first step, evaluating matrix coherence, involves organizing the rows and columns of the site × species matrix with an ordination procedure so sites with similar species compositions and species with similar ranges are placed together, after which ‘coherence’ is measured by the number of unfilled cells (‘embedded absences’) in the matrix (Dallas 2014). In short, the method measures deviations from a ‘coherent’ community in which species occupy every site in their respective range. If the number of embedded absences does not differ from the number in randomized matrices, one can rule out patterns consistent with nested subsets, Clementsian/Gleasonian turnover, or competitive exclusion. One can think of coherence as the degree to which species are ‘mixed-up’ among discrete sites with respect to each other. Coherence was calculated using the function ‘Coherence’ in the package ‘metacom’ (version 1.5.2; Dallas 2014) in R (version 3.5.1; R Development Core Team 2018) for each of the 1000 draws from the probabilistic site × species matrix. By recording the z-score (the standardized difference between the observed and expected number of embedded absences) for each of these iterations, I produced a posterior distribution for coherence from the combined posteriors of all site × species breeding probabilities. To calculate null matrices, I preserved species frequencies (i.e. species commonness) but allowed site-specific species richness to vary, as I could find no reason to suspect that the number of high or low richness sites would be conserved.

In addition to the Leibold and Mikkelson (2002) coherence-based approach, I used non-metric multi-dimensional scaling (NMDS) on the median site × species matrix to look for any patterns of variation among sites in their species composition that might not have been identified by embedded absences. The Jaccard index was used as the dissimilarity metric and retained three axes in the NMDS (‘metaMDS’ function in the R package ‘vegan’; Oksanen et al. 2019). The three-axis NMDS site scores were then converted into unique colors by assigning axes one, two, and three to red, green, and blue color values, respectively. In this way, each community was assigned a color, with more similar communities being more similar in color than those that were more distinct. Placing these points on a map according to their geographic location allowed me to visually identify any geographic clustering in community similarity (Ferrier et al. 2007). I also calculated pairwise orthodromic distance (i.e., the shortest distance around the surface of a sphere) between all sites using the haversine method (R package ‘geosphere’), which then was compared to the pairwise Jaccard dissimilarity in community composition.

To look for a potential relationship between species richness and the area of bare rock available for nesting, I used results from the species-accumulation curve analysis from Chapter 3 and obtained site areas by manually annotating the bare-rock layer produced by Burton-Johnson et al. (2016). Sites that did not have clearly identifiable boundaries to the accessible rock area were excluded, as were sites with fewer than five years of visitation data (the criterion for inclusion in the metacommunity analysis).

Abundance data for the *Pygoscelis* penguins came from the Mapping Application for Penguin Populations and Projected Dynamics (MAPPPD; Humphries et al. 2017), while data on shag abundance came from the analysis in Chapter 2. For penguins, I included all sites north of 68.5°S and between 70.0°W and 44.3°W, which included the entirety of the Antarctic Peninsula, the South Shetland Islands, and the South Orkney Islands. I used the median of the posterior estimate for population size in 2016. As uncertainty compounds in sequential years without direct field observation, I used the last available count rather than the model estimate in cases where no abundance survey had been completed since 2006. The entire range of the Antarctic shag was included, including the birds in the South Orkney Islands of uncertain taxonomy, using the most recent estimate of population size provided (Chapter 2). Given the effort expended in documenting the presence of these densely-aggregating, surface-nesting species (the easiest to detect among all of the region’s seabirds), including in some cases via satellite imagery (Lynch et al. 2012b), this likely represents nearly-complete information about all breeding sites in the region.

To standardize abundance patterns for more effective comparison among species, a species-specific kernel density estimate was calculated for each set of colony locations, weighted by the abundance at each colony. The sites were first reprojected with a Lambert equal-area projection centered near the midpoint of all sites, at 64.411°S, 56.789°W. I used the bandwidth parameter suggested by Venables and Ripley (2002) as a way to visualize where, if at all, each species had concentrated collections of high-abundance colonies.

4.4: RESULTS

Among the 56 sites included in the full community analysis, predicted species richness ranged from 7 to 13 (mean = 8.8). The most common species was the gentoo penguin, and the least common species was the black-bellied storm-petrel (*Fregetta tropica*). Of the comprehensive list of 515 sites with abundance estimates of pursuit-diving birds, 140 (27%) included at least two members of the guild. All three species of *Pygoscelis* penguin breed together at fifteen of those sites.

The distribution of coherence z-scores had a median of -0.24 with 95-percent quantiles of -2.25 and 1.47, providing no evidence of either positive or negative coherence (Figure 4.1). The three-axis NMDS (stress = 0.0908) identified a single cloud of points with no discernable community clusters (Figure 4.2), and there was little to no geographic pattern in community composition, except at the most southerly sites (Figure 4.3; see Appendix 9 for maps with individual axis results). The orthodromic distance between pairs of sites was not strongly correlated with the pair-wise Jaccard dissimilarity of community composition, except at extremely large distances (> 500km; Figure 4.4). Sites within a few kilometers of each other exhibited the full range of community dissimilarity, as did sites hundreds of kilometers apart. Both the NMDS pattern and high levels of dissimilarity among neighboring sites were consistent with a single community pool for the majority of sites, potentially with subtle gradients in species composition. For the very small subset of sites (n = 14) that had high confidence estimates of both bare rock area and species richness, there was not enough evidence to demonstrate a significant linear relationship between the natural log of area and the natural log of richness (Figure 4.5; $F = 2.201$, $df = 1,13$, $p = 0.1618$), providing no evidence for a species-area relationship.

Unlike the metacommunity patterns from occupancy data, maps of population density from abundance data (i.e., the concentration of abundance in geographic space) for the pursuit-diving seabirds displayed strikingly non-overlapping patterns (Figure 4.6). Abundance was most strongly concentrated among the three species of *Pygoscelis* penguins, with Adélie penguins concentrated in the northeast (Figure 4.6A), chinstrap penguins on the major island groups to the north (Figure 4.6B), and gentoo penguins in two areas in the South Shetland Islands and central Antarctic Peninsula coastline (Figure 4.6C). All three penguin species had widespread distributions, but uniformly low abundances over much of their range compared to within their respective abundance hotspots. With the exception of the South Shetland Islands, where their concentrations were low, Antarctic shags were more uniformly distributed and overlapped many of the penguin hotspots (Figure 4.6D).

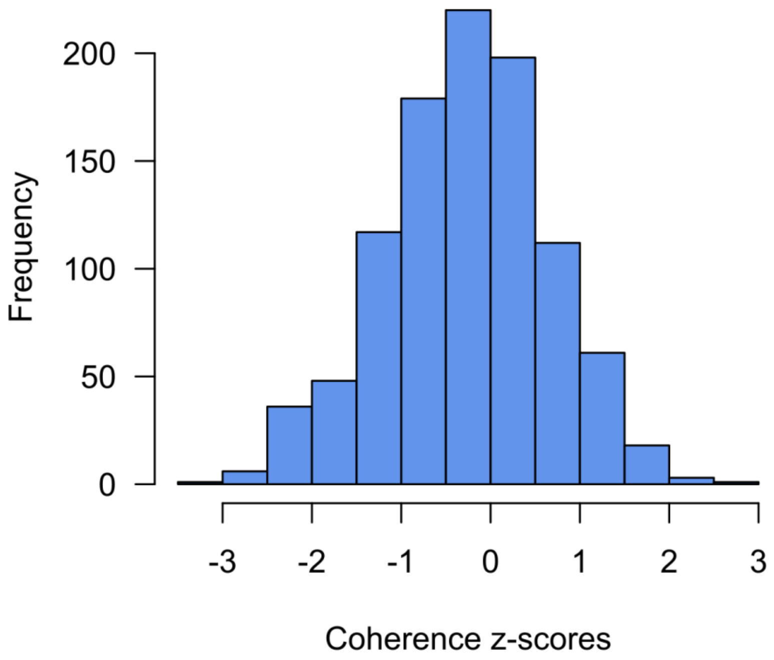

Figure 4.1: Distribution of coherence z-scores from 1000 site × species matrices drawn from the matrix of site x species probabilities.

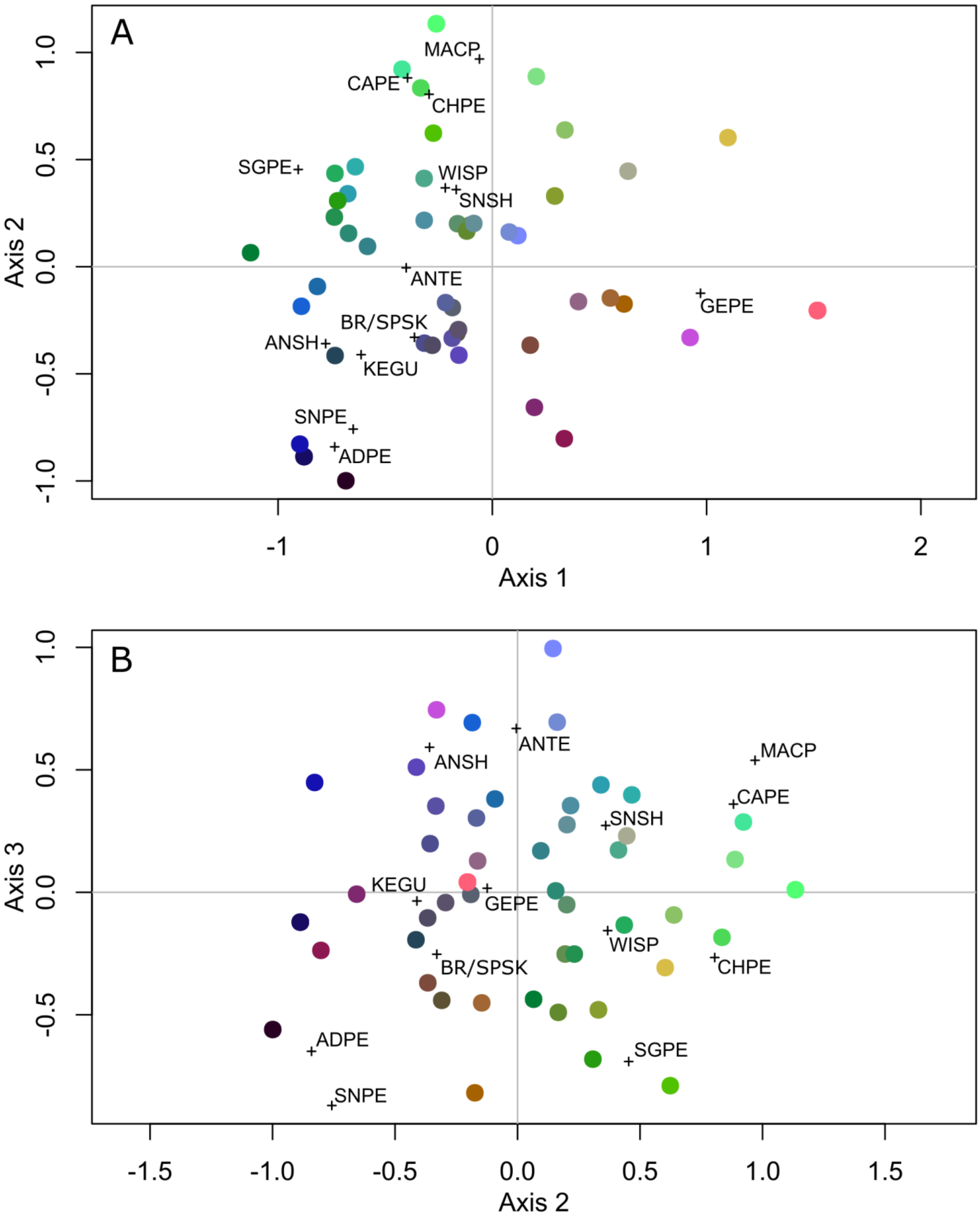

Figure 4.2: Site scores (colored points) and species loadings (crosses) from a three-axis non-metric multidimensional scaling of median occupancy state of all species at each site with at least 5 years of data collection. See Table 1.1 for species codes; note that both species of skua are combined. A: Retained axes 1&2; B: axes 2&3. Colors were created by assigning red, green, and blue values to Axes 1, 2, and 3, respectively.

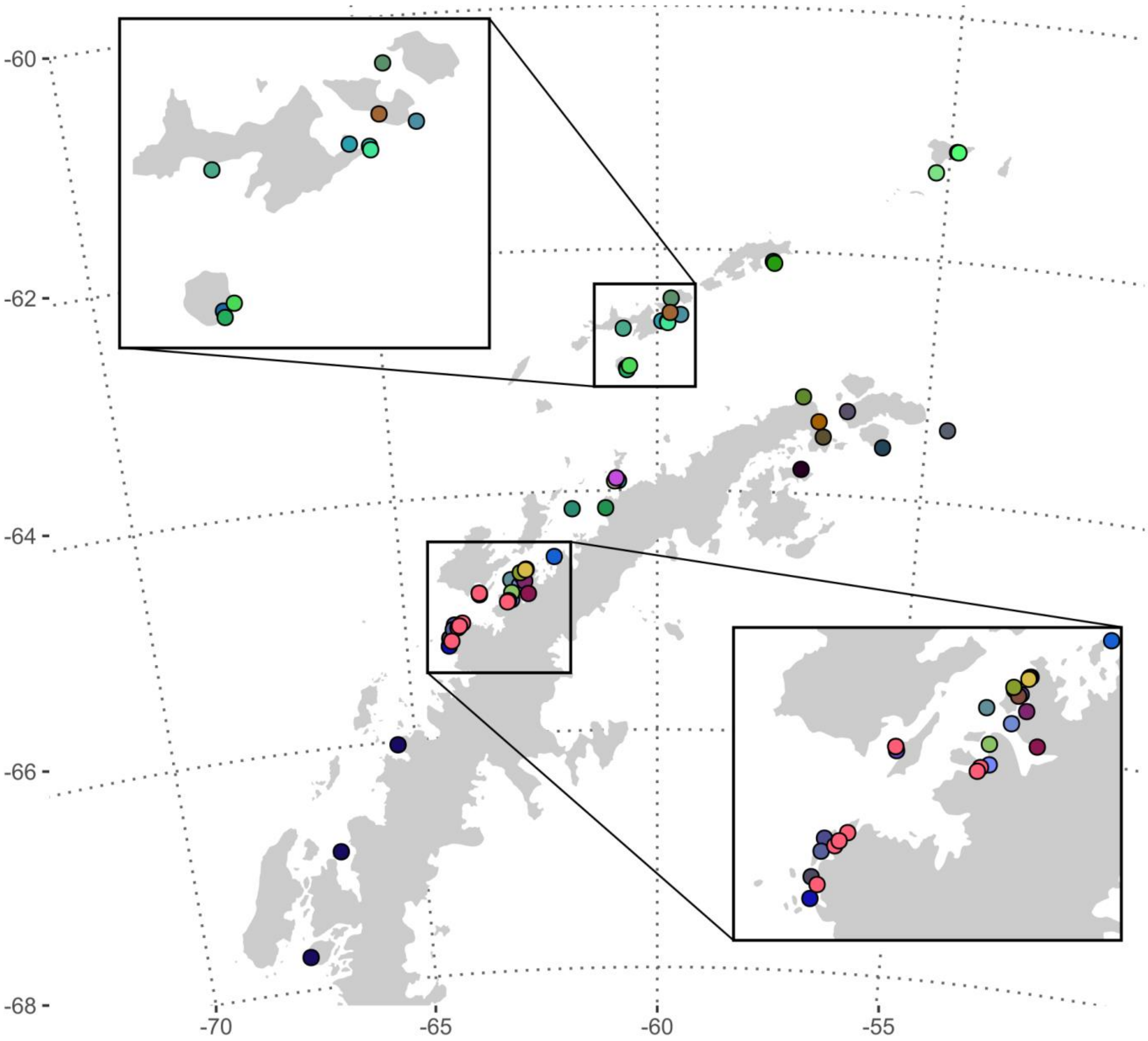

Figure 4.3: Map of sites with at least 5 years of occupancy data, displayed with the red-green-blue color assigned from the three retained NMDS axes. Insets enlarge areas with higher site density.

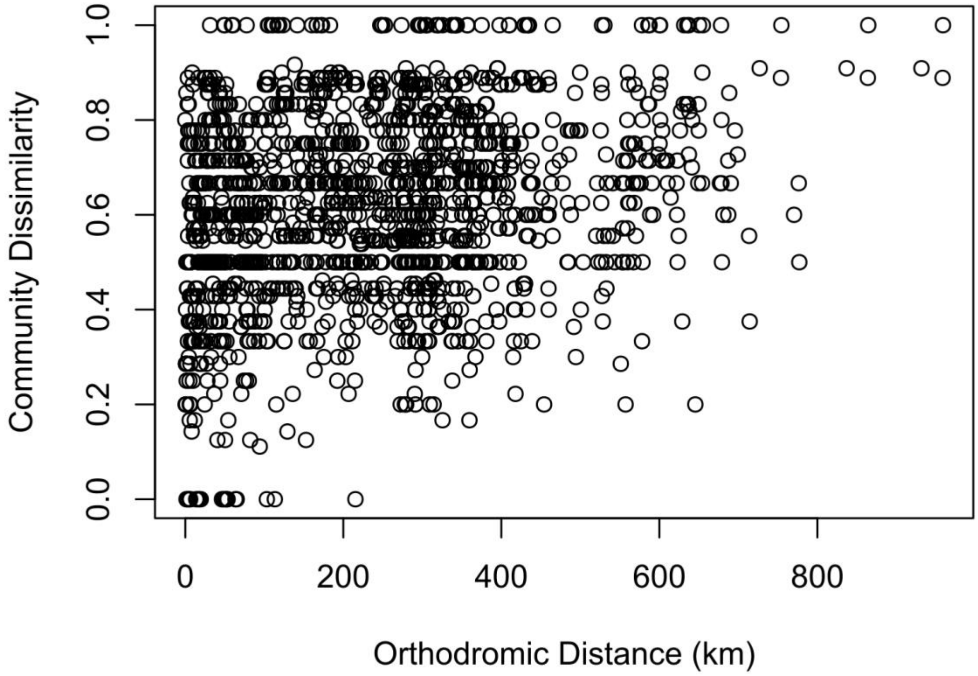

Figure 4.4: Pair-wise orthodromic (i.e., across the planet's surface) distance between sites vs. pair-wise Jaccard dissimilarity.

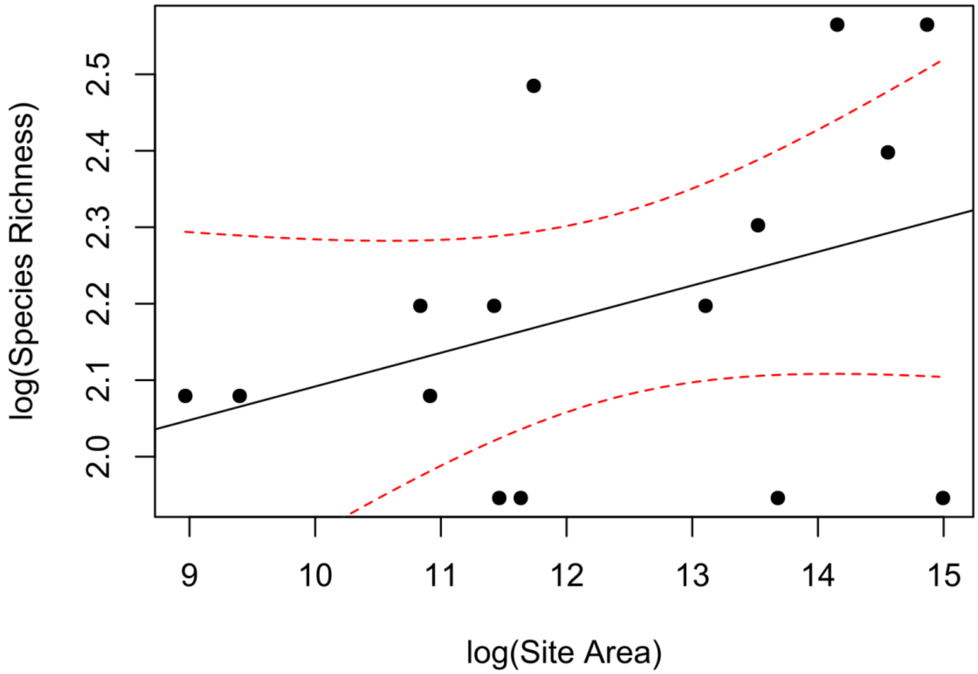

Figure 4.5: Species-area relationship for sites that had both high confidence estimates of total bare-rock area and at least five years of occupancy data. Best-fit linear slope of the relationship between log(area) and log(richness) equals 0.067 (t = 2.373, *d.f.* = 12, p = 0.035). Dotted red lines indicate 95% confidence interval around the best-fit line.

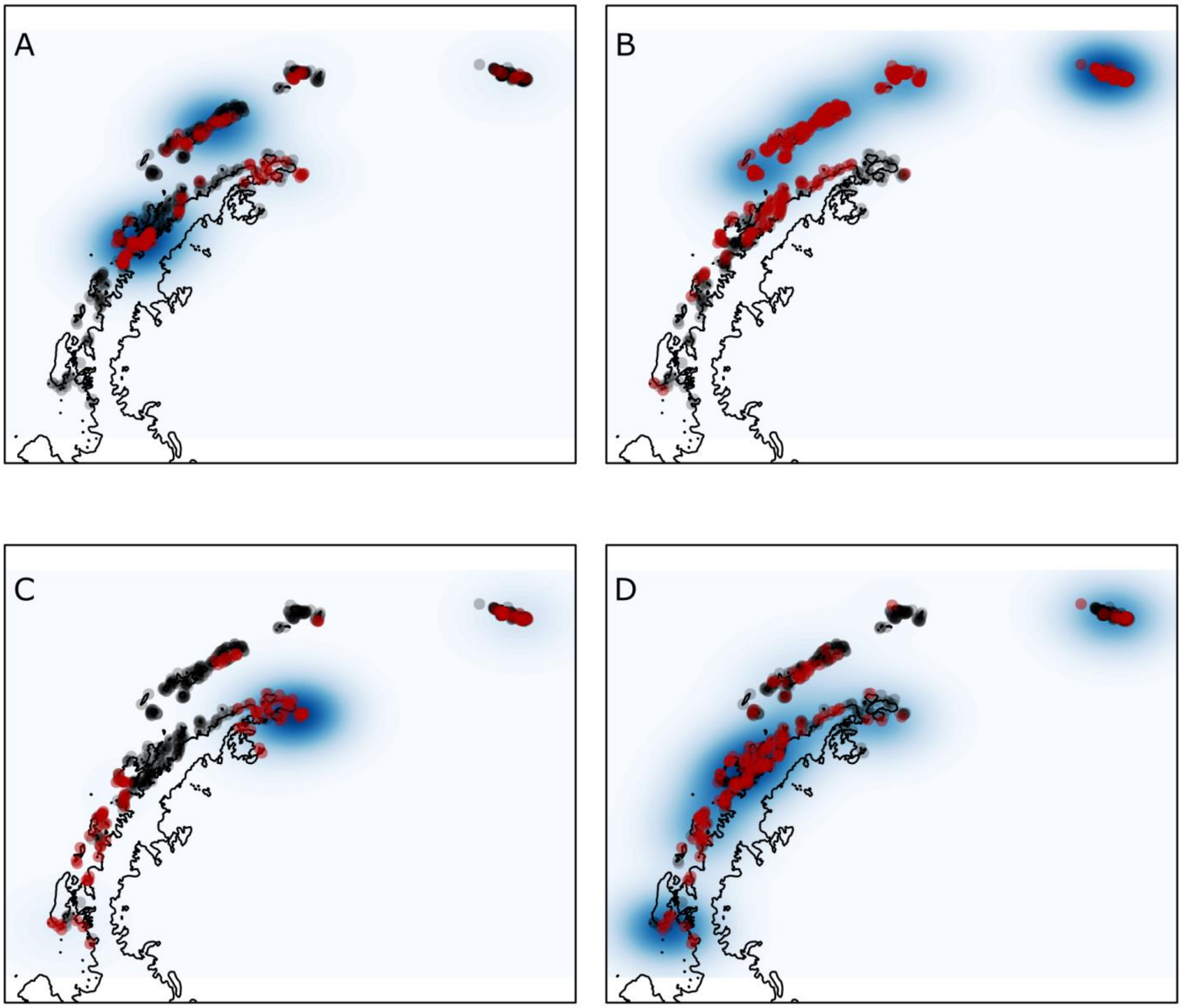

Figure 4.6: All known colony locations (points) and local population density (blue shading) of the four main pursuit-diving seabirds in the Antarctic Peninsula region: the three *Pygoscelis* penguins (A: gentoo, B: chinstrap, and C: Adélie) and D: Antarctic shag. Point color indicates sites occupied (red) and not occupied (black) by each species.

4.5: DISCUSSION

Species incidence patterns can be influenced by a variety of factors, often obscuring the role that stochastic and deterministic forces might play in creating a metacommunity structure. By incorporating both occupancy and abundance data I provide a clearer picture of how seabird life-history and landscape-scale aspects of the Antarctic Peninsula environment combine to structure this seabird metacommunity. No strong patterns emerged from the occupancy data, consistent with a metacommunity of patches colonized by a stochastic process. In contrast, available abundance data at the same regional scale showed clear non-overlapping, species-specific concentrations, suggesting niche differentiation due to deterministic processes. The addition of Antarctic Peninsula seabirds to the body of metacommunity literature highlights how differences in methods can lead to a diversity of observed ecological patterns.

Several lines of evidence point toward stochastic patch occupancy among species. There was no significant coherence in species incidence across sites, nor did the NMDS analysis reveal any clusters of sites with similar species composition in either ordination space or geographic space. In addition, sites only a few kilometers from each other often had just as dissimilar species assemblages as sites that were hundreds of kilometers apart. While it is difficult to prove the absence of a spatial pattern, the simplicity of the terrestrial environment (i.e., mostly bare rock with minimal vegetation and few elements of habitat that would conceivably impact seabird breeding) makes it unlikely that unaccounted-for site-level variation in habitat suitability has strong deterministic effects on what species colonize any given site. From the occupancy point of view, therefore, there is nothing to distinguish this metacommunity from a null expectation that species colonize sites stochastically.

Many sites have long histories of occupation by species that are currently present, and there is little reason to suspect that the observed occupancy pattern represents a snapshot of a dynamic metacommunity characterized by rapid cycling of active and inactive patches. Many of the penguin sites on the Antarctic Peninsula have evidence of initial colonization dating to ~600 years ago (Emslie et al. 2014). Adélie penguins have been breeding in the southern Antarctic Peninsula for at least 6000 years (Emslie and McDaniel 2002). Sites with small populations can therefore persist for hundreds or even thousands of years without going extinct, and such populations may be out of equilibrium with the environmental factors present during colonization. Occupancy status may, therefore, be only weakly informative in understanding a species' habitat suitability, unlike abundance, which is highly heterogeneous and may better reflect optimal environmental conditions. Similar relationships between occupancy and abundance have been found in a variety of species distribution modeling efforts (e.g., Estrada and Arroyo 2012, Howard et al. 2014).

The idea that communities can be stochastically assembled (i.e., neutral) is one of the fundamental cornerstones of metacommunity theory (Leibold and Chase 2018), however empirical evidence for neutral patterns has been difficult to document (McGill et al. 2006). For example, random processes may be more obvious at only certain spatial scales (Viana and Chase 2019), or if one also takes intraspecific mechanisms into account (McPeek and Siepielski 2019). To my knowledge, this study is only the second case (after the study of freshwater fish by Henriques-Silva et al. 2013) in which the use of the Leibold and Mikkelson's (2002) framework has identified a vertebrate metacommunity exhibiting neutral characteristics.

The neutral theory of biodiversity was first developed with the community of tropical trees on Barro Colorado Island in mind (Hubbell 2001b). Tropical trees are similar to seabirds in that adults are long-lived and have high site-fidelity once established, though a tree metacommunity interprets ‘sites’ as individual trees. In the Antarctic avian system there is a similar neutral-like pattern, even when measuring occupancy at the level of the colony. Of particular importance is the fact that in this system the dispersal limitation at the level of a colony is quite a bit stronger than in a system like the Barro Colorado Island trees. The strong site-fidelity of seabirds, capable of locking each community in its initial, stochastically colonized state, may be the crucial feature responsible for such a pattern. Data on the long-term dynamics at these sites is scarce. If nesting remains of non-penguin species are sufficiently well preserved, a historical analysis of multi-species occupation at abandoned sites, similar to the work by Emslie et al. (2020) for the Pygoscelis penguins at one location, would help to better resolve the metacommunity colonization process.

Unlike the lack of consistent patterns in species occupancy, the largest colonies of each species of *Pygoscelis* penguin were concentrated in specific and non-overlapping geographic areas. Colony size, therefore, was neither random nor evenly-spaced. These findings are consistent with Ainley et al. (1995), though the increased precision of the abundance data available now makes it clear that the populations are more clustered than Ainley et al. were able to distinguish. This strikingly non-overlapping pattern of abundance among the three species has not been previously documented and suggests that differences in species’ environmental preferences result in disproportionate population growth across their range.

The concentration of abundance in species-specific areas raises the question: how are these hotspots of high-population sites maintained? Seabird colony size has been demonstrated to follow log-normal and power laws, with few large and many small colonies (Jovani et al. 2008). Jovani et al. (2016) explained such distributions in the Northern Hemisphere with evidence of food availability (i.e., ‘Ashmole’s Halo’). However, there is very little evidence of density dependence in population time series of penguin populations on the Antarctic Peninsula (Che-Castaldo et al. 2017). In addition, all three *Pygoscelis* penguins consume primarily the same food (Hinke et al. 2007). The reason for the striking non-overlap in population concentration, when breeding conditions are clearly ‘suitable’ enough for smaller populations to be maintained for hundreds of years (or more) in areas very distant from these population ‘hotspots’ remains unknown.

This study highlights the value of diverse ecological systems for examining metacommunity structure. In this case, occupancy data suggest that stochastic processes control metacommunity structure. I hypothesize that the original colonization process was stochastic and the resulting random patterning of species incidence has been maintained by strong philopatry. However, abundance data for the four pursuit-diving species point toward species-specific differences in habitat suitability across the landscape, differences that deterministically impact the concentration of large colonies. Despite the challenges of collecting data in the Antarctic, this dichotomy between deterministic and stochastic patterns was possible to explore because the system is composed of discrete patches, inhabited by a relatively small number of species. Of particular importance was the confidence with which I was able to measure the geographic concentration of abundance for the pursuit-diver guild of seabirds, owing to a dedicated effort over the past several decades to collect and catalog the relevant abundance data. I encourage the Antarctic research community to now focus on expanding data collection of abundance to other species, to aid a more complete analysis of the entire species pool. Similar efforts in other systems may yield equally interesting case studies of the role that various factors play in shaping metacommunity structure.

CHAPTER 5: The role of wind fetch in structuring Antarctic seabird breeding occupancy

5.1: ABSTRACT

Avian breeding sites located along shorelines may allow easy access to aquatic food sources, but risk exposing birds and nests to high wind and wave action. One measure of exposure is wind fetch, the distance of open water over which wind can blow uninterrupted. By calculating fetch that is weighted by average prevailing wind direction for breeding colonies of pursuit-diving seabirds in the Antarctic Peninsula, I show that different members of this guild have opposite relationships to coastline exposure. Gentoo penguins occupied more enclosed sites with lower fetch, while chinstrap penguins and Antarctic shags occupied more exposed sites. While considerable research has been devoted to understanding Antarctic seabird habitat suitability, the role of wind and wave exposure has not been considered in depth, in part because comprehensive data on colony presence and absence has only recently been made available. I propose several mechanisms for why fetch may act to differentiate niches among this guild. These findings may increase our ability to identify suitable breeding areas for Antarctic species as they respond to climate change.

5.2: INTRODUCTION

Breeding sites of aquatic bird species need to be accessible to individuals leaving or returning to their nests and are therefore often located along or near the shore. Nests may be well-placed to provide easy access to aquatic or littoral food resources, but too much exposure to wind and waves can have detrimental effects on breeders, including but not limited to difficulty in accessing nest sites (Shepard et al. 2019), increased costs of incubation (Hilde et al. 2016), and nest flooding (Viera et al. 2006, Allen et al. 2008). One way of quantifying the exposure of a breeding site is by calculating fetch, the distance of open water between a point and the closest shoreline in a particular direction over which wind can blow uninterrupted. High fetch allows the production of larger waves, resulting in increased exposure of a coastline to the physical forces of wave action. Several studies have linked either higher or lower fetch to the presence of coastal breeding sites for different species of shorebirds, alcids, and loons (Rönkä et al. 2008, Haynes et al. 2014). Dalgarno et al. (2017) found evidence of a trade-off in black oystercatchers (*Haematopus bachmani*), which nested most commonly in moderately-high fetch areas that provided good foraging resources, even though breeders were excluded from the most exposed areas where the risk of nest-washout was too high. Given the variety of different mechanisms that may link wind and wave exposure to breeding success and nest-site location, and the diverse ways that aquatic bird species interact with the shoreline environment, it is possible that fetch may be one measure that distinguishes niche space in a breeding bird assemblage.

My interest in fetch originated with a casual observation that the breeding sites of gentoo penguins seemed to be clustered in particularly enclosed and protected stretches of coastline, at least when compared to other members of the genus. Several studies have examined the terrestrial components of *Pygoscelis* habitat suitability (e.g., Volkman and Trivelpiece 1981, Cobley and Shears 1999), but the exposure of the coastline has received surprisingly little attention. Identifying aspects of Antarctic Peninsula environment that determine the suitability of locations to *Pygoscelis* breeding is useful because as the region experiences large ecological changes, the gentoo penguin has experienced population increases and range expansion, while the other two members of the genus, the chinstrap penguin and Adélie penguin, have undergone population declines (Lynch et al. 2012a). As densities and distributions of these species shift, and ongoing projects attempt to disentangle the effects of climate change, industrial fishing, and recovery of whale populations on birds (Che-Castaldo et al. 2017, Trathan et al. 2018, McMahon et al. 2019), it is important to understand which habitats might or might not provide suitable places for colonization or population growth in the future. Identifying which factors may play a role in niche differentiation is of particular importance in regions where closely related species occur in sympatry.

My primary goal was to assess whether gentoo penguins were more likely than other pursuit-divers to nest in low-fetch areas, as my anecdotal observations suggested. Given that penguins must enter and exit the water from the shore, it seemed logical that a calmer shoreline would, in general, be advantageous for any penguin breeding site, and that the other *Pygoscelis* penguins may show a similar negative relationship to fetch. Alternatively, a positive relationship to fetch may exist if exposed coastlines provide more direct access to prey resources. I hypothesized that Antarctic shag nesting areas would have no relationship to fetch since, unlike penguins, they are able to fly, and thus arrive and depart their nests irrespective of wave conditions at the coast.

5.3: METHODS

Data on *Pygoscelis* penguin breeding sites were obtained from the Mapping Application for Penguin Populations and Projected Dynamics (MAPPPD; Humphries et al. 2017), which contains a comprehensive list of any colonies ever reported. I used the list of Antarctic Shag breeding sites reviewed in Chapter 2. For this analysis I included any site which contains a breeding population of any of the four species in the central-west region, defined here as all of the coastline between 63.563°S and 65.443°S latitude and 60.212°W and 64.895°W longitude. These boundaries fall at natural breaks in the distribution of pursuit-diver colonies in the region, and also encompass the region identified in Chapter 3 as a hotspot for gentoo penguin population density. It is one of the few areas in the Antarctic Peninsula that contains a reasonably large number of breeding sites of all four species in the guild.

Coastline data were obtained from the Antarctic Digital Database (ADD: https://www.add.scar.org/). I chose the medium resolution polygon layer from which to calculate fetch, because it provided the best balance between the spatial resolution required for accurate calculation and the computing power necessary to handle file size. Because fetch must be calculated from a point, and available methods required points to not overlap the coastline, the ‘QChainage’ plugin in QGIS 3.4 (QGIS Development Team 2020) was used to create a set of points exactly 1 m off of the coast, spaced every 200 m along the shore. A total of between one and approximately twenty of those points were chosen to represent each breeding bird site, using the authors’ knowledge and satellite images available on Google Earth (https://www.google.com/earth/). If a site encompassed a relatively large number of points (generally greater than fifteen), the points were subsampled by choosing one on the edge of the site and selecting every second or sometimes third point. This was done to limit the time required to calculate fetch for the entire collection of sites. The mean number of points selected per site was seven. To compare fetch at breeding sites to the remainder of the coastline, I randomly selected an equal number of points that were at least 1 km away from locations associated with birds. Because the method of using multiple points to represent the fetch at each breeding site had the effect of smoothing the final estimate of average fetch, I also selected seven points (three on either side of the randomly selected point) to summarize the fetch at random points. Finally, in an effort to visualize coastline fetch patterns directly, I calculated a high resolution map of fetch along the coastlines of two areas with a diversity of breeding colonies: Paradise Harbor, an enclosed bay near the southern part of the study area, and Trinity Island, a relatively exposed island near the northern part of the study region. Because fetch is a measure of distance, and because many traditional map projections do a poor job of conserving distance relationships at high latitudes, all geographic data were transformed into a Lambert equal-area coordinate reference system centered on the midpoint of the Antarctic Peninsula sites extracted from MAPPPD (64.411°S, 56.789°W).

Wind data came from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA5 reanalysis product and were obtained from the Copernicus Climate Change Service (C3S: https://cds.climate.copernicus.eu/about-c3s). I used summer season monthly (November through February) means of u- and v-component (i.e. east-west and north-south) wind velocity from 1979-2019, that have a spatial resolution of 0.25° × 0.25°. Each monthly mean raster layer was converted into a layer of wind direction, and the prevailing wind direction was extracted from each layer for each point of interest, including the points representing breeding sites, randomly-selected points, and the example points around Paradise Harbor and Trinity Island. The average wind direction was extracted from the raster cell for each summer month in the 41-year time period (total n = 164) overlapping each point, allowing the production of a frequency histogram of prevailing wind direction for each point.

Fetch was calculated in R, version 3.6.2 (R Development Core Team 2019), using the package ‘fetchR’ (Seers 2018). Fetch was calculated for 36 lines emanating from each point along the coastline, spaced ten degrees apart, and measured as the distance to the closest point of land in each direction. Each of these ten-degree bins was then weighted by multiplying the fetch by the proportion of the 164 monthly wind values for that point that came from that bin. The resulting distribution of wind-weighted fetch was summed across all 36 ten-degree bins to arrive at a wind-weighted fetch value for each point. Fetch for breeding bird sites and random locations were then averaged across all points chosen to represent each location.

Sites were grouped according to whether they did or did not contain each of the four study species to create comparable distributions of wind-weighted fetch. Similar distributions were created for all sites with birds, and for all randomly-selected locations. Fetch was confirmed to be lognormally distributed using a Kolmogorov-Smirnov test, and was then log-transformed for easier analysis and visual interpretation. I used t-tests to compare the mean log-transformed fetch between sites with and without each species, and between all breeding sites and random locations. Resulting p-values were adjusted using the Šidák method to account for multiple comparisons.

5.4: RESULTS

The combined data from the MAPPPD database and Chapter 2 resulted in 130 sites in the central-west region of the Antarctic Peninsula with at least one breeding species of pursuit-diving seabird. Each species occupied between 14 and 62 of the total sites in the region (Table 1). The species of primary interest, gentoo penguins, had some overlap with other species (present together with Adélie penguins at seven sites, chinstrap penguins at fifteen sites, and Antarctic shags at seventeen sites). Four sites contained all four pursuit divers.

The distribution of weighted fetch across all sites was lognormally distributed (Kolmogorov-Smirnov test, $D = 0.0737$, $p = 0.4796$), and when log-transformed showed a geographic pattern similar to expectations, with generally higher fetch to the north and along the exposed western sides of the major islands (Figure 5.1). Prevailing winds during the study period were often westerly (i.e. onshore) along the exposed western shore of those large islands, resulting in some of the highest weighted fetch values. Winds through the center of the study region were often easterly, presumably originating from the high-elevation glaciated Antarctic Peninsula to the east, resulting in relatively low weighted fetch along the eastern shore of the Gerlache Strait compared to the western shore.

Of the four members of the guild, only gentoo penguins occupied sites with significantly lower fetch than sites at which they were absent (Figure 5.2A; Table 5.1). In contrast, sites occupied by chinstrap penguins and Antarctic shags had higher fetch than those without (Figure 5.2B,D; Table 5.1). Distributions of fetch at sites with and without Adélie penguins could not be distinguished, although the ratio of sample size between both categories was much more uneven than for the other species (Figure 5.2C; Table 5.1). The distribution of fetch at sites with birds was not significantly different from randomly-selected locations along the entire coastline of the central-west region of the Antarctic Peninsula (Figure 5.2E; Table 5.1).

Paradise Harbor (Figure 5.3A) and Trinity Island (Figure 5.3B) exemplify some of the patterns seen throughout the entire study area. Trinity Island generally had higher fetch along its entire coast, and hosted mostly chinstrap penguin colonies with a couple of gentoo penguin colonies at its southern end in one of the few protected bays. By contrast, Paradise Harbor was almost entirely protected and, consistent with my overall findings, primarily hosted gentoo penguin colonies.

Species	Number of Colonies		Difference in log(weighted fetch)	t	Šidák-corrected p-value
	With	Without			
gentoo penguin	53	77	-1.2909	-6.875	<0.0001
chinstrap penguin	55	75	0.7529	3.378	0.0051
Adélie penguin	14	116	-0.4828	-2.222	0.1615
Antarctic shag	62	68	0.6557	3.009	0.0157
any species	130	130 (random)	0.0021	0.011	1.000

Table 5.1: Results of two-sample t-tests between the distributions of the natural log of weighted fetch at pursuit diver breeding colony sites that did and did not sustain populations of each species, as well as a t-test between all breeding colony sites and an equal number of randomly selected coastline locations greater than 1 km away from any breeding colony. Displayed p-values were Šidák-corrected for multiple comparisons.

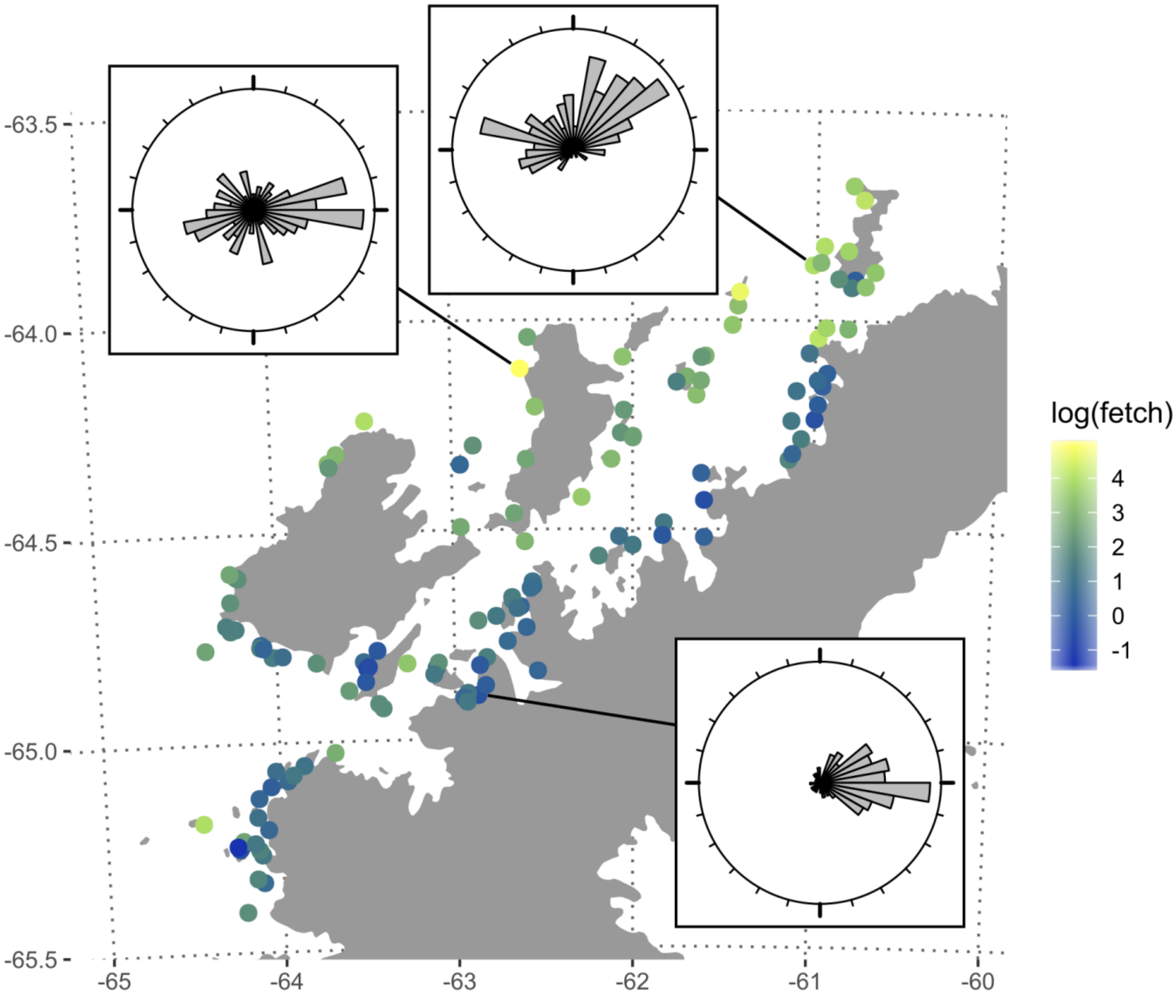

Figure 5.1: Log-transformed average wind-weighted fetch at each breeding bird site in the central-west region of the Antarctic Peninsula. Insets show distribution of prevailing summer wind direction at three representative points.

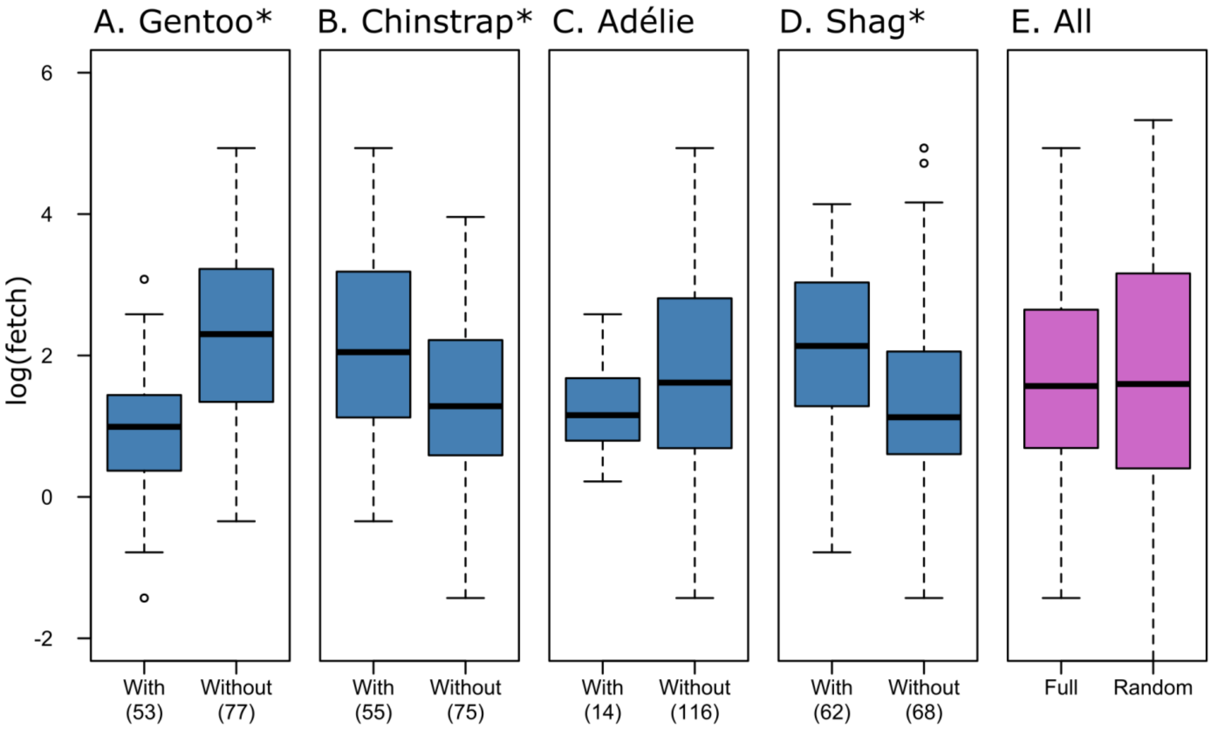

Figure 5.2: The distribution of the natural log of wind-weighted fetch at sites with and without each species of pursuit diving seabird (A: gentoo penguin, B: chinstrap penguin, C: Adélie penguin, D: Antarctic shag) in the central-west region of the Antarctic Peninsula. Total number of sites in each category listed on the x axis. Panel E. shows the distribution at all 130 sites, compared to the randomly selected locations at least 1 km away from bird sites. Asterisks (*) indicate species for which the difference in mean fetch was significant (Table 5.1).

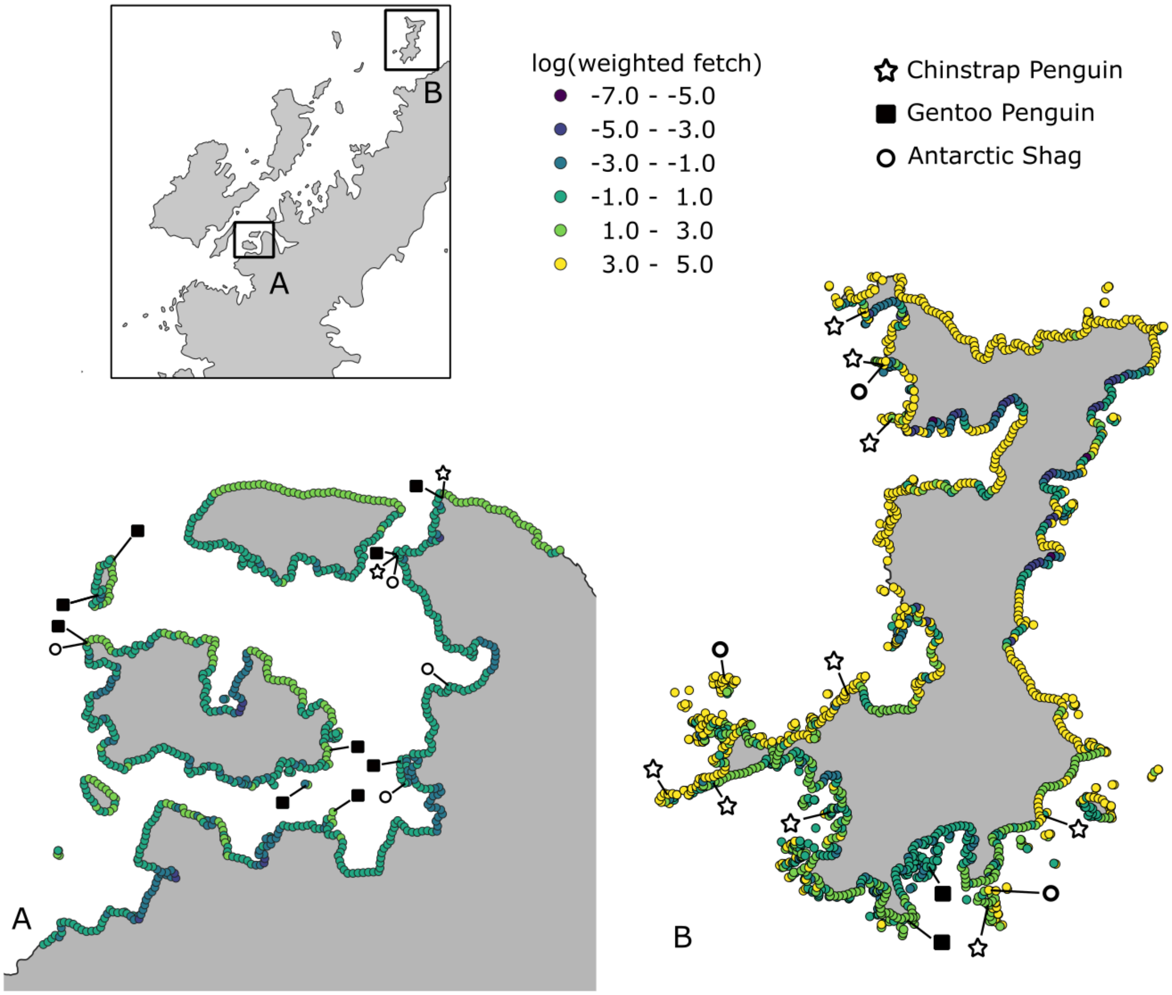

Figure 5.3: Log-transformed wind-weighted fetch along the coastline in two representative areas: (A) relatively protected Paradise Harbor and (B) relatively exposed Trinity Island. Breeding instances of pursuit divers indicated by stars, squares, and circles (chinstrap penguin, gentoo penguin, and Antarctic shag, respectively).

5.5: DISCUSSION

The divergent responses to wind fetch exhibited by different pursuit-diving seabirds in the central-west region of the Antarctic Peninsula highlight a previously underappreciated aspect of the guild's niche space. Gentoo penguins occupied breeding sites with significantly lower weighted fetch, as I initially expected from my casual observations. In contrast, both chinstrap penguins and Antarctic shags occupied sites with higher fetch. Although Adélie penguins did not show a significant relationship, it is possible that the small number of nesting sites in the study region masked such a relationship. My results demonstrate that a coastline's level of exposure has the capability to act as an environmental filter, determining which seabird species are most likely to succeed at establishing or growing colonies at a very local scale.

Before exploring possible mechanisms for the relationship with fetch in Antarctic bird occupancy, it is worth considering the evidence of mechanisms for similar relationships in other waterbirds with nests along shorelines. In their analysis of 15 species breeding in a Finnish archipelago, Rönkä et al. (2008) found positive relationships between mean fetch and both turnstone (*Arenaria interpres*) and black guillemot (*Cepphus grille*) breeding presence, although they also found some evidence that it may positively affect lesser black-backed gull (*Larus fuscus*), redshank (*Tringa totanus*), and common ringed plover (*Charadrius hiaticula*) breeding. Those authors did not expand on the exact nature of the relationships, other than to indicate that those species were considered to favor more maritime, exposed islands. Both gulls and shorebirds obtain much of their food from littoral shorelines, which is not the case for either of the Antarctic species with positive relationships to fetch. Fetch was one of several variables that affected the location of Pacific (*Gavia pacifica*) and yellow-billed (*G. adamsii*) loon nests, both of which were more likely to nest in areas with less exposure (Haynes et al. 2014). Exposure to high winds also impacted western grebe (*Aechmophorus occidentalis*) nest placement, although differences in fetch were not appreciable enough for the authors of that study to examine it specifically (Allen et al. 2008). Black oystercatcher nests were found predominantly in areas with higher fetch, likely due to greater prey abundance along more exposed coasts, but declined sharply at extremely high exposure sites, presumably due to the risk of washout (Dalgarno et al. 2017). Therefore, risk of flooding or damage to the nest was a common mechanism used to explain many negative relationships to fetch, even if balanced by the benefits of being located near a food source. Loons, grebes, and oystercatchers all generally nest right along the shoreline, rather than in colonies that may be set back from shore on more elevated ground, as is the case for all of the Antarctic pursuit-divers. Both loons and grebes are also limited physically, because they would be unable to fly to the water from a more inland nest.

Antarctic birds may relate to fetch and exposure in diverse ways, including some combination of access to food and physical risk of exposed shorelines. Several aspects of gentoo penguin ecology and nest-site selection differ from that of the chinstrap and Adélie, perhaps providing insight on whether a physical risk, such as flooding or damage to nests, may be responsible for the difference in affinity for fetch at breeding sites. Compared to the other two *Pygoscelis* penguins, gentoos have been shown to occupy lower elevations when breeding at the same site (Volkman and Trivelpiece 1981). If gentoos also nest at lower elevations when not sympatric with other species, which is, as yet, untested, then they would be at higher risk of flooding from abnormally heavy surf, possibly explaining an affinity for areas with calmer shorelines. However, the mean elevation of gentoo colonies is still well above sea level (Volkman and Trivelpiece 1981), making flooding from heavy surf unlikely. Gentoos generally feed further inshore than other *Pygoscelis* penguins and have shorter nest relief intervals

(Trivelpiece et al. 1987), meaning that over the course of a breeding season each adult likely makes more transits to and from the water than its congeners. Although the difference is small, this may also make it more advantageous to breed in areas where adults are less likely to be subjected to strong forces when coming ashore. At large spatial scales, chinstrap penguins avoid areas with higher sea-ice concentrations (Fraser et al. 1992, Trivelpiece et al. 2007), suggesting that areas with large concentrations of ice might also be unfavorable at the local scale around breeding sites. It is possible that by nesting at areas more exposed to wave action, such as prominent points and along the more exposed sides of islands, chinstrap colonies are located in areas that are less likely to entrain dense mats of ice, which occasionally choke enclosed stretches of water in the Antarctic summer. I suggest that if physical risks from heavy surf do play a role in the divergent relationships to fetch among Antarctic birds, it may relate more to risks associated with coming and going from the colony than damage to eggs and nestlings.

Other means of ecological separation in foraging exist among the three *Pygoscelis* penguins, which may relate to the relationship of fetch to food supply. When breeding at the same site, these species often segregate their marine foraging areas, with gentoo penguins generally foraging closest to shore (Trivelpiece et al. 1987, Kokubun et al. 2010, Cimino et al. 2016b, Oliver et al. 2019). Of course, fetch may affect local currents (Mao and Heron 2008), and therefore the concentration of marine food sources, but fine-scale data on currents and prey distribution for most of the central-west Antarctic Peninsula are extremely limited. Antarctic shags feed almost entirely on demersal fish, likely feeding very close inshore (Casaux and Barrera-Oro 2006), which suggests that having local areas that are ice-free might be important, similar to my hypothesis above for chinstrap penguins. However, Antarctic shags nest much further south along the western coast of the Antarctic Peninsula, as well as in the northeast region near the Weddell Sea (Chapter 2), where sea-ice concentrations are much higher. It is, therefore, difficult to imagine colony locations in the central-west region being constrained by ice. I was not able to investigate any relationship between fetch and marine habitat use directly; however, spectacled eiders (*Somateria fischeri*) wintering in the Bering Sea rely on sea-ice leads that are affected by fetch (Bump and Lovvorn 2004). Given that all four Antarctic pursuit-divers examined here have close relationships with sea-ice environments, both during the breeding and over-wintering seasons, it is reasonable to expect that fetch may play a variety of roles in their habitat suitability. I also did not attempt to investigate the possible effects that fetch and wind-related ocean mixing may have on the marine community on which Antarctic seabirds rely. In other systems, birds often interact with fetch and wind via vegetation structure or food supplies (Allen et al. 2008, Dalgarno et al. 2017). Examining whether long-term changes in average wind direction have occurred at local scales was not possible in this analysis, but such changes are likely given larger scale changes in prevailing winds in the Southern Ocean (Thompson and Barnes 2014). Whether or not fetch impacts availability of prey in coastal Antarctica, and whether or not the effect of prevailing winds has changed over time would be interesting topics for future study.

All Antarctic pursuit-diving birds are dense, colonial nesters, and one hypothesis for the advantage of colonial nesting involves the passing of information at the colony, when members of the colony are able to take directional cues from birds returning from a food source (Ward and Zahavi 1973). Although evidence for this hypothesis was initially difficult to find (Richner and Heeb 1995), recent work has established that seabirds roosting on the water's surface just offshore a colony in "rafts" can act as "information exchange" centers (Weimerskirch et al. 2010, Machovsky-Capuska et al. 2014, Boyd et al. 2016). Penguins also occasionally form rafts near colonies and, given that penguins returning from foraging are only visible as high as they can "porpoise" (leap) out of the water, it is possible that heavy seas could make it difficult for other birds sitting on the water to observe the direction from which successful foragers are arriving. If gentoo penguins are relying on this strategy more than other *Pygoscelis* species, this could be another plausible mechanism to explain their affinity for protected sites, though considerably more work is needed to investigate the issue.

The examination of wind-weighted fetch along the entire coastline in two example sections of the study region (Figure 5.4) revealed that regions with exposure levels consistent with areas that had breeding birds were not particularly rare. Naturally many other factors likely contribute to making a site suitable for breeding, and prior work has suggested that these birds may not inhabit all suitable breeding sites available to them (Chapter 3). This study identified a habitat feature, wind-weighted fetch, that had previously unknown effects on the breeding occupancy of Antarctic Peninsula pursuit-diving seabirds. Fetch positively influenced two species and negatively influenced another, suggesting that it may also play a role in niche differentiation via terrestrial nesting habitat, a factor that has received little attention as important to the community of Antarctic breeding birds. Future studies that can investigate the effects of fetch on foraging and over-winter habitat may provide useful insights into how the Antarctic environment shapes the avifauna of the region. In particular, the gentoo penguin's apparent affinity for low-fetch sites, combined with the amount of low-fetch coastline currently covered by glaciated ice-cliffs (making such coastlines unsuitable for breeding *Pygoscelis* penguins), provides an intriguing opportunity for a semi-natural experiment as anthropogenic warming causes glaciers to recede (Cook et al. 2016). Gentoo penguins have begun colonizing new sites in this region and will likely continue to do so (Lynch et al. 2012a). Future attempts to predict where birds may colonize should incorporate measurements of fetch, perhaps allowing a better understanding of a colonization process that is difficult to observe directly.

CHAPTER 6: Conclusion

This body of work represents a new case study in community ecology, in an environment that lends itself well as a natural laboratory to investigating associations among species. The summary of Antarctic shag abundance (Chapter 2) and multi-state species occupancy (Chapter 3) resulted in more detailed maps of those species distributions than were previously available, which will have direct impacts on conservation efforts in the region. The results from my first two chapters then allowed an exploration of the metacommunity structure of the entire suite of Antarctic Peninsula breeding birds (Chapter 4), revealing how species overlap patterns that are subtle when viewed through the lens of occupancy data may be quite striking when measured with population density or abundance. The non-overlap of *Pygoscelis* penguin population density distributions posed additional questions regarding features of the habitat that were not well understood, prompting an investigation into the importance of wind fetch (Chapter 5), which had not previously been seen as relevant to most seabird breeding site locations.

6.1: *Randomness and environmental filtering*

Possibly the most striking result to emerge from this dissertation is the nature of the difference between the metacommunity analysis showing apparent random patterns, and the strongly non-overlapping pattern in population density among the guild of pursuit-divers (Chapter 4). Perhaps the most logical explanation for this is that environmental filtering more strongly affects population density than occupancy. Species can exist in many locations, but only thrive at some. Much of my inspiration for beginning this work came from the observation of many species clustered at small rocky outcrops, often with apparently identical terrestrial habitat scattered throughout the local area. Only a few kilometers away, a second site would host also several species, and often the overlap in species composition would be very low (as evidenced by Figure 4.4). While the abundance results from the pursuit-divers suggests that the population size of those two colonies may differ, random colonization, perhaps coupled with interspecific interactions as yet undescribed, is a likely cause for the pattern.

The effect of fetch on occupancy described in Chapter 5 may at first seem at odds with the subtle differences observed in occupancy of the entire metacommunity in Chapter 4. Fetch obviously represents an environmental factor that can affect the breeding state of certain species at breeding sites, while at the same time the sites at which species breed appear to be largely governed by random former colonization. It should be noted, however, that the magnitude of the relationship with fetch is small, with large variability, consistent with the subtle nature of the differences in community structure. The analysis of fetch was also constrained to an area dominated by high densities of gentoo penguins, and it remains to be seen how the relationship compares to other parts of the region, at which scale the differences in abundance become obvious. There is much left to learn about other potential factors that have small, but real effects on both occupancy and abundance.

6.2: *Site fidelity*

Another important conclusion stemming from this body of work is evidence for the powerful the effect of site fidelity on ecological patterns. The breeding probabilities from my species occupancy models were heavily influenced by site fidelity. In fact, in many cases site fidelity overwhelmed the effects of environmental conditions. In a region that has a rapidly changing environment, this could lead species to be out of equilibrium with suitable habitat conditions, in turn leading to population sinks that “trap” species in population declines. The results from the metacommunity analysis suggested that the colonization process may have been random in the past, and that subsequent differences in population growth may have led to the current pattern in population density seen in pursuit-divers. If true, environmental changes for these site-faithful species may not only have direct effects on each species, but also alter the community patterns. Whether or not that would have conservation implications is unclear for this system, but I suggest that analyses on communities across entire regions, such as I have done here, may be important next steps as ecologists continue to monitor the effects of large-scale anthropogenic alterations to natural systems.

Dispersal in Antarctic breeding birds, particularly the movement of young birds prior to reproductive maturity, is especially poorly studied. Given how infrequently new colonies are observed, it is likely that social attraction is strong enough to constrain most species from quickly expanding into new areas, however the vast majority of attention in this regard has been given to penguins. Even among the well-studied penguins, however, gene flow among sites is very poorly understood. Given that measurements of dispersal are crucially important to a full understanding of metacommunity dynamics (Leibold and Chase 2018), such studies would be an important next step to pursue.

6.3: *Value of exploration*

I believe that this work highlights the value of exploratory studies, by which I mean the collection of basic data on occurrence, abundance, and natural history of species, as well as the search for patterns in those data. Much of my motivation for this dissertation came not from specific hypotheses, but a desire to better understand connections, or lack thereof, among the seabirds in a particular place. Not only did this effort lead to interesting realizations about niche differentiation, site fidelity, and stochastic processes in metacommunities, but it resulted in a marked improvement in distribution maps for many of the region's birds. In exploring those maps, a casual observation led to the hypothesis that fetch may play a previously unrecognized role in habitat suitability.

Exploratory analyses require data, obtained through literal exploration. This obviously includes exploration in space, i.e., visiting previously unexplored stretches of coastline to document breeding bird sites, which is perhaps the most useful type of data collection to aid efforts to document a region's wildlife, as I did in Chapter 2 for the Antarctic shag. It is worth emphasizing how important specific voyages were to that effort. For example, the herculean effort by Poncet and Poncet (1987) set a baseline for not only the populations of penguins outlined in their manuscript (informing many of the population estimates I use in Chapter 4), but also their unpublished shag data, without which the historical comparison in Chapter 2, and therefore the realization that the distribution of shags may be shifting, would not have been possible. Dedicated expeditions are valuable, but so too are data gleaned from opportunistic visits, many of which were used to build the occupancy maps in Chapter 3.

While abundance data may be better suited to distinguish subtle distribution and metacommunity patterns, presence/absence data are still able to provide useful results, especially if those data are collected in long time series with replication to permit the calculation of detection probabilities. In the case of the occupancy models presented here, sometimes as many as ten years of data were required to have high confidence in the species richness at a site. The presence/absence data collected by Antarctic Site Inventory researchers is relatively easy to obtain while present at a site collecting other information. This serves as a reminder of just how important long-term data collection efforts remain, especially in a region like the Antarctic that can serve well as a natural laboratory for understanding ecological principles. While my results also indicate that abundance data are often “better”, for many species the simple act of recording occupancy in a time series provides us with at least a starting point for evaluation their distributions, bringing to mind the adage “don’t let perfect be the enemy of good”.

6.4: *Future directions*

It is my hope that what I have presented about the Antarctic Peninsula allows others to continue to use it as a laboratory to examine fundamental questions in community ecology, and that, in general, future work monitoring wildlife can similarly be used to explore the structure of other metacommunities. In the Antarctic, much more work is needed on the distributions and population size of most non-penguin bird species. In some cases, such as the snowy sheathbill or Antarctic tern, these needs even extend to basic natural history. Of paramount importance is the need to study dispersal of and colonization by virtually all the region’s birds. Long time series of both occupancy and abundance are especially useful, and those efforts should be continued.

More broadly, work on the relative role of both site-fidelity and random colonization in altering the structure of metacommunities would be worthwhile, particularly for other highly colonial organisms, which gather in large population densities. The Antarctic may be useful as a model system for such investigations, but they are relevant far beyond polar ecosystems. Hopefully these will remain in the minds of ecologists as they continue to explore the natural world.

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APPENDIX 1: Probability density of missing Antarctic shag popualtion

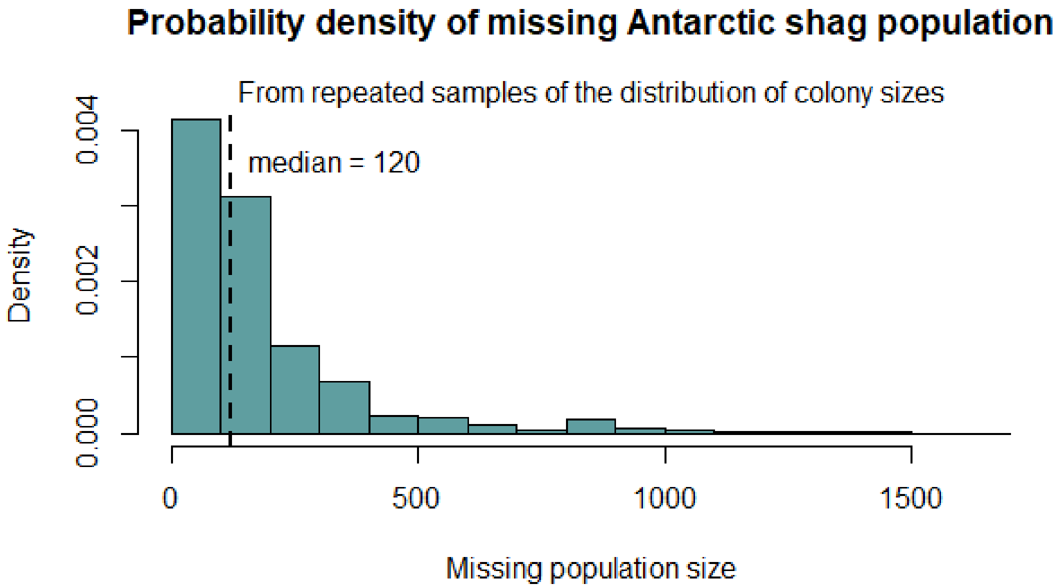

Figure A1.1: Probability density of the number of Antarctic shags missing from the population estimate in Chapter 2, calculated by bootstrapping the existing list of colony sizes.

APPENDIX 2: Size distribution of Antarctic shag colonies

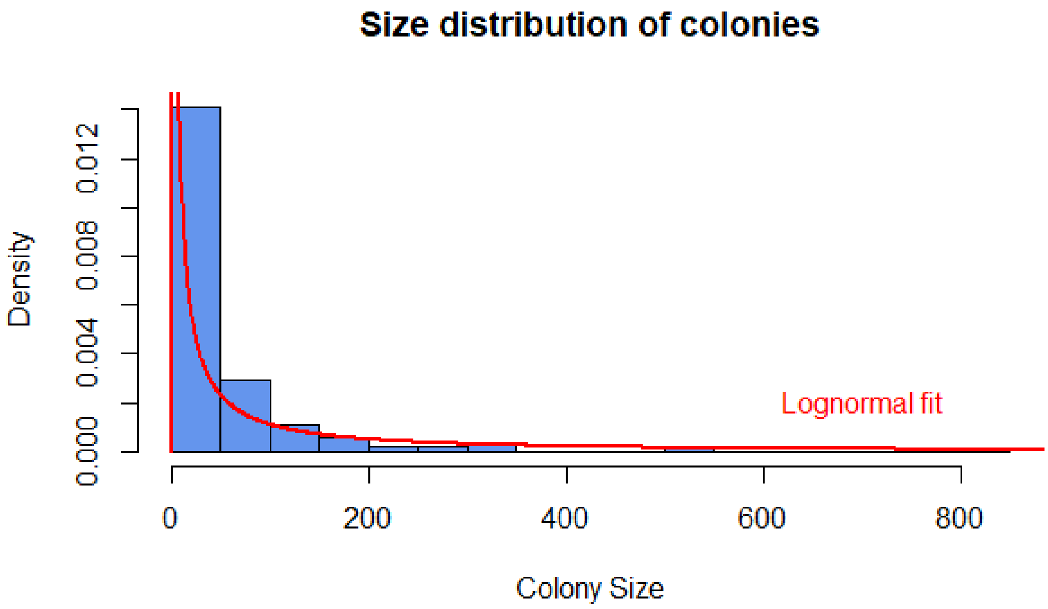

Figure A2.1: Histogram of Antarctic shag colony sizes, demonstrating that the distribution fits a lognormal distribution well.

APPENDIX 3: Ternary probability

In Chapter 3, the multi-state occupancy model relies on a three-state system, which when parameterized in the way chosen for that analysis, presents a counterintuitive result. For two independent probabilities, ψ, the probability of being present, and r, the probability of breeding, then the probability of being in one of the three possible states can be expressed as:

$$\phi = \begin{bmatrix} 1 - \psi \\ \psi \times (1 - r) \\ \psi \times r \end{bmatrix} \tag{A3.1}$$

where $1 - \psi$ is the probability of not being present, $\psi \times (1 - r)$ represents the probability of being present, but not breeding, and $\psi \times r$ is the probability of being both present and breeding. Of course, rather than derive and interpret ϕ directly, I interpreted the latent state, which was drawn from linked Bernoulli distribtions. However, ϕ is also useful, and in this case represents the probability of being in one of the three breeding states based purely on the underlying characteristics of the site in a given year. The logit of both ψ and r is modeled with a number of covariates representing the site characteristics, and vague priors are used for both parameters.

At first glance, one may believe that if both ψ and r are independent, then the multi-state probability of ϕ would also be independent, and should be characterized by a Dirichlet distribution, placing equal probability of being anywhere in the three-state space, which can be shown as a null model from simulated data (Figure A3.1A). However, if draws from both ψ and r are simulated with flat draws from a Uniform distribution, and then ϕ calculated from equation A3.1, the resulting distribution is weighted towards the first case, in which the species is not present (Figure A3.1B). When the logit link model from equation 3.4 is also simulated, the results are nearly identical: heavily weighted towards no presence (Figure A3.1C). These results demonstrate how the model in Chapter 3 is conservative when interpreting only ϕ, and the reason why I interpret the latent state results instead.

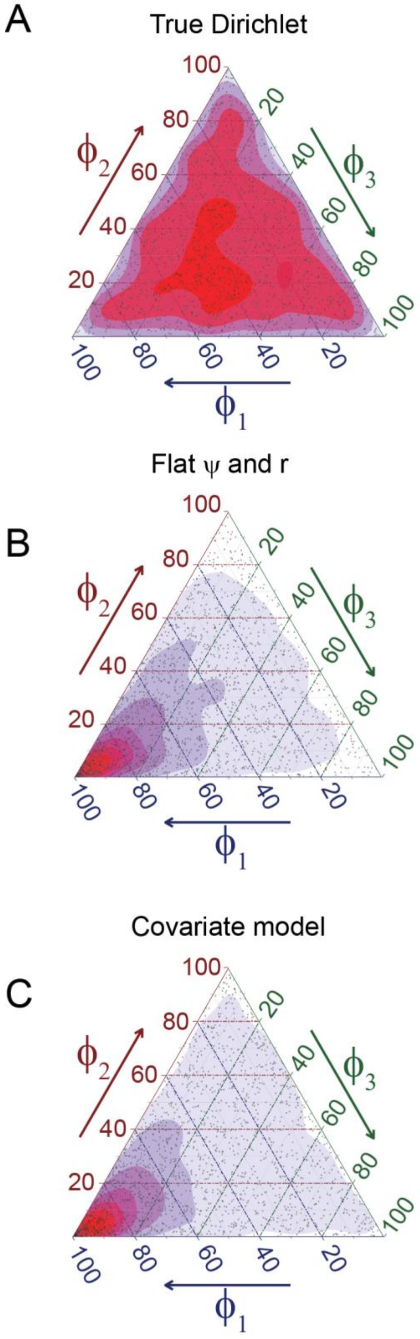

Figure A3.1: Ternary diagrams for a process that (A) chooses a three-state probability with a true Dirichlet process, (B) calculates probability using two uninformative and independent probabilities (ψ and r), and (C) with vague priors on covariates in a logit link model, simulating the occupancy model from Chapter 3. Color represents the kernel density of the random points.

APPENDIX 4: Occupancy model posterior predictive check

The posterior predictive check for each single-species occupancy model (Chapter 3) was completed by first drawing a set of simulated observed states for each site, year, and visit during each iteration of the MCMC sampler. Recall that the probability of recording each state in each site and year, named “eval” in the model code, was returned in the model output. It was calculated as the sum of the products of each true state probability and the detection probabilities that would have resulted in recording the observed state in question:

$$E_{state_{s,y,v}} = \sum_{i=1}^{3} (\phi_{s,y} * p_{i,state})$$

Test statistics were then calculated as follows:

for the simulated (i.e. predicted) data:

$$T_{pred} = \sum_{state=1}^{3} \sum_{s=1}^{181} \sum_{y \in Y} \sum_{v=1}^{V_{s,y}} \frac{(Simulated_{s,y,v} - E_{state_{s,y,v}})^2}{E_{state_{s,y,v}}}$$

and for the actual data:

$$T_{actual} = \sum_{state=1}^{3} \sum_{s=1}^{181} \sum_{y \in Y} \sum_{v=1}^{V_{s,y}} \frac{(Observed_{s,y,v} - E_{state_{s,y,v}})^2}{E_{state_{s,y,v}}}$$

Bayesian p-values were then calculated as the proportion of iterations for which $T_{pred} > T_{actual}$. R code for extracting the correct values from the model output are included in the model code, and the code for re-loading that output, calculating the Bayesian P-value, and making a figure for a single species is included in the R script ‘Posterior_Pred_Check.R’, at the online repository for Chapter 3 (https://github.com/lynch-lab/Schrimpf_etal_PolarBiology_Occupancy)

Posterior Predictive Check results:

Bayesian p-values (Table A3.1) for all species except the Antarctic shag ranged between 0.434 and 0.853, indicating that the models returned reasonable simulated data, and were not over-fit. The Antarctic shag model was under-fit (Bayesian p-value = 0.978) suggesting that additional, un-modeled factors (e.g., interspecific interactions) may play an important role in determining multistate occupancy for that species.

Species	P-value
Adélie penguin	0.645
Antarctic shag	0.978
Antarctic tern	0.550
black-bellied storm-petrel	0.479
brown skua	0.721
cape petrel	0.434
chinstrap penguin	0.533
gentoo penguin	0.853
kelp gull	0.695
macaroni penguin	0.826
snow petrel	0.689
snowy sheathbill	0.535
south polar skua	0.605
southern fulmar	0.463
southern giant petrel	0.788
Wilson's storm-petrel	0.473

Table A4.1: Bayesian p-values from the posterior predictive check. Values greater than 0.9 are highlighted in bold.

APPENDIX 5: Additional occupancy model posterior distributions

This appendix displays additional parameter posterior distributions for the site-fidelity covariate (gamma; Figure A5.1, A5.2) and intercept (alpha; Figure A5.3, A5.4), for both presence (A5.1, A5.3) and breeding (A5.2, A5.4). Source code can be found at the online repository for Chapter 3 (https://github.com/lynch-lab/Schrimpf_etal_PolarBiology_Occupancy).

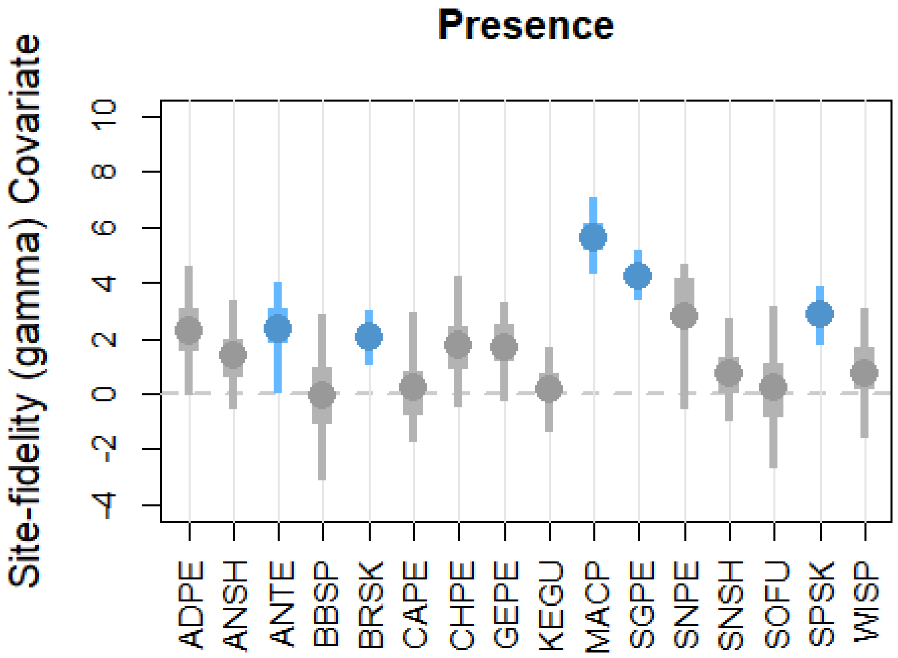

Figure A5.1: Site-fidelity parameter posteriors for presence. Circles indicate medians, while wide and narrow bars indicate the 50% and 95% HDIs, respectively. Blue posteriors do not overlap zero. See Table 1 of the paper for species codes.

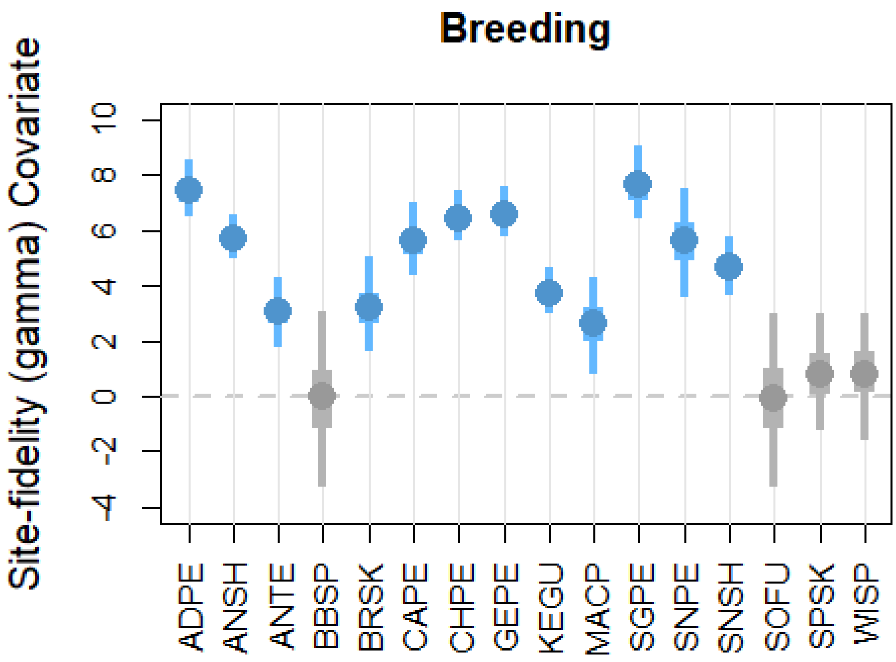

Figure A5.2: Site-fidelity parameter posteriors for breeding. Circles indicate medians, while wide and narrow bars indicate the 50% and 95% HDIs, respectively. Blue posteriors do not overlap zero. See Table 1 of the paper for species codes.

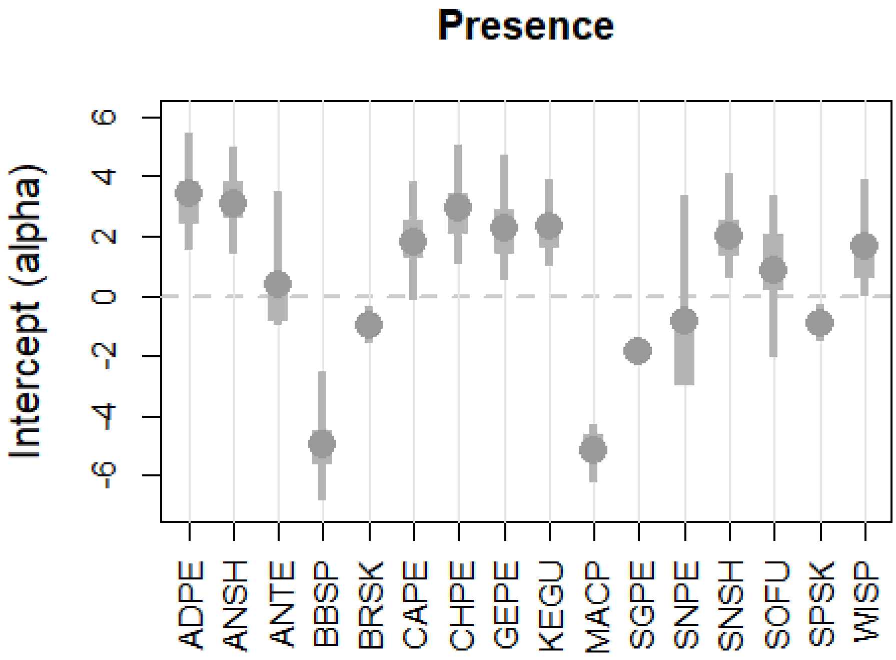

Figure A5.3: Intercept parameter posteriors for presence. Circles indicate medians, while wide and narrow bars indicate the 50% and 95% HDIs, respectively. See Table 1 of the paper for species codes.

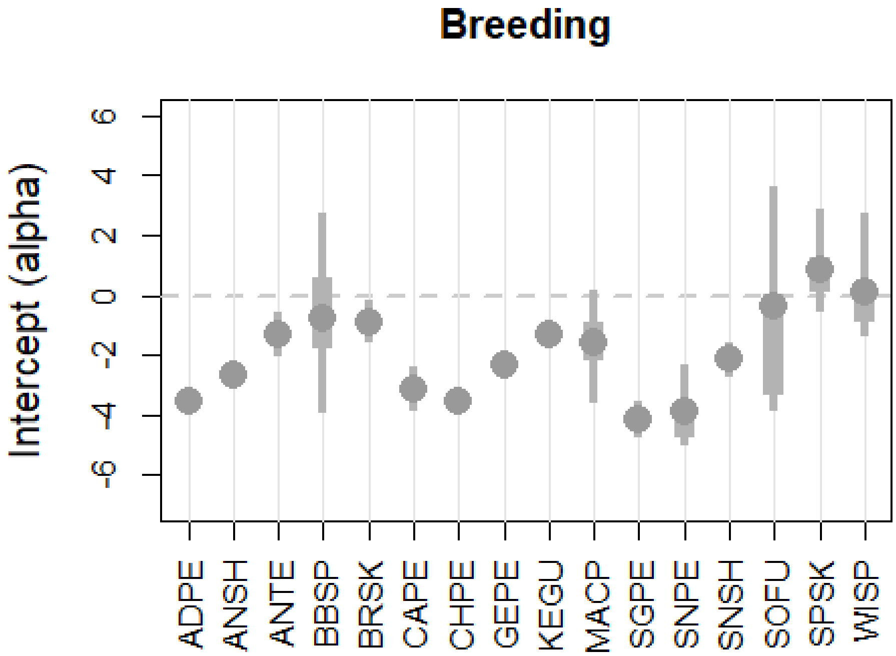

Figure A5.4: Intercept parameter posteriors for breeding. Circles indicate medians, while wide and narrow bars indicate the 50% and 95% HDIs, respectively. See Table 1 of the paper for species codes.

APPENDIX 6: Effect of removing site-fidelity

I explored the role that site-fidelity played in the occupancy model results by re-running each of the single-species models without the site-fidelity (gamma) term included. Many of the sea-ice covariates in the models without site-fidelity had more extreme impacts on the probability of presence (Figure A6.1A) and breeding (Figure A6.1B), suggesting that our interpretation of the effect of environment on species occupancy is biased by not explicitly modeling site fidelity. Species with larger median site-fidelity terms also had a larger difference between the sea-ice (beta) terms before and after removing site-fidelity, and 95% HDIs of the posteriors of that difference more often excluded zero (Figure A6.2).

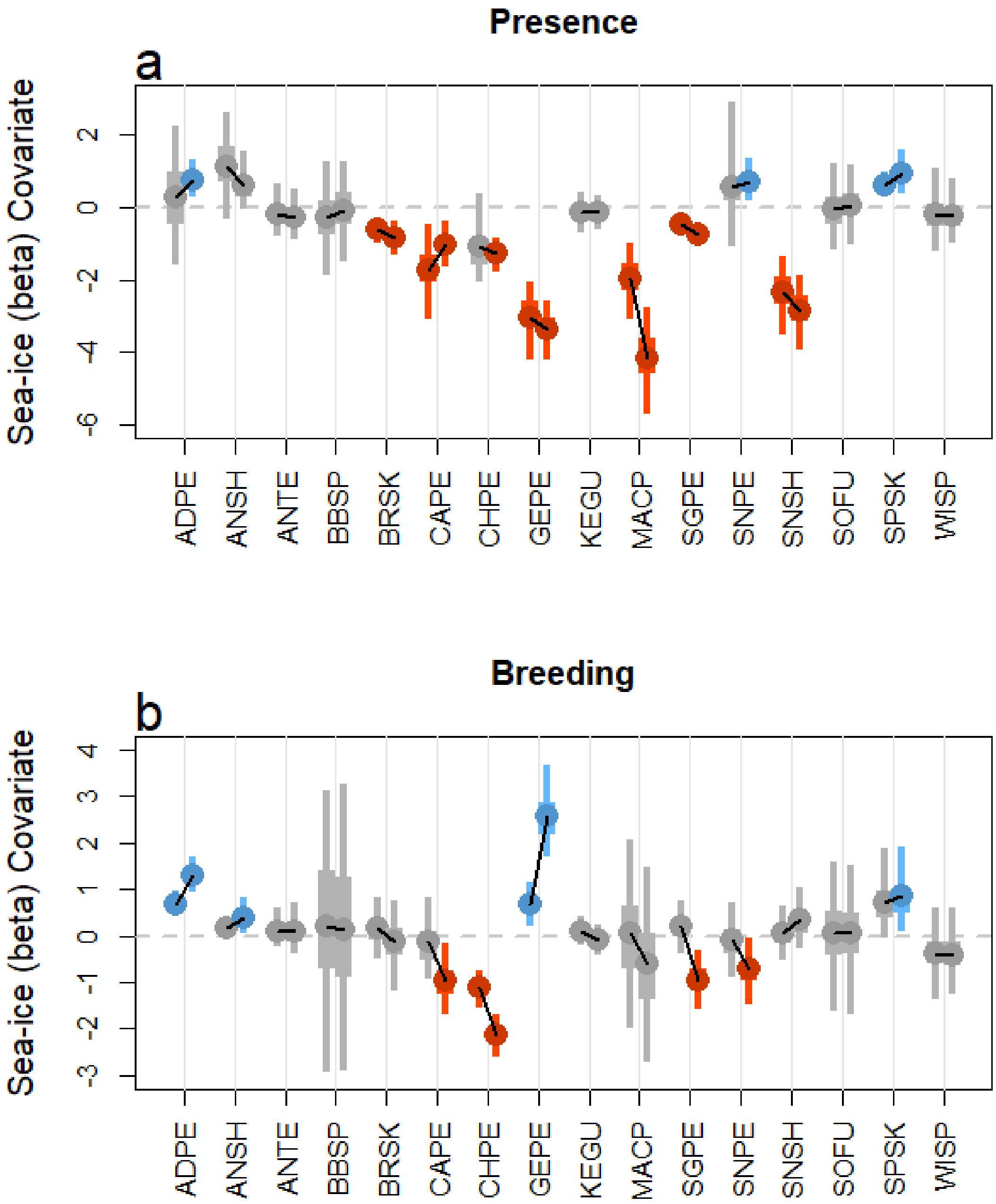

Figure A6.1: Sea-ice covariate (beta) posterior distributions before (left) and after (right) removing the site-fidelity term (gamma) from the model. Circles indicate medians, while wide and narrow bars indicate the 50% and 95% HDIs, respectively. Small black lines connect each median before and after removal. Results are shown for presence (A), breeding (B).

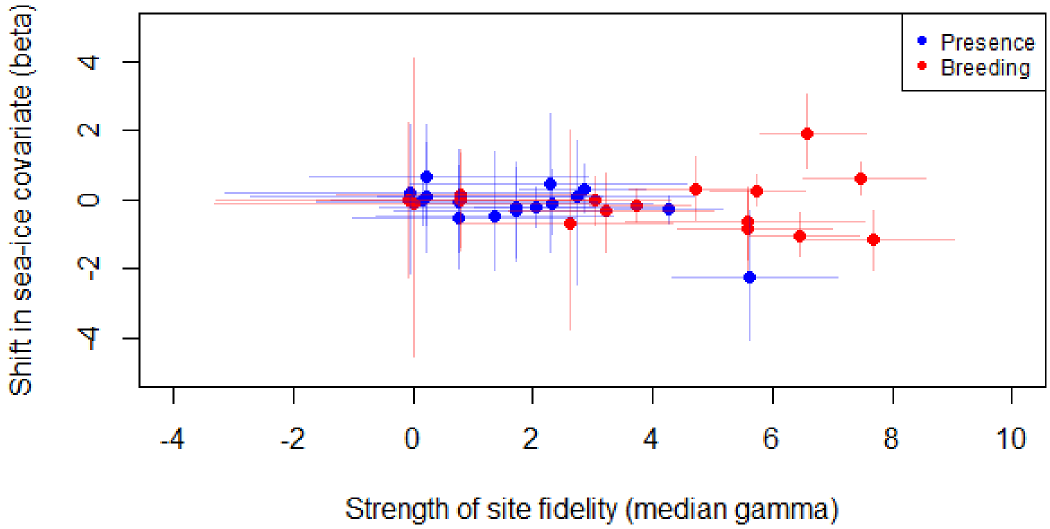

Figure A6.2: Relationship between the strength of the site-fidelity term and the difference (post-removal minus pre-removal) in the sea-ice covariate.

APPENDIX 7: Species-specific breeding probabilities

Maps of the breeding probability of all species, using the proportion of the latent breeding state posterior indicating occupancy for all years during which each site was visited. See Table 1.1 for species codes.

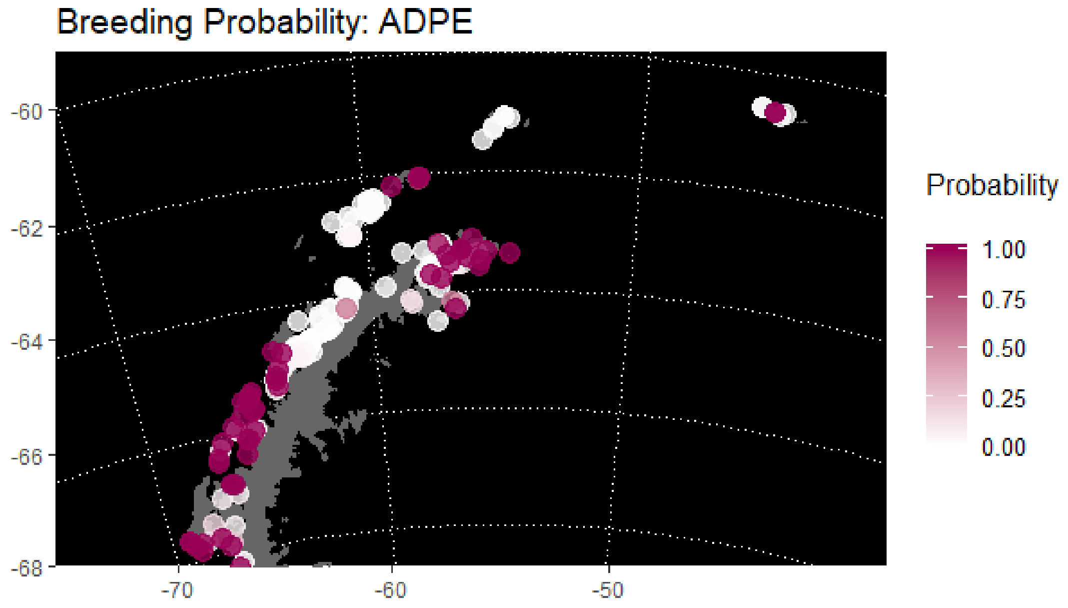

Figure A7.1: Map of breeding probability for Adélie penguin.

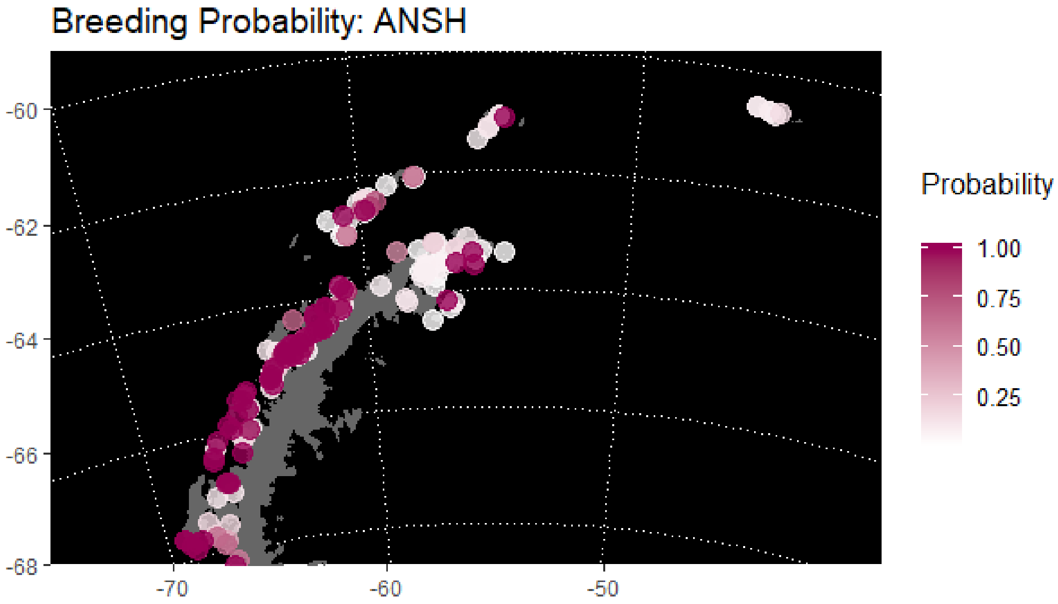

Figure A7.2: Map of breeding probability for Antarctic shag.

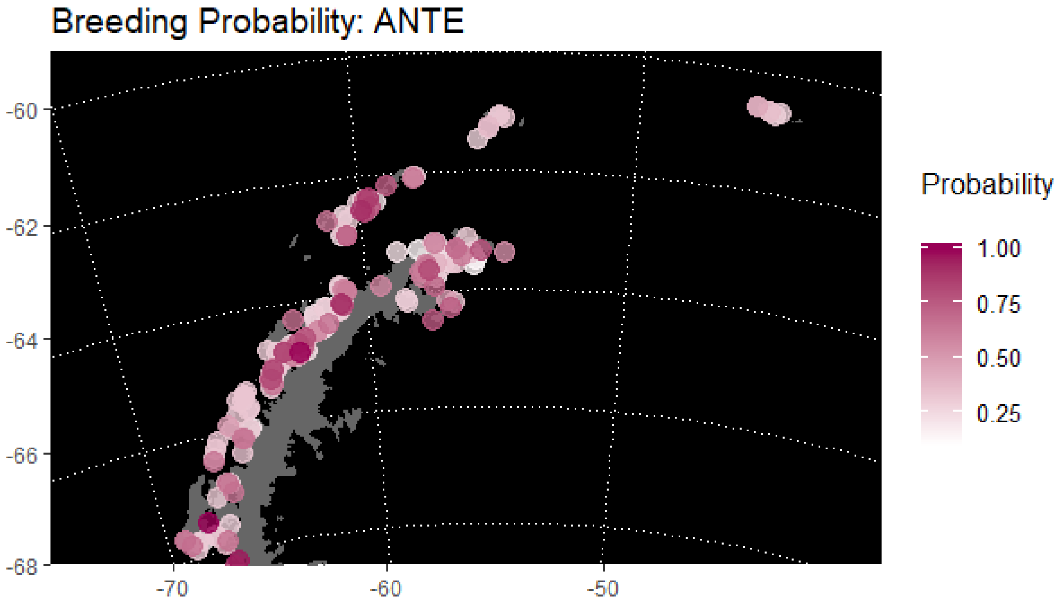

Figure A7.3: Map of breeding probability for Antarctic tern.

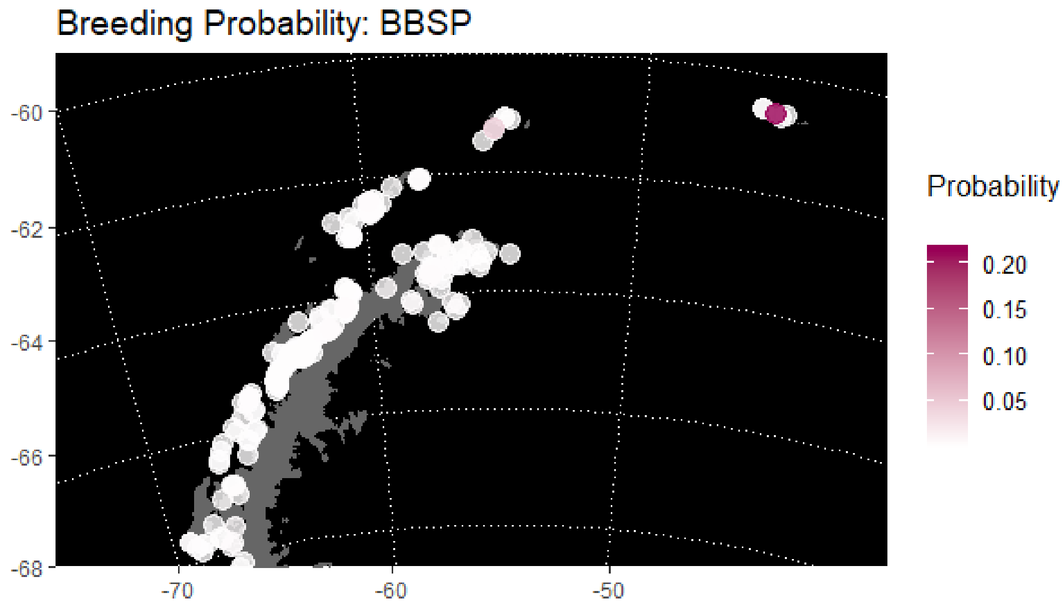

Figure A7.4: Map of breeding probability for black-bellied storm-petrel.

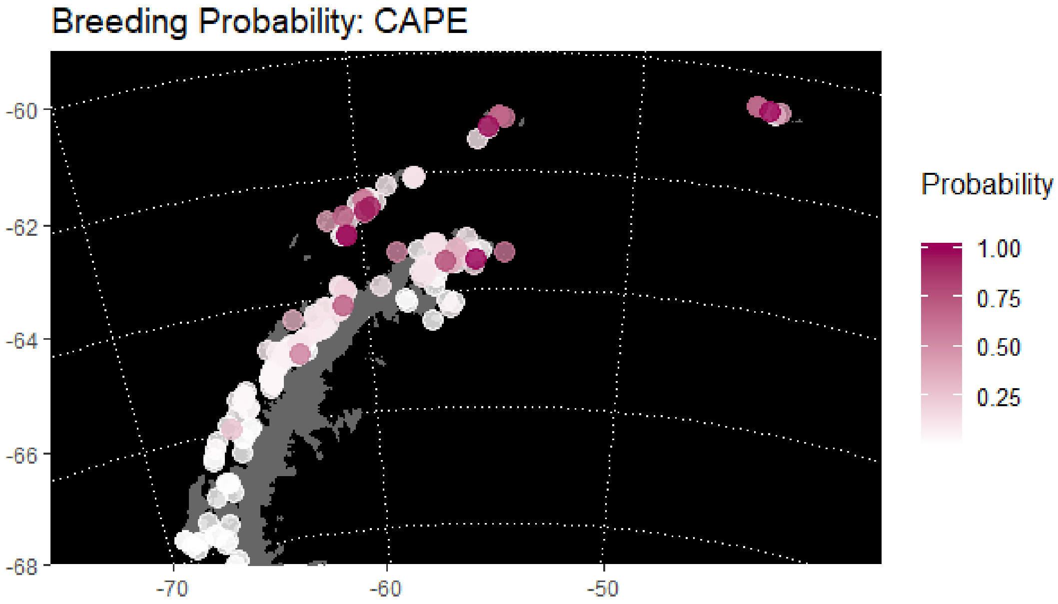

Figure A7.5: Map of breeding probability for cape petrel.

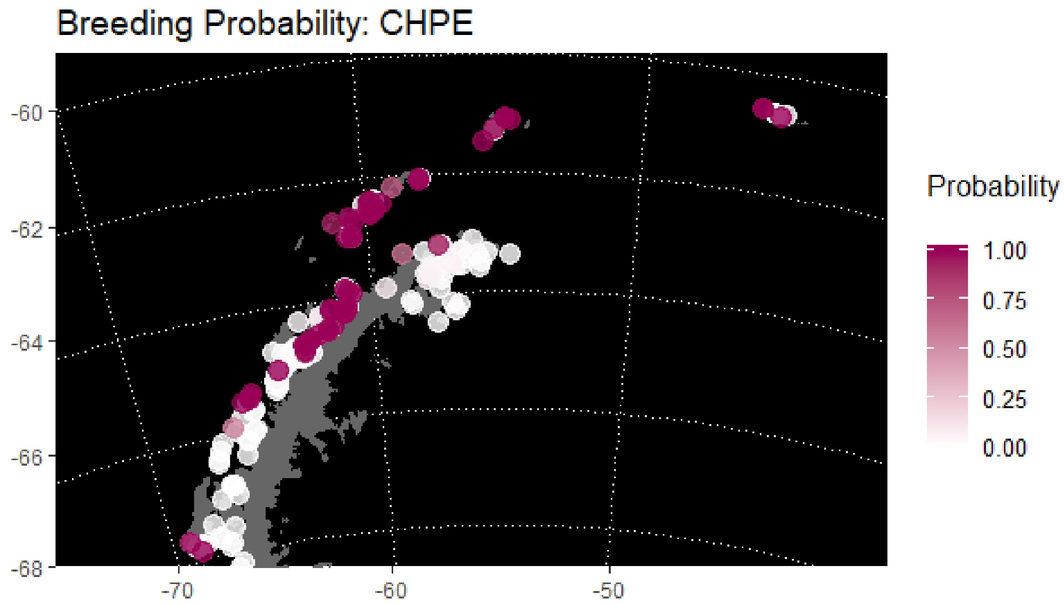

Figure A7.6: Map of breeding probability for chinstrap penguin.

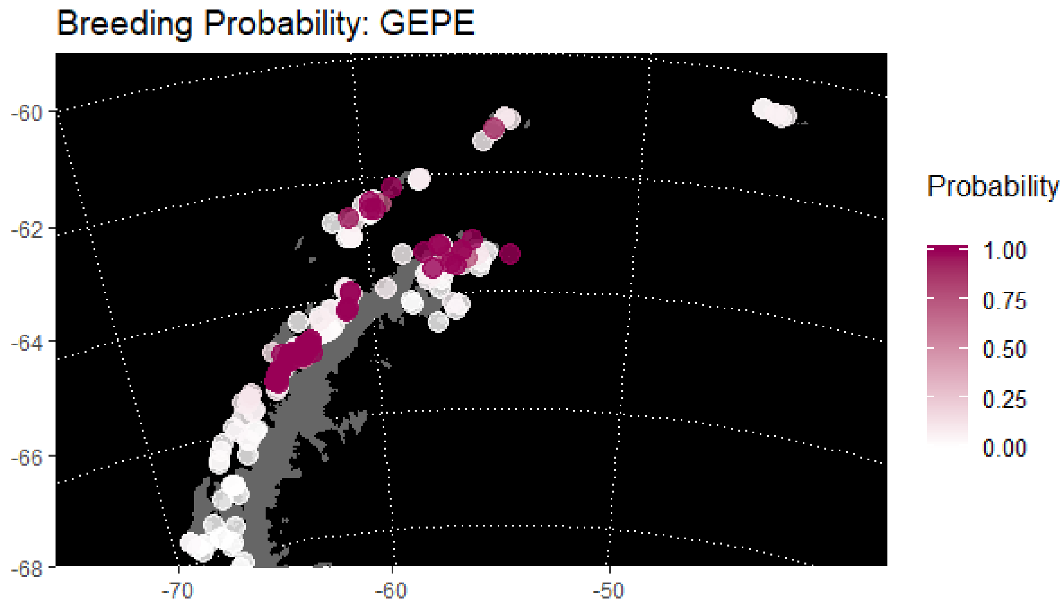

Figure A7.7: Map of breeding probability for gentoo penguin.

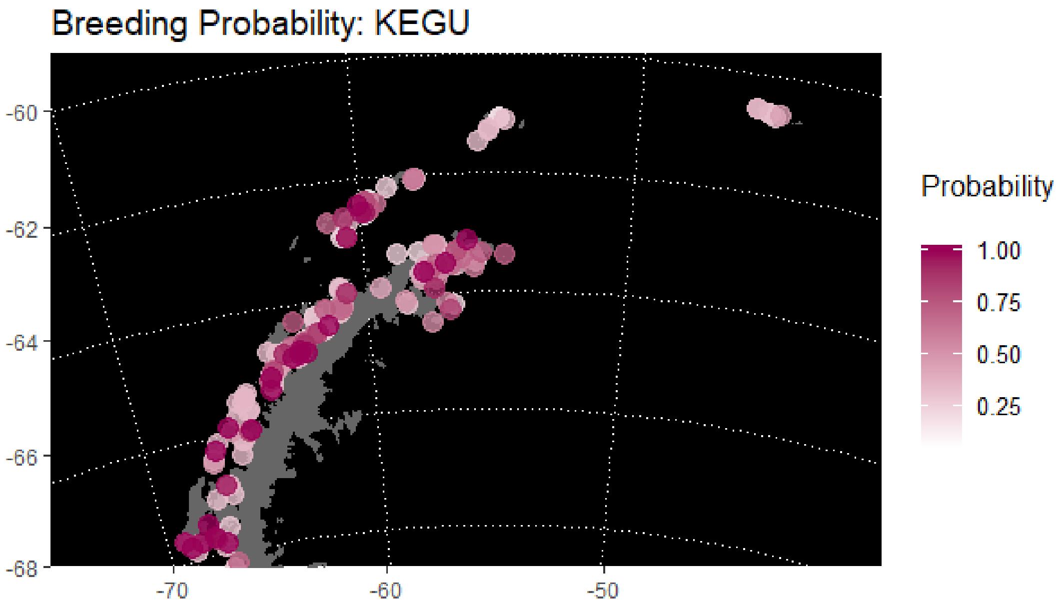

Figure A7.8: Map of breeding probability for kelp gull.

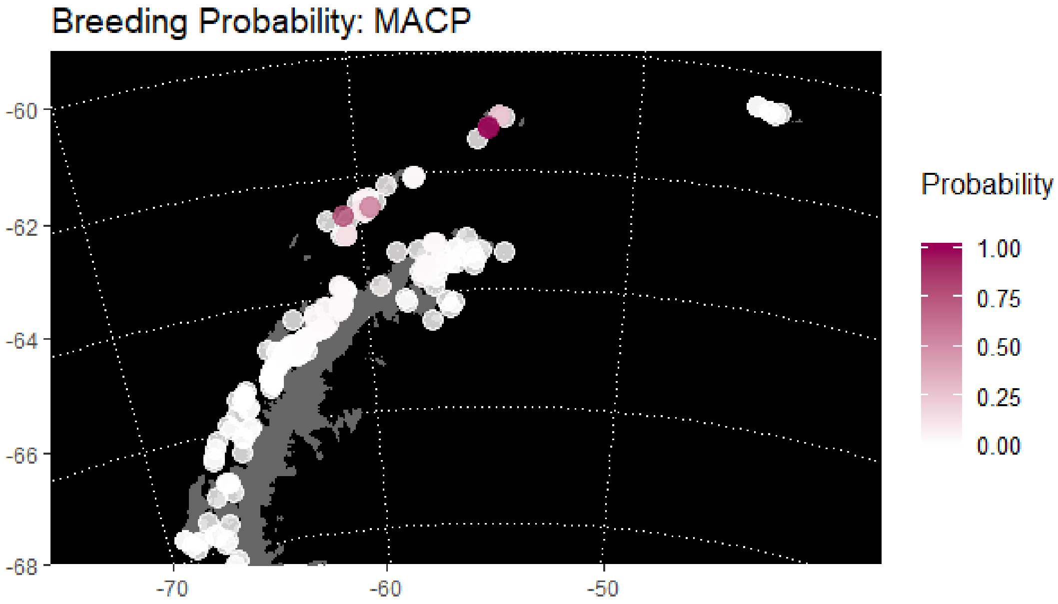

Figure A7.9: Map of breeding probability for macaroni penguin.

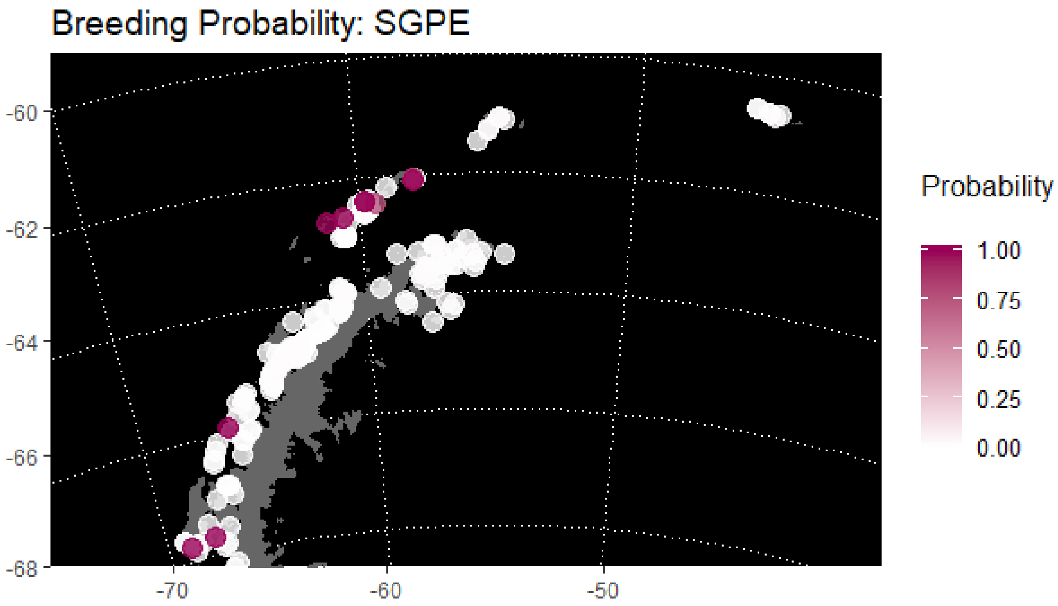

Figure A7.10: Map of breeding probability for southern giant petrel.

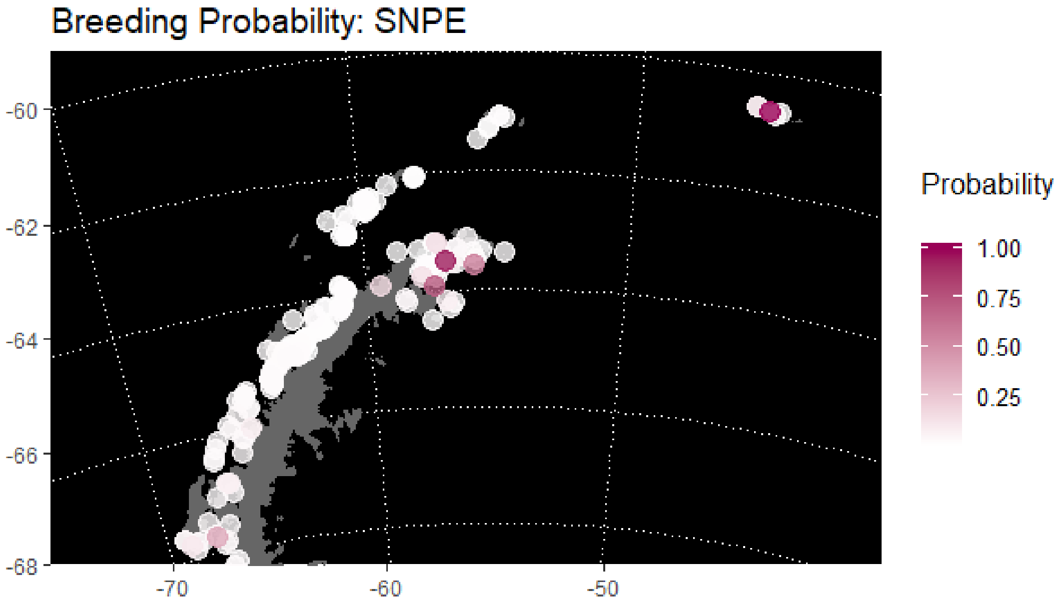

Figure A7.11: Map of breeding probability for snow petrel.

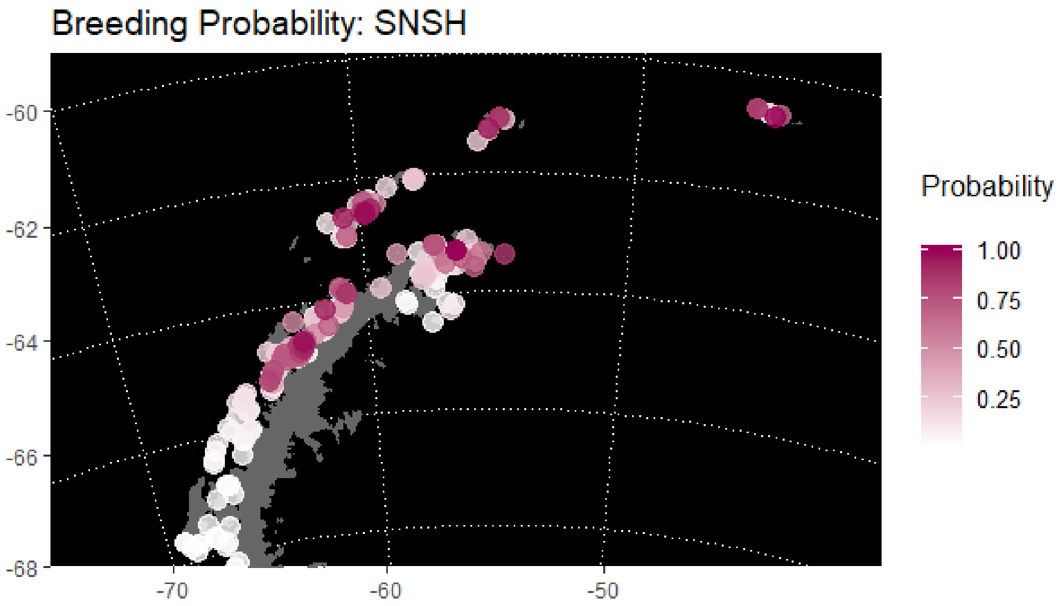

Figure A7.12: Map of breeding probability for snowy sheathbill.

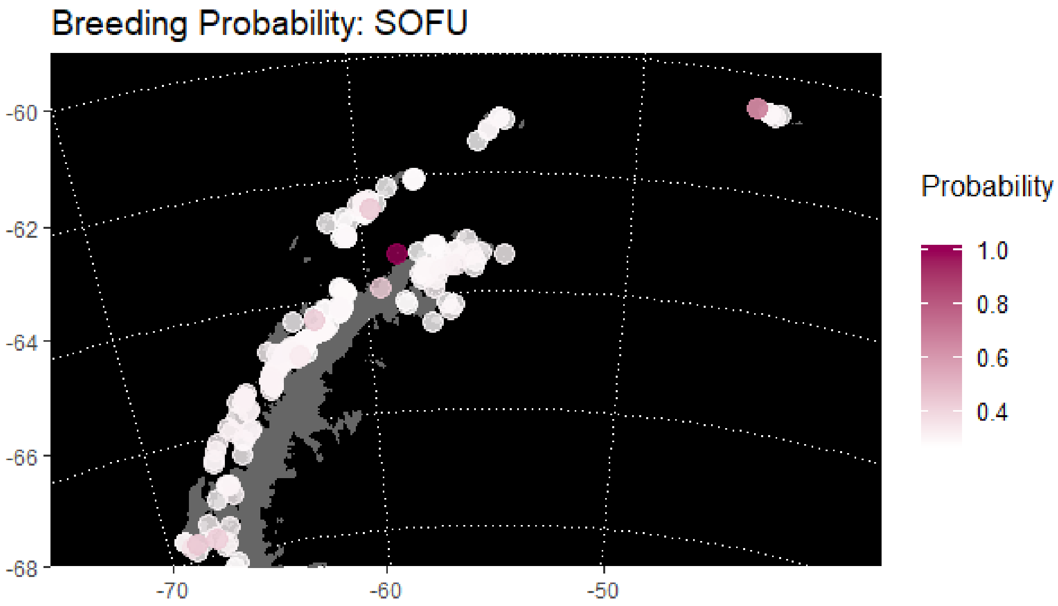

Figure A7.13: Map of breeding probability for southern fulmar.

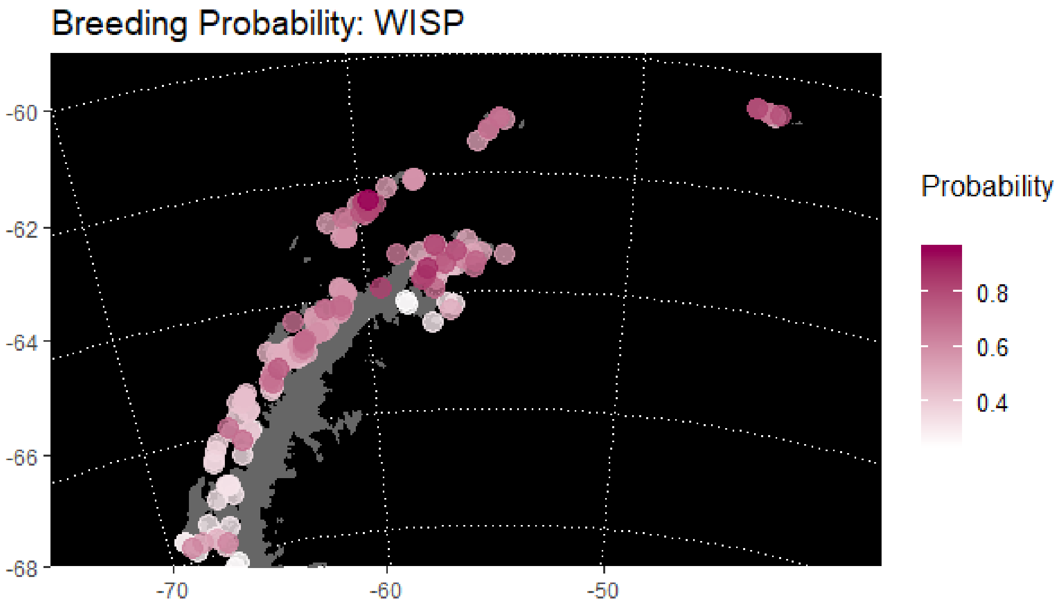

Figure A7.14: Map of breeding probability for Wilson's storm-petrel.

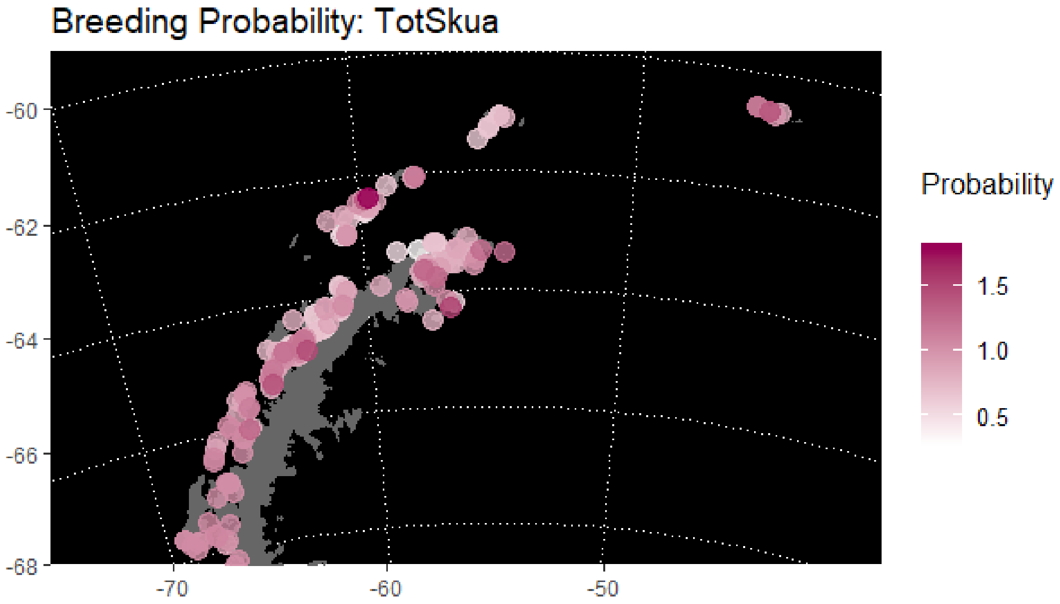

Figure A7.15: Map of breeding probability for both brown and south polar skuas, including unidentified skuas. Note that because the two species of skua were combined with the model results of all skuas for this figure, and hence takes values over the interval 0:2, representing the mean posterior estimate for the number of skua species breeding at each site.

APPENDIX 8: Downsampling Procedure

In Chapter 3 it was necessary to determine how many years of visitation to a site it would require before the Chao2 estimated species richness approached the final Chao2 value, and how quickly the uncertainty in that estimate decreased. For the ten sites with the longest histories of visitation (ranging from 17 to 22 years), I calculated the Chao2 and Chao2 standard error using the vegan package for each year of visitation (for each site), using all of the species accumulation results for any years up to and including that year of visitation. Both Chao2 and its standard error were calculated for each iteration of the species accumulation posterior, and then the median value (of each the estimate and SE) was used as the summary statistic. That estimate (+/- one standard error) was plotted on top of the model-based species accumulation curves (as displayed in Figure 3.3), and visually assessed the overlap (Figures A8.1-A8.10). In every case the Chao2 estimator took almost as long as the model results to reach an asymptote, suggesting that it provides little benefit in estimating true species richness at under-sampled sites. See the GitHub repository for source code for accumulation curves.

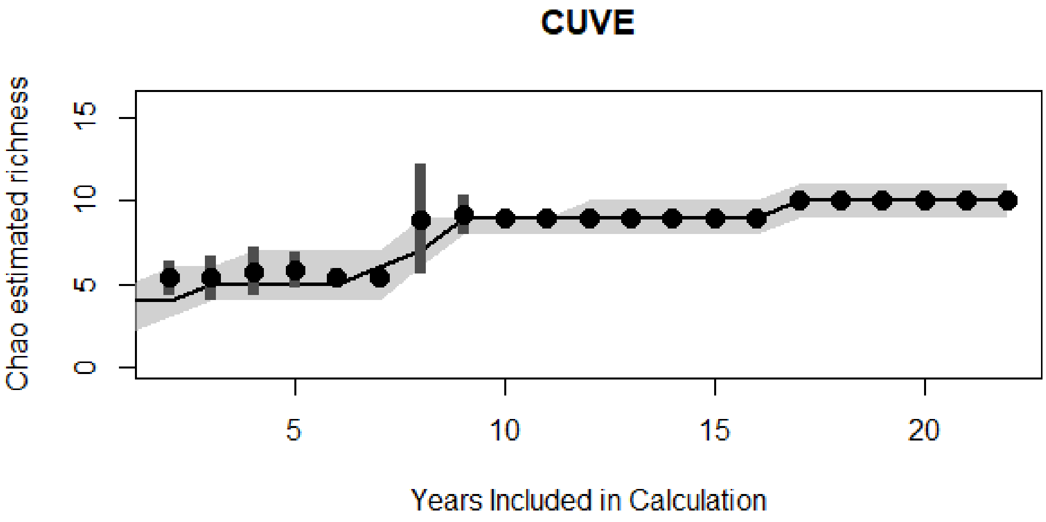

Figure A8.1: Downsampled median values of Chao2 estimated richness (points) +/- median values for Chao2 standard error (thick bars) at Cuverville Island. Model-based species accumulation (solid line = median; shaded region = 95% HDI) as described in Figure 3.3.

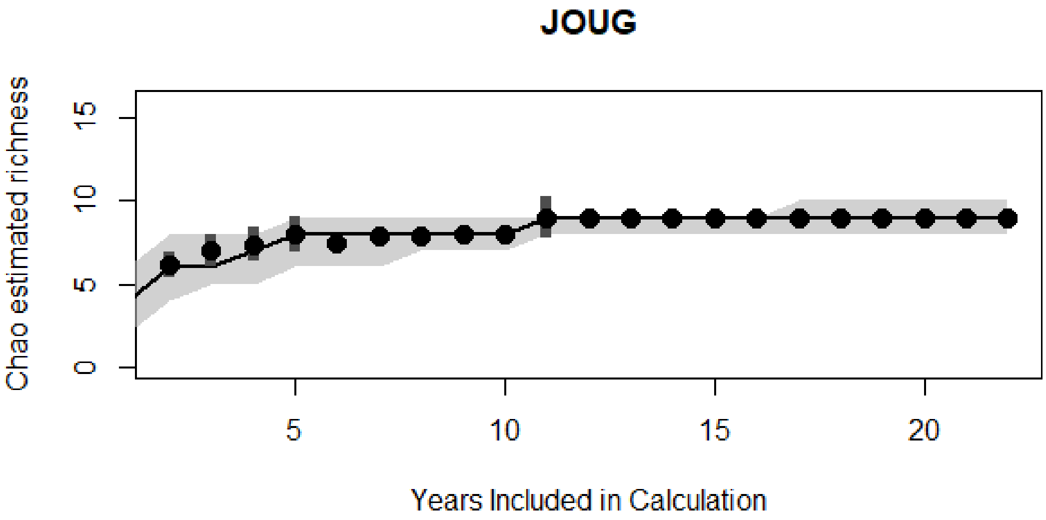

Figure A8.2: Downsampled median values of Chao2 estimated richness (points) +/- median values for Chao2 standard error (thick bars) at Jougla Point. Model-based species accumulation (solid line = median; shaded region = 95% HDI) as described in Figure 3.3.

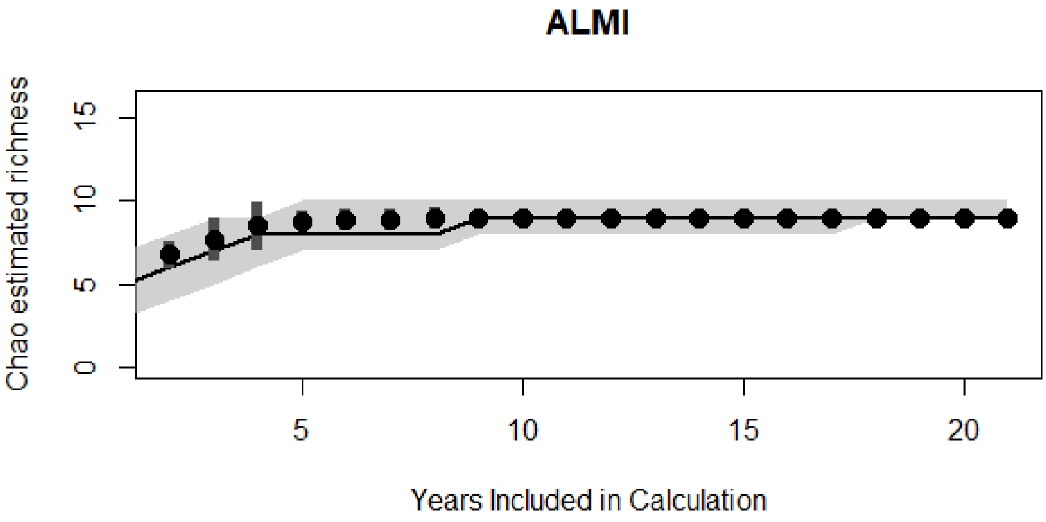

Figure A8.3: Downsampled median values of Chao2 estimated richness (points) +/- median values for Chao2 standard error (thick bars) at Brown Station. Model-based species accumulation (solid line = median; shaded region = 95% HDI) as described in Figure 3.3.

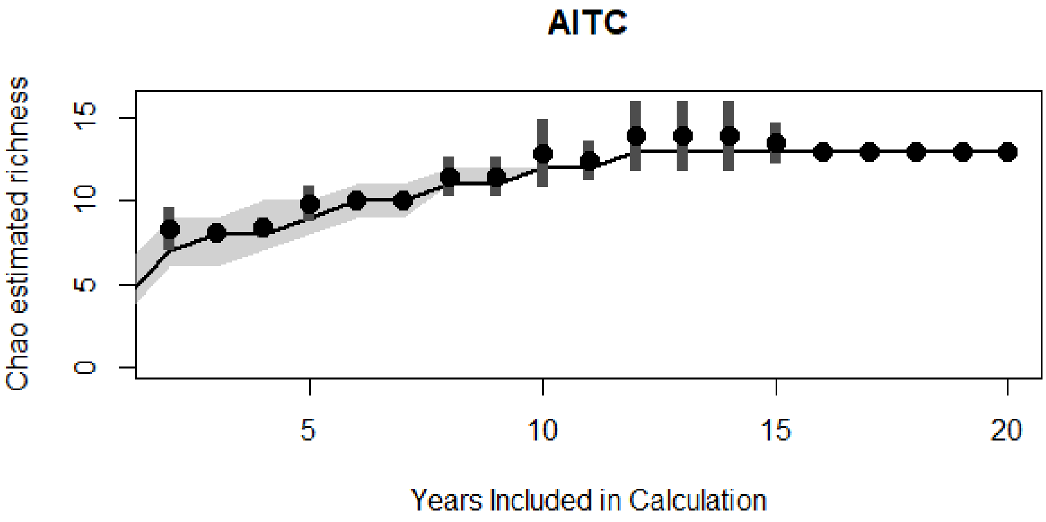

Figure A8.4: Downsampled median values of Chao2 estimated richness (points) +/- median values for Chao2 standard error (thick bars) at Barrientos Island (Aitcho Islands). Model-based species accumulation (solid line = median; shaded region = 95% HDI) as described in Figure 3.3.

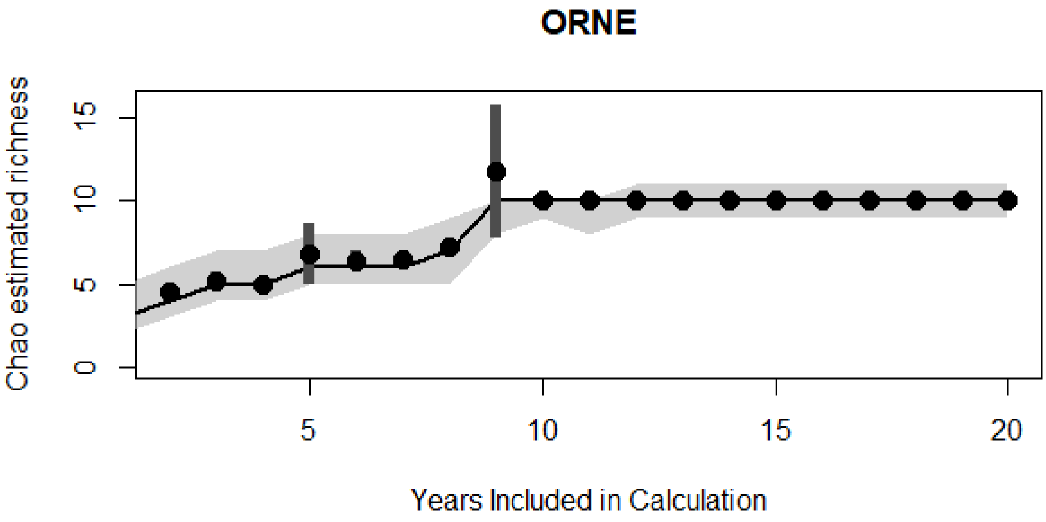

Figure A8.5: Downsampled median values of Chao2 estimated richness (points) +/- median values for Chao2 standard error (thick bars) at Orne Islands. Model-based species accumulation (solid line = median; shaded region = 95% HDI) as described in Figure 3.3.

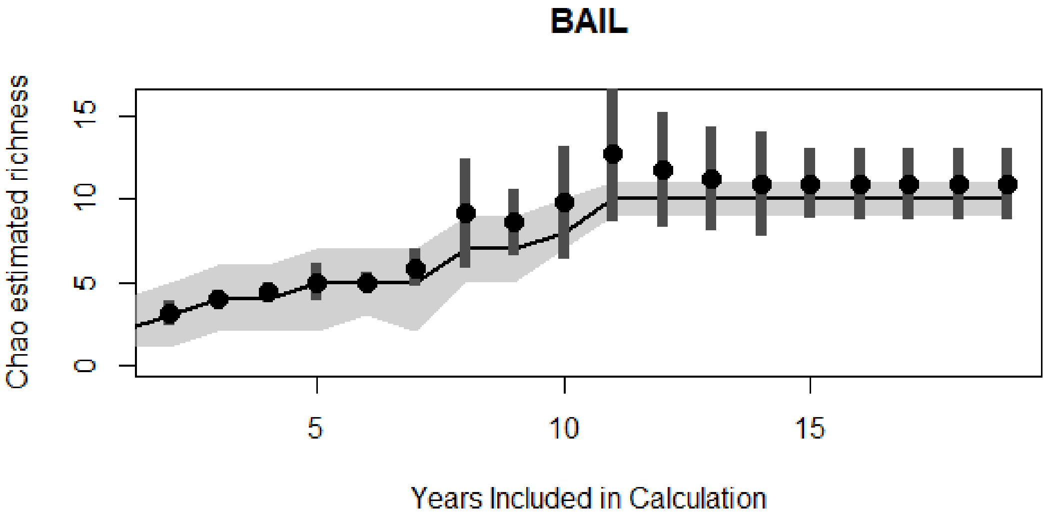

Figure A8.6: Downsampled median values of Chao2 estimated richness (points) +/- median values for Chao2 standard error (thick bars) at Bailey Head. Model-based species accumulation (solid line = median; shaded region = 95% HDI) as described in Figure 3.3.

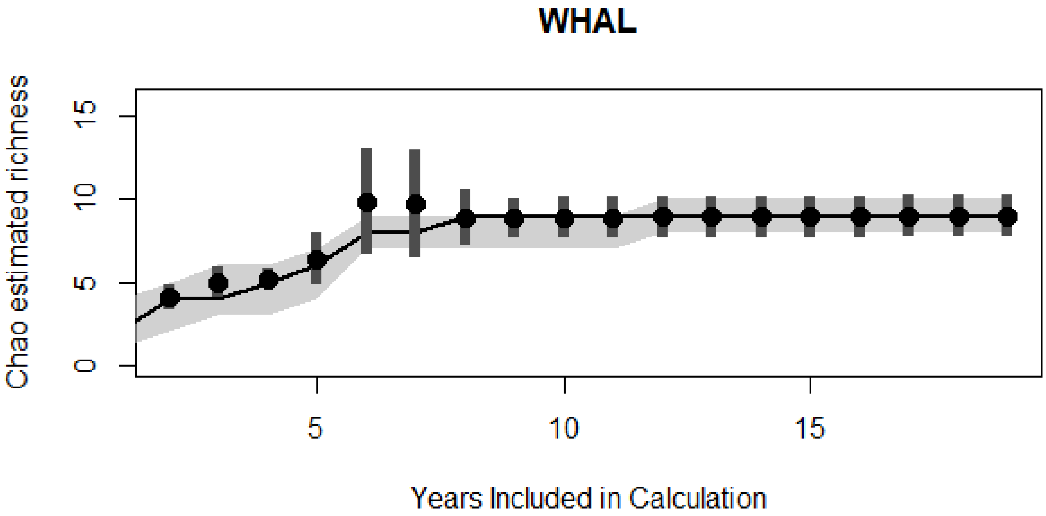

Figure A8.7: Downsampled median values of Chao2 estimated richness (points) +/- median values for Chao2 standard error (thick bars) at Whaler's Bay. Model-based species accumulation (solid line = median; shaded region = 95% HDI) as described in Figure 3.3.

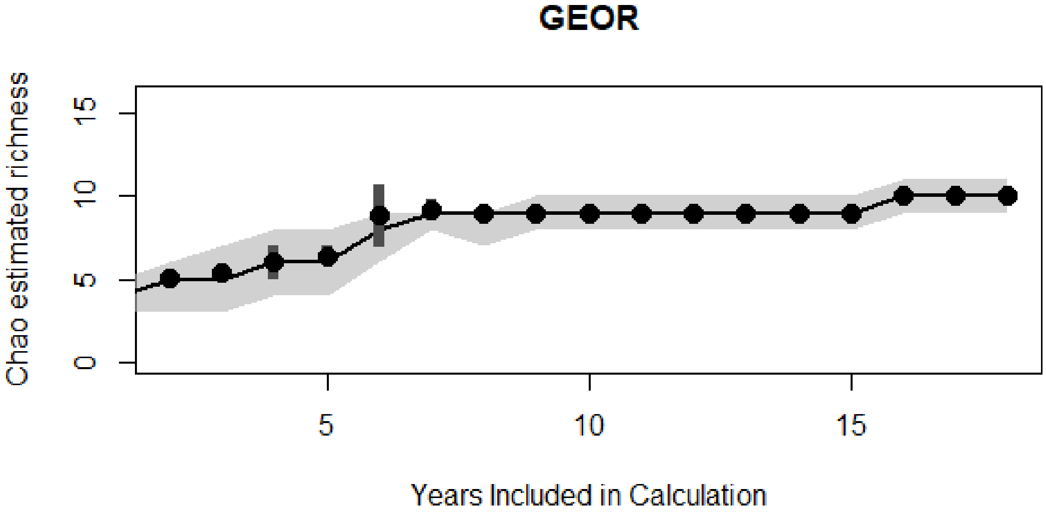

Figure A8.8: Downsampled median values of Chao2 estimated richness (points) +/- median values for Chao2 standard error (thick bars) at George’s Point. Model-based species accumulation (solid line = median; shaded region = 95% HDI) as described in Figure 3.3.

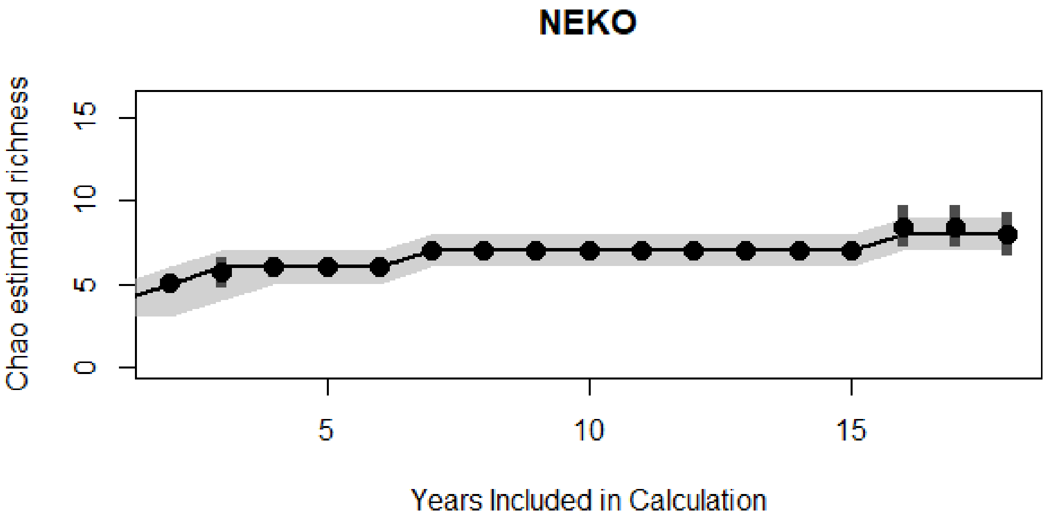

Figure A8.9: Downsampled median values of Chao2 estimated richness (points) +/- median values for Chao2 standard error (thick bars) at Neko Harbor. Model-based species accumulation (solid line = median; shaded region = 95% HDI) as described in Figure 3.3.

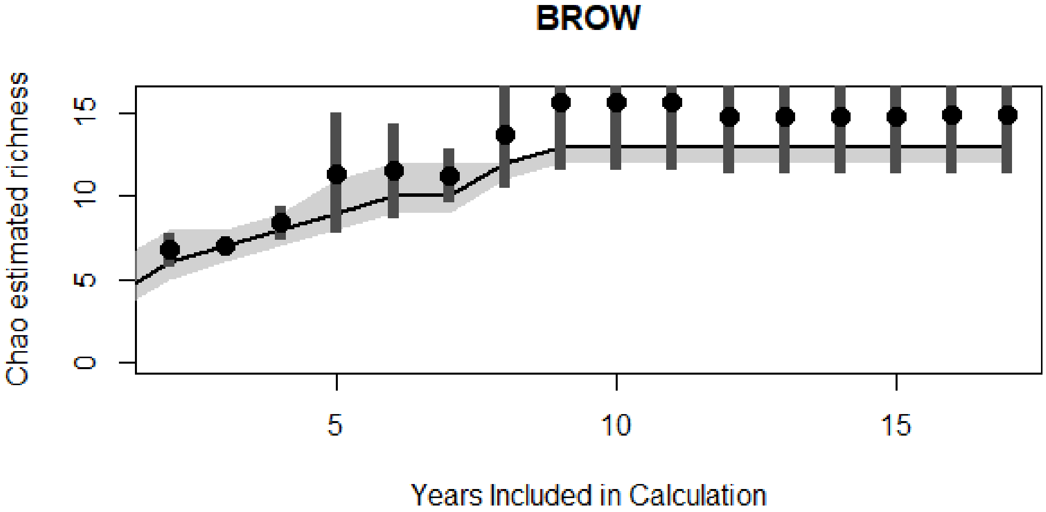

Figure A8.10: Downsampled median values of Chao2 estimated richness (points) +/- median values for Chao2 standard error (thick bars) at Brown Bluff. Model-based species accumulation (solid line = median; shaded region = 95% HDI) as described in Figure 3.3.

APPENDIX 9: Single-axis community maps

To facilitate interpretation of the NMDS results in geographic space for readers with a form of color blindness, maps showing each of the three axis scores are displayed here.

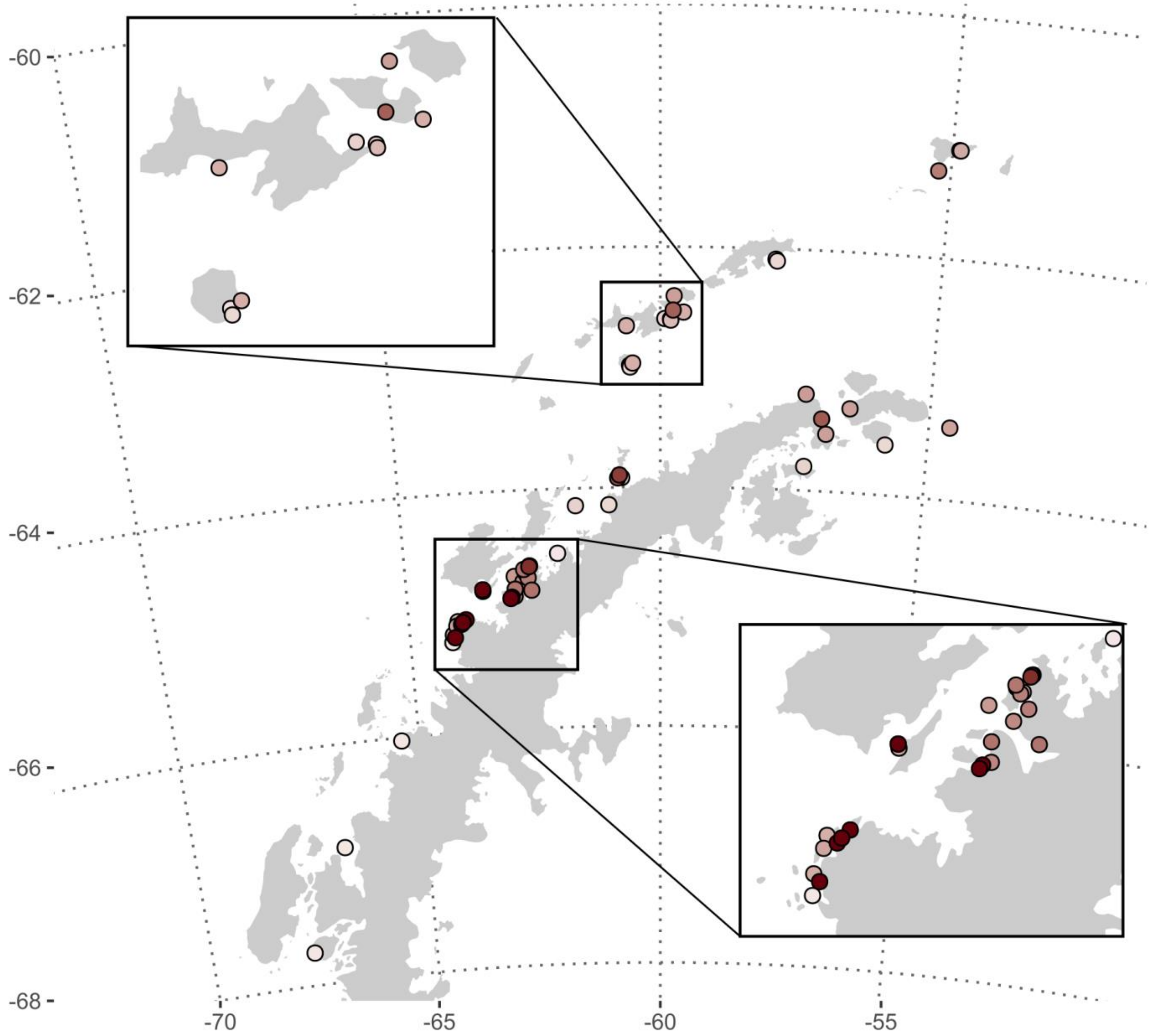

Figure A9.1: Map of sites with at least 5 years of occupancy data, displayed with results from NMDS axis 1 (which was the red component of the score in Figures 4.2 and 4.3). Light color indicates a low axis score, and dark indicates a high axis score. Insets enlarge areas with higher site density.

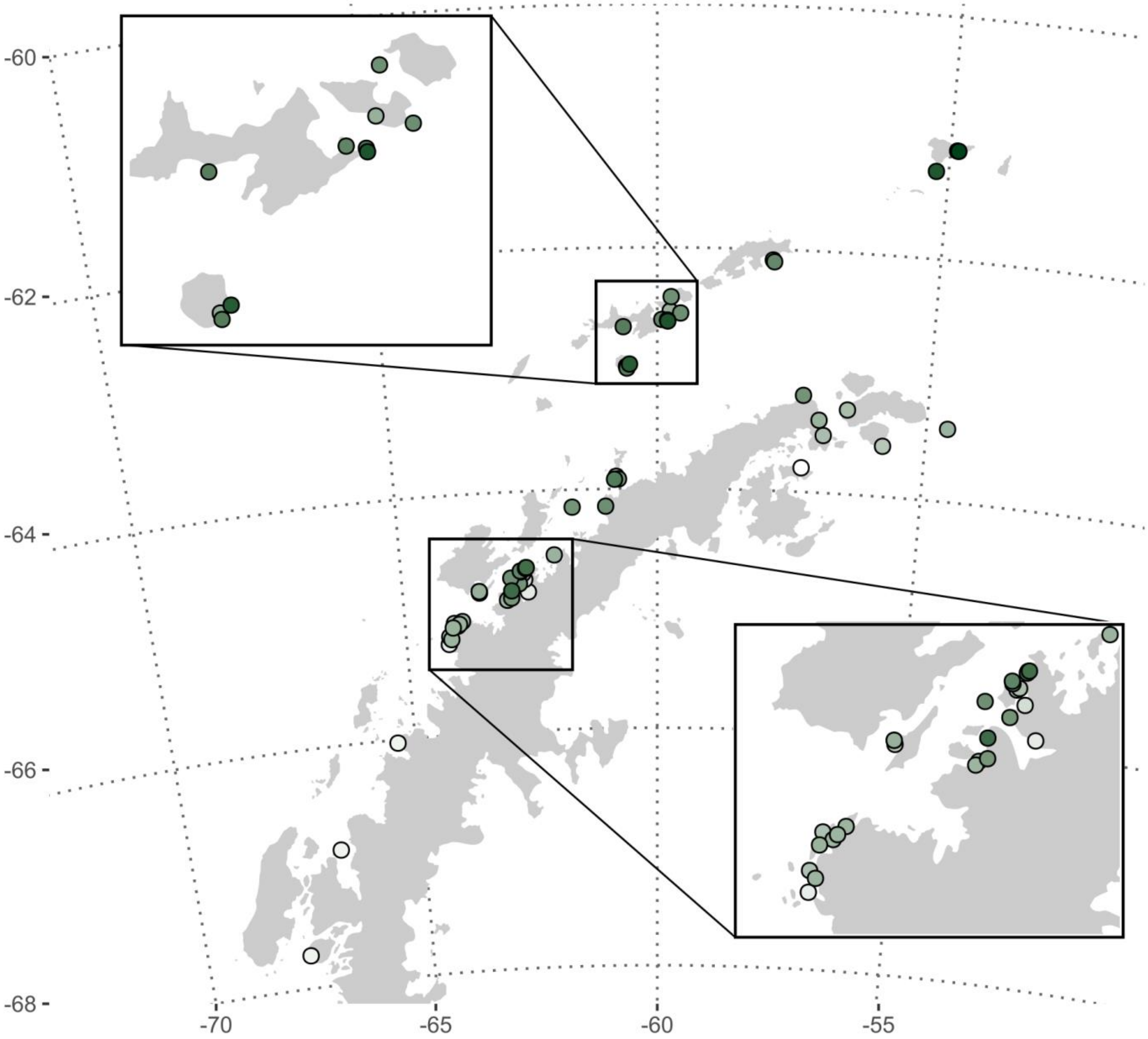

Figure A9.2: Map of sites with at least 5 years of occupancy data, displayed with results from NMDS axis 2 (which was the green component of the score in Figures 4.2 and 4.3). Light color indicates a low axis score, and dark indicates a high axis score. Insets enlarge areas with higher site density.

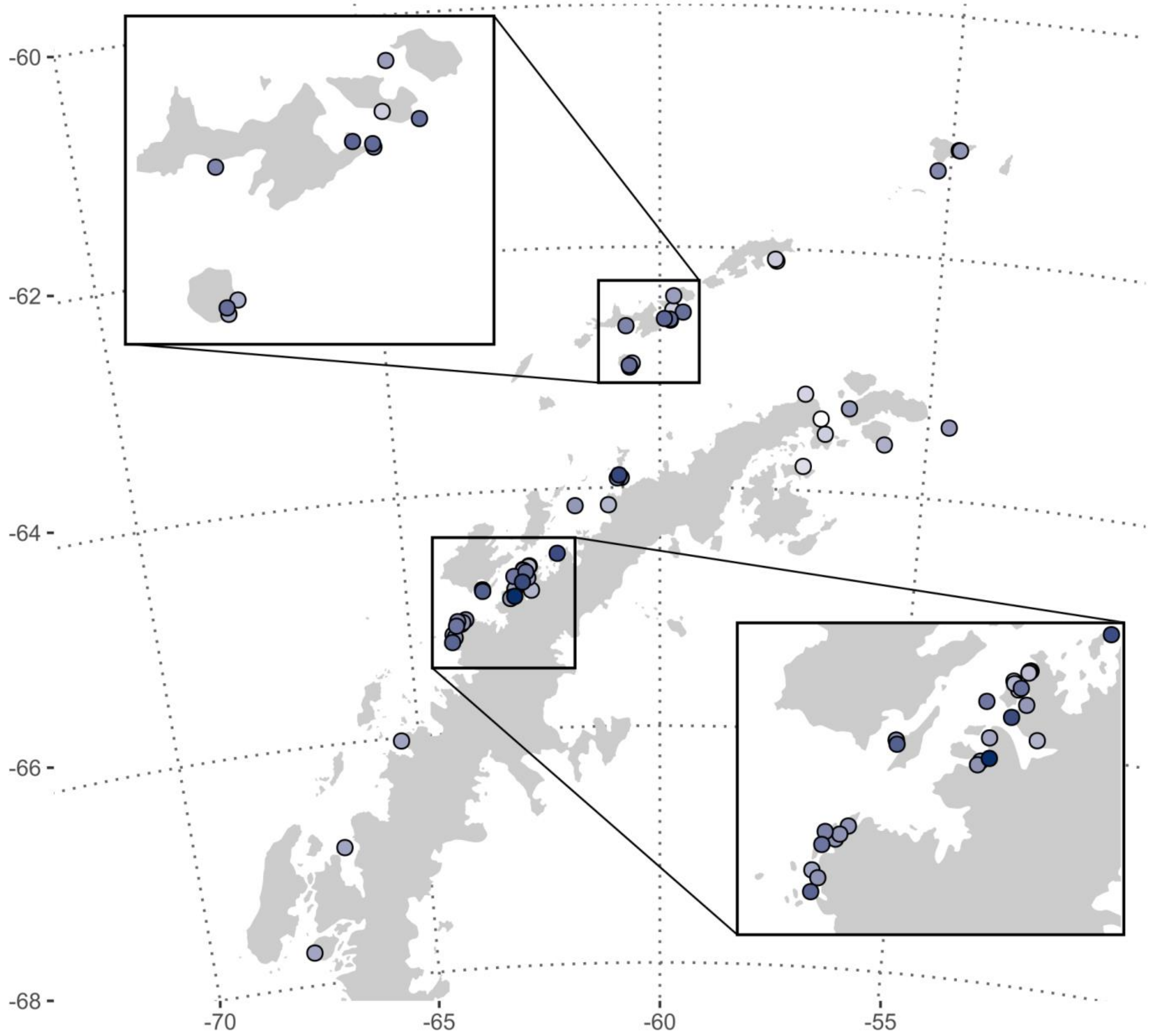

Figure A9.3: Map of sites with at least 5 years of occupancy data, displayed with results from NMDS axis 3 (which was the blue component of the score in Figures 4.2 and 4.3). Light color indicates a low axis score, and dark indicates a high axis score. Insets enlarge areas with higher site density.

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